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# Tip dating supports a Middle Ordovician origin for total-group chondrichthyans and a rapid radiation of acanthodian-grade taxa

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**The early evolutionary history of acanthodians, a paraphyletic group of Palaeozoic stem chondrichthyans, is reconstructed using a comprehensive and updated morphological phylogenetic dataset consisting of 429 characters scored for 87 articulated taxa. Results of a time-calibrated Bayesian analysis suggest a Middle Ordovician origin for total-group Chondrichthyes, coinciding with the end of the Great Ordovician Biodiversification Event, and an Early Devonian age for the most recent common ancestor of crown Chondrichthyes. Further, major acanthodian lineages are inferred to originate towards the end of the Late Ordovician. This supports a diversification model in which interordinal cladogenesis occurred in the Middle-Late Ordovician and most intraordinal cladogenesis occurred in the Silurian. Divergence dates and short internodes inferred by the tip-dating analysis indicate a relatively rapid pattern of successive cladogenetic splits for major groups of acanthodians that diverged from the chondrichthyan stem in the Darriwilian and Sandbian. These speciation events possibly produced daughter lineages that remained morphologically similar to their ancestors before undergoing other cladogenetic splits, as suggested by the relatively low rates of morphological evolution (number of morphological changes per million year) reconstructed for the same branches. The lack of synapomorphies resulting from such a compressed pattern of divergences is likely the cause of low branch support and the topological instability that characterizes acanthodian relationships. The results presented in this study confirm that underlying evolutionary processes such as rapid radiations, in conjunction with the fragmentary nature of the fossil record, can further negatively impact phylogenetic reconstruction based on morphological data.**

Acanthodii | ancient rapid radiation | Bayesian phylogenetics | Chondrichthyes | tip-dating

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## Introduction

Acanthodii are a globally distributed and morphologically distinct grade of Palaeozoic cartilaginous fishes, with a fossil record ranging from the early Silurian (Andreev et al., 2022b; Zhu et al., 2022) to the Permian (Schultze, 1985). Found in both marine and freshwater palaeoenvironments (Schnetz et al., 2022), their most distinctive and easily preserved features are the fin spines, located anteriorly to all fins except the caudal one, and the characteristic micromeric scales (Moy-Thomas, 1971). Except for lineages that possess pectoral dermal plates (e.g., climatiids and diplacanthids) and for the body scale bases, which are composed of bone, the skeleton of acanthodians is primarily cartilaginous. This limited their conservation potential and caused a scarcity of morphological information, which hindered our understanding of their anatomy and phylogenetic relationships. In turn, this is corroborated by the variety of hypotheses regarding their systematic position on the jawed vertebrates tree (Nelson, 1969; Denison, 1979; Janvier, 1996; Sansom, 2009; Davis et al., 2012).

In recent years, due to advancements in methods of phylogenetic reconstruction and in data collecting practices, with phylogenetic datasets containing an ever-growing number of characters and taxa (Laing et al., 2018), almost all the large-scale phylogenetic analyses recovered Acanthodii as a paraphyletic array leading to crown-group Chondrichthyes (Burrow et al., 2016; Qiao et al., 2016; King et al., 2017, Brazeau et al., 2023; Cui et al., 2025). Despite this seemingly robust consensus and the wealth of new information about the early evolutionary history of the group (Burrow and Rücklin, 2014; Andreev et al., 2022b, Zhu et al., 2022), relationships along the chondrichthyan stem remained obscure, with different analyses recovering the four main acanthodian orders in a variety of arrangements. Climatiids are usually retrieved as either the earliest diverging clade of total-group Chondrichthyes (Burrow et al., 2016, Frey et al. 2019, Klug et al., 2023) or as more closely related to crown-group chondrichthyans by more inclusive analyses (King and Rücklin, 2020, Cui et al., 2025). The respective systematic positions of the other three orders, Acanthodiformes, Diplacanthifomes and Ischnacanthiformes, are equally elusive, with the three groups generally recovered as a clade (Burrow et al., 2016) or with Diplacanthiformes as the earliest diverging clade of 'Acanthodii', followed crownwards by Ischnacanthiformes and then Acanthodiformes (Zhu et al., 2022).

The recovery of conflicting phylogenetic hypotheses is possibly due to the different taxon and character samples used in different analyses and in the methods of tree inference used (Fonseca et al., 2024) or can be a direct consequence of underlying complex evolutionary processes (Whitfield and Lockhart, 2007). Moreover, new data about the early evolutionary history of the group, represented by the recently described early Silurian taxa *Shenacanthus* (Zhu et al., 2022) and *Fajingshania* (Andreev et al., 2022b) have never been incorporated in a tip-dating analysis and used to infer the timing of the early radiation of 'Acanthodii'. The aim of this study is to construct a new comprehensive morphological dataset focused

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on early total-group chondrichthyans' relationships, including all the informative characters available in the literature and most of the better known and reasonably complete acanthodian taxa. The matrix will then be used to test previously proposed phylogenetic hypotheses and to infer divergence ages for major acanthodian-grade and early crown chondrichthyan clades.

## Materials and methods

### Dataset assembly

To construct a comprehensive morphological dataset focused on the relationships of stem chondrichthyans and early crown chondrichthyans, the matrix presented in Zhu et al., (2022) was used as a starting point. First, all extinct total-group chondrichthyan taxonomic units present in the dataset were selected, excluding those above the genus level, together with 9 osteichthyans and 2 placoderm outgroups. Second, all the parsimony informative characters for the chosen taxa were selected and included in the matrix. Twenty-six direct autapomorphic traits were also included in the dataset because they provide information and influence estimation of the duration of terminal branches in morphological clock-type analyses (Matzke and Irmis, 2018) and considering future expansions. Lastly, the dataset was complemented with 9 additional taxa, scored using the primary literature and examination of tomographic slices and 3D renderings. The newly added taxonomic units are: *Acanthodes lopatini* Rohon, 1889 (scored based on Beznosov, 2009), *Diplacanthus crassissimus* Duff, 1842 (scored based on Burrow et al., 2016), *Fallodentus davidsoni* Newman et al., 2020 (scored based on Newman et al., 2020), *Fanjingshania renovata* Andreev et al., 2022b (scored based on figures and tomographic data in Andreev et al., 2022b), *Howittacanthus kentoni* Long, 1986 (scored based on Long, 1986), *Lodeacanthus gaujicus* Upeniece, 1996 (scored based on Upeniece, 1996), *Orcadacanthus pusillus* Agassiz, 1844 (scored based on Newman et al., 2023), *Tricuspicanthus gannitus* Blais, Hermus and Wilson, 2015 (scored based on Blais, Hermus and Wilson, 2015 and tomographic data in Blais, 2017) and *Utahacanthus guntheri* Schultze, 1990 (scored based on Schultze, 1990). Furthermore, characters 24, 25 and 26 of the current character list were rescored in *Entelognathus primordialis* based on new data in Cui et al. (2023).

The complete matrix comprises 429 characters (of which 403 are parsimony informative) scored for 87 taxa. Nexus files used for phylogenetic analyses, a complete character list, and all the recovered trees are present as supplementary material.

### Phylogenetic analyses

A Bayesian inference analysis integrating both morphological and stratigraphic data was performed using MrBayes ver. 3.2.7 (Ronquist et al., 2012). 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 time-calibrated analysis was conducted using the fossilized birth-death (FBD) model (Gavryushkina et al., 2014; Heath et al., 2014) with a relaxed clock, and the Mkv model (Lewis, 2001) of character evolution. Uncertainty regarding stratigraphic occurrences of all the included taxa was accounted for using uniform prior distributions for tip ages (Barido-Sottani et al., 2019), except for the age of *Tribodus* Brito and Ferreira, 1989, which was fixed at 106 millions of years ago (Mya) because MrBayes ver. 3.2.7 requires the age of the most recent taxon to be fixed if the sample is composed of fossil taxa only.

Stratigraphic information for each terminal taxon was obtained from the Paleobiology Database (2024) and from Zhu et al. (2022). The tree age prior was specified using a uniform distribution set between 433.4 and 486.85 millions of years ago (a maximum age conservatively set in the Early Ordovician based on results presented in Marjanović, 2021). The crown Gnathostomata node was also calibrated, following Marjanović (2021), using a uniform prior distribution with a minimum age of 465 Mya and a maximum age of 475 Mya. *Dicksonosteus* Goujet, 1975 and *Entelognathus* Zhu et al., 2013 were used as successive outgroups, based on results of most previous phylogenetic analyses on total-group gnathostomes (Zhu et al., 2016; Li et al., 2021).

Two runs of four chains each were performed for 15,000,000 generations, with the temperature set at 0.10 and sampling every 500 generations. The first 25% of the sampled trees were discarded as burn-in and all characters were unordered. Results of the FBD analysis were summarized in a maximum clade credibility tree. Convergence of independent runs was assessed examining the MrBayes output and visually using Tracer ver. 1.7.2 (Rambaut et al., 2018): effective sample size was greater than 200 for the tested parameters and average standard deviation of split frequencies was 0.0137 at the end of the analysis.

A maximum parsimony analysis was performed in PAUP* ver. 4.0a169 (Swofford, 2002), using a heuristic search with tree bisection and reconnection (10,000 replicates) a maximum of 10 trees per replicate with a score above 1, maxtrees set at 100.000 and all characters set as having equal weights.

### Phylogenetic networks

The consensus network method is adopted here to further explore and visually summarize topological uncertainty and instability of taxa in the set of most parsimonious trees recovered by the parsimony analysis. Phylogenetic consensus networks show all taxon relationships reconstructed by a phylogenetic analysis over a specified proportion of the recovered set of trees, presenting conflicting phylogenetic hypotheses that are usually not displayed by traditional consensus trees (Holland and Moulton 2003; Moon, 2017). Consensus networks were computed in SplitsTree v. 6.4.13 (Huson and Bryant, 2006) with default options, and frequency thresholds of 33%, 20%, 10% and 0% were used (Serra Silva, 2024). Additionally, cluster networks were also computed in SplitsTree using the same set of most parsimonious trees and the same thresholds and default options.

## Results

### Phylogenetic results

The topology recovered from the FBD analysis is presented in Figures 1 and 2 and is in overall agreement with previous large-scale phylogenetic analyses of stem chondrichthyans and total-group gnathostomes, such as Chevrinais et al. (2017), Andreev et al. (2022b) and Zhu et al. (2022). A clade formed by Ischnacanthiformes plus Diplacanthiformes is recovered as the earliest diverging group of acanthodians (posterior probability:

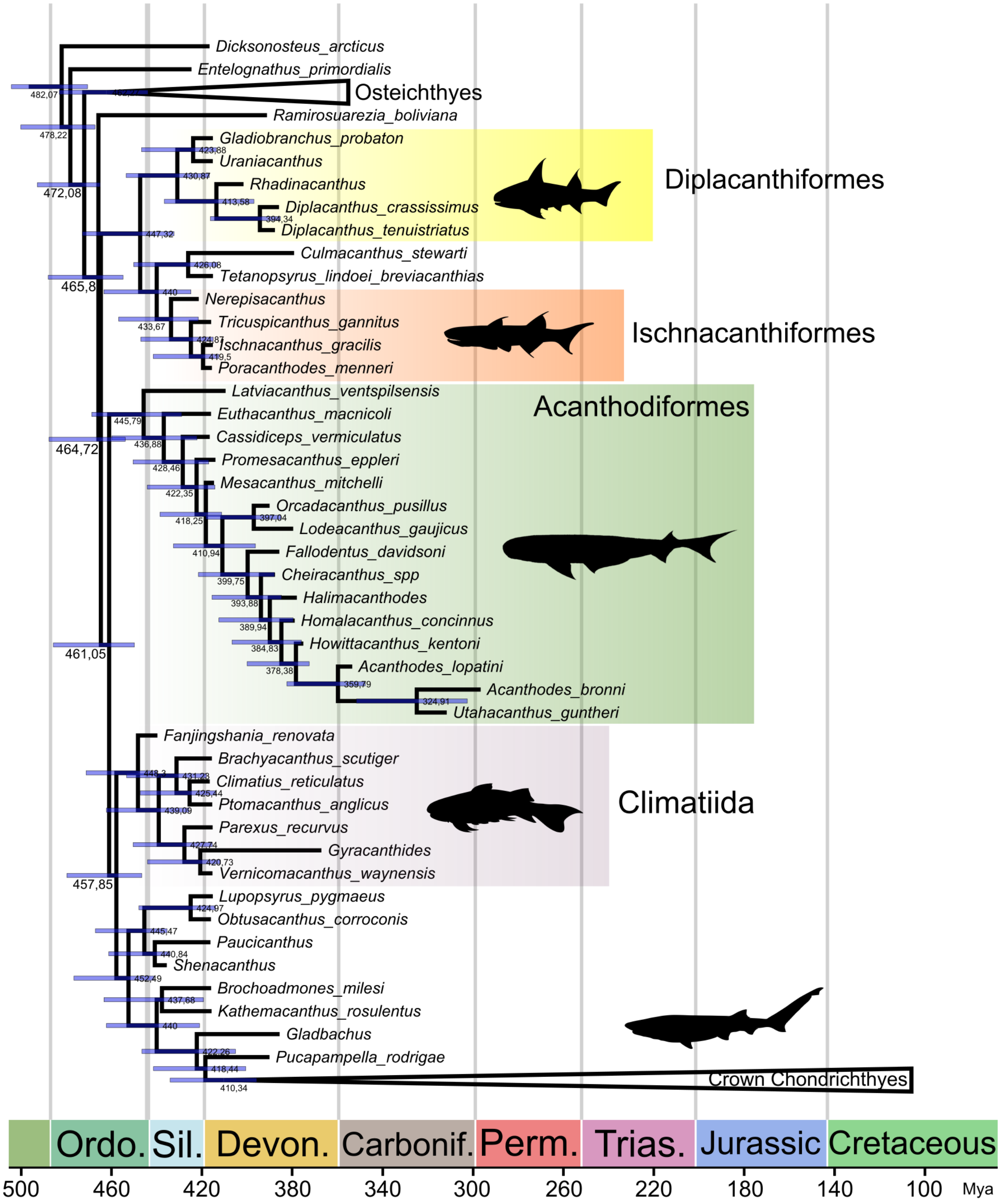

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**Figure 1.** Maximum clade credibility tree recovered by the Bayesian time-calibrated analysis. Numbers at nodes are median age values inferred by the analysis. Silhouettes are taken from Phylopic: *Ptomacanthus anglicus* by T. Michael Keesey used under CC0 1.0 Universal Public Domain Dedication, *Diplacanthus crassisimus* by RP Dearden used under CC0 1.0 Universal Public Domain Dedication, *Hexanchus griseus* by Ignacio Contreras used under Attribution 3.0 Unported, *Acanthodes bronni* by Nobu Tamura used under Attribution 3.0 Unported, *Ischnacanthus gracilis* by RP Dearden used under CC0 1.0 Universal Public Domain Dedication.

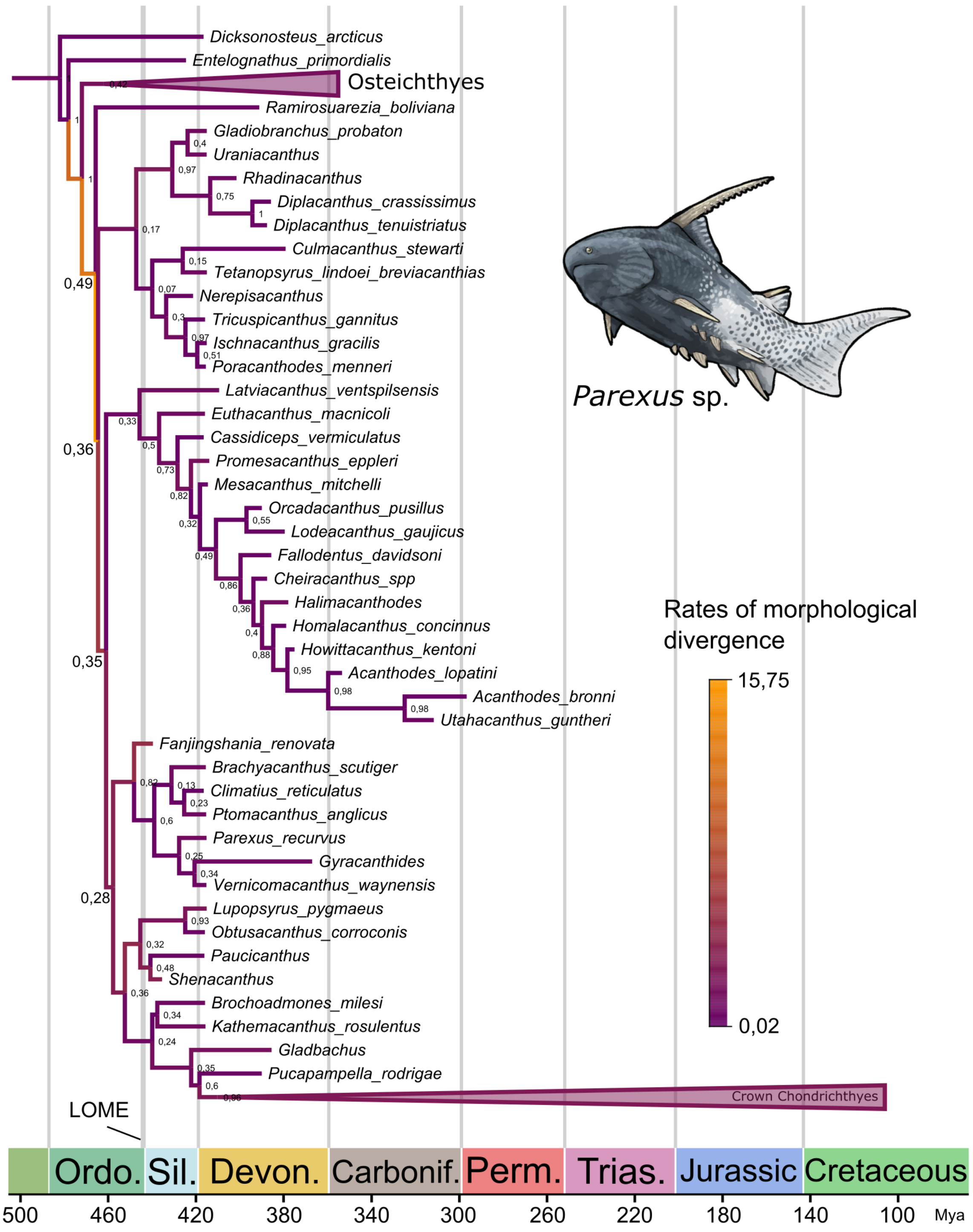

**Figure 2.** Maximum clade credibility tree recovered by the time-calibrated Bayesian analysis. Numbers at nodes are posterior probability values, branches coloured according to median rates of morphological evolution. *Parexus* sp. by SeismicShrimp, used under a Creative Commons Attribution 4.0 International license. Abbreviations: LOME, Late Ordovician Mass Extinction.

0.17). This clade is followed crownwards by Acanthodiformes, the latter including *Euthacanthus* and *Latviacanthus* (posterior probability: 0.33). Acanthodiformes, in turn, is recovered as sister taxon to Climatiida + a paraphyletic array composed of the more crownward acanthodians and other stem chondrichthyans (including *Brochoadmones*, *Kathemacanthus*, *Gladbachus* and *Pucapampella*, here termed the '*Brochoadmones* grade') + crown Chondrichthyes (posterior probability: 0.28). This arrangement is not consistent with the topology found by the tip-dating Bayesian analysis performed by Klug et al. (2023) and parsimony analyses in Burrow et al. (2016), in which Climatiida is recovered as the earliest diverging clade of 'Acanthodii', and Ischnacanthiformes and Diplacanthiformes are found closely related to Acanthodiformes. Differently from the results in Zhu et al. (2022), *Janusiscus* is recovered as the earliest diverging osteichthyan in the tip-dating analysis, and *Culmacanthus* and *Tetanopsyrus* are found forming a clade, which in turn is closely related to Ischnacanthiformes, albeit with very low support (posterior probability: 0.07). Furthermore, in Klug et al. (2023) Pucapampellidae is recovered as monophyletic, a hypothesis not supported by phylogenetic results presented herein.

*Ramirosuarezia* (Pradel et al., 2009) is recovered as the earliest diverging total-group chondrichthyan in the tip-dating analysis, although support for this hypothesis is low (posterior probability of a clade comprising all total-chondrichthyans excluding *Ramirosuarezia*: 0.36). *Fanjingshania* is recovered as the earliest diverging climatiid, whereas in phylogenetic analyses presented by Andreev et al. (2022b) this taxon is recovered in a more derived position. Immediately crownwards of Climatiida, the FBD analysis recovered a clade containing *Shenacanthus*, *Paucicanthus*, *Lupopsyrus* and *Obtusacanthus* (posterior probability: 0.32). Relationships retrieved among crown Chondrichthyes are mostly consistent with the results of the Bayesian analysis in Zhu et al. (2022). Congruence of topologies retrieved herein with results presented in the latter study possibly suggests a good stratigraphic fit for this arrangement of the chondrichthyan stem.

Divergence dates retrieved from the time-calibrated analysis are summarized in Table 1. Total-group Chondrichthyes is inferred to originate in the Darriwilian, 465.8 millions of years ago (Mya), right after the Great Ordovician Biodiversification Event (Servais et al., 2008; Harper et al., 2019). The clade composed of Acanthodiformes + Climatiida + the '*Brochoadmones* grade' + crown chondrichthyans and the clade comprising Climatiida, the '*Brochoadmones* grade' and crown chondrichthyans are inferred to originate at 464.72 and 461.05 Mya, respectively. The origins of major acanthodian lineages are placed in the Katian: the clade comprising Ischnacanthiformes and Diplacanthiformes is reconstructed to originate 447.32 Mya, whereas the most recent common ancestor of Acanthodiformes is placed at 445.79 Mya. Climatiida is inferred to originate 448.3 Mya. The most recent common ancestor of crown-group chondrichthyans is placed at 410.34 Mya by the tip-dating analysis, an age consistent with the divergence dates inferred by Inoue et al. (2010) and Renz et al. (2013) for crown Chondrichthyes. Furthermore, the Chondrichthyes-Osteichthyes split is inferred to occur in the Floian, 472.08 Mya.

Median rates of morphological divergence (number of morphological changes per million year) inferred by the FBD analysis are relatively high on the branches leading to crown-group Gnathostomata and total-group Chondrichthyes (values of 10.74 and 12.18, respectively), as shown in Figure 2 and Supplementary Figure 1. They gradually decrease on branches leading to major acanthodian-grade clades (values of 1.74, 5.75 and 3.07), after the *Ramirosuarezia* split. Relatively low rates of morphological evolution are also inferred among crown chondrichthyans (Suppl. Fig. 1).

**Table 1.** Divergence dates of major crown gnathostome clades inferred by the Bayesian time-calibrated analysis.

| Clade | Median age inferred (in millions of years) |
|---|---:|
| Crown Gnathostomata | 472.08 |
| Total-group Chondrichthyes | 465.8 |
| Ischnacanthiformes | 433.67 |
| Diplacanthiformes | 430.87 |
| Acanthodiformes | 445.79 |
| Climatiida | 448.3 |
| Crown Chondrichthyes | 410.34 |
| Total-group Osteichthyes | 462.27 |

The parsimony analysis recovered 1530 most parsimonious trees of length 1043, these are summarized as a strict consensus tree shown in Supplementary Figure 2. The tree is generally poorly resolved, the only well resolved part of the topology being the clade formed by Climatiida, more crownward stem chondrichthyans and crown Chondrichthyes. *Shenacanthus* is recovered as sister taxon to crown chondrichthyans as in the parsimony analysis in Zhu et al. (2022).

### Consensus networks results

Results of the consensus network analyses are shown in Figure 3, and, regardless of the used split frequency threshold, all show that most of the split incompatibilities are found in the area corresponding to the early radiation of total-group Chondrichthyes. The same area displays low support values in the Bayesian maximum clade credibility tree and corresponds to an unresolved polytomy in the strict consensus tree recovered by the parsimony analysis. In this area of the chondrichthyan stem, four cladogenetic events are concentrated and very close to each other (less than 10 millions of years from the appearance of the common ancestor of total-group chondrichthyans to the Climatiida divergence), with very short internodes. This, coupled with relatively low rates of morphological divergence inferred by the tip-dating analysis, possibly suggests little morphological change in daughter lineages compared to their inferred ancestor. The results of the cluster network analyses are shown in Supplementary Figures 3-6 and are consistent with the consensus networks.

## Discussion and Conclusion

Here, I have provided a revised and expanded phylogenetic analysis of acanthodians and early crown chondrichthyans. The tip-dating Bayesian analysis inferred divergence dates consistent with previous molecular estimates for the crown-group (Inoue et al., 2010; Renz et al., 2013) and with the fossil record of total-group Chondrichthyes (Sansom and Andreev, 2018; Andreev et al., 2022a). Nevertheless, the results presented here are not congruent with a previous morphological clock analysis of stem chondrichthyans (Klug et al., 2023), which recovered significantly younger divergence dates. However, this discrepancy in the results is not unexpected, given their comparatively reduced taxon sample and the absence of the key Silurian acanthodian-grade taxa *Shenacanthus* and *Fanjingshania* in their matrix.

Differently from the time-adjusted parsimony analyses in Andreev et al. (2022a,b) and Zhu et al. (2022), the tip dating analysis

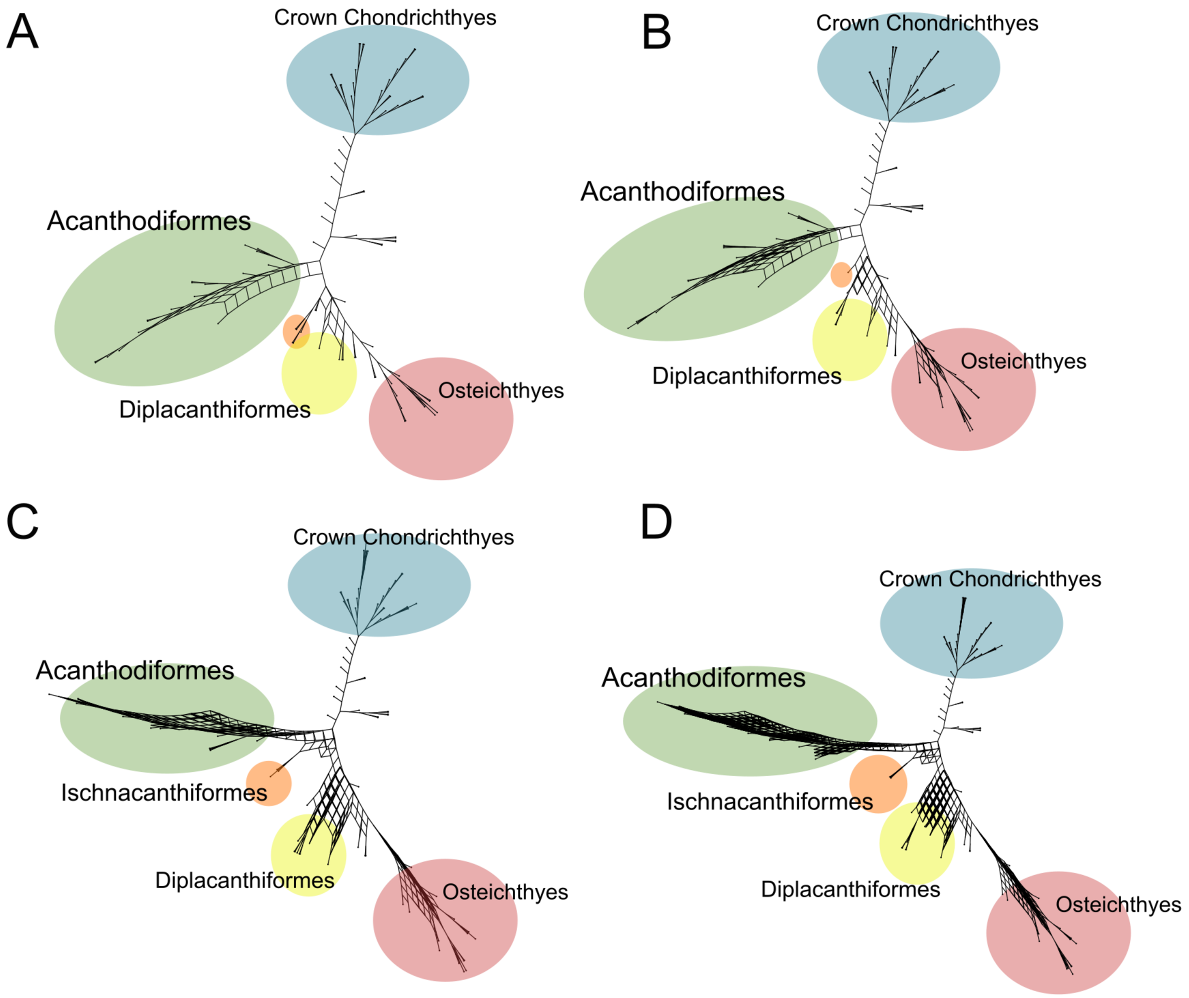

**Figure 3.** Consensus networks computed using 1530 most parsimonious trees recovered by the parsimony analysis. **A**, 33%; **B**, 20%; **C**, 10% and **D**, 0% split frequency thresholds. Some taxa have been omitted for clarity.

presented herein recovered an Early Ordovician (Floian) age for crown gnathostomes, a Middle Ordovician (Darriwilian) age for total-group chondrichthyans and Late Ordovician dates for the origin of major acanthodian groups. For acanthodians, this suggests a 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 the group occurred in the Silurian. Such a diversification pattern would also imply a relatively low taxonomic diversity in the Middle-Late Ordovician and for most of the Silurian, consistent with the patchy fossil record of the group in these time periods.

Older divergence dates recovered herein could be explained by the more complete ingroup taxon sample and the smaller sample of outgroup taxa in 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).

Both Bayesian and maximum parsimony analyses yielded generally poorly supported topologies, in which nodes along the chondrichthyan stem, right after the Osteichthyes-Chondrichthyes split, display very low posterior probability values or are collapsed, respectively. This area of the topology corresponds to a region of instability of the recovered relationships among taxa, as evidenced by the network analyses. The same problematic nodes and branches display relatively low rates of morphological evolution compared to more rootward clades. Comparatively low rates of divergence could be due to the sparse fossil record of jawed vertebrates in the Late Ordovician and early Silurian. Cryptic morphological diversity caused by preservation bias could have artificially lowered rates of morphological evolution in this case. Alternatively, this could mean that during the initial interordinal diversification of acanthodians, daughter lineages remained relatively similar, from a morphological point of view, to their inferred ancestors. After cladogenetic events, they had relatively little time to accumulate potential synapomorphies before undergoing other evolutionary splits (Whitfield and Lockhart, 2007). This is supported by the very short internodes, and hence temporal proximity of major cladogenetic events along the chondrichthyan stem (see Shaffer et al., 1997), starting after the Osteichthyes-Chondrichthyes split and reaching up to the Climatiida divergence. Such instances of rapid successive speciation episodes, similarly to cryptic or budding cladogenesis (i.e. when two or one of the daughter lineages resulting from a cladogenetic event remain morphologically undifferentiated from their ancestor, see Bapst, 2013), pose a challenge to morphological phylogenetic reconstruction, due to the intrinsic unresolvability, given by the possible lack of phylogenetic signal, of clades that originated in this way (Rokas and Carroll, 2006; Bapst 2013).

While short internal branch lengths do not directly represent budding speciation events (see Caetano and Quental, 2023), short internodes and low rates of morphological divergence suggest little morphological change in at least one of the daughter lineages after a bifurcation, as the amount of phylogenetic signal of a given branch is proportional to the duration of that branch (Rokas and Carroll, 2006). Therefore, they support an ancient rapid radiation hypothesis for early clades along the chondrichthyan stem and, possibly, for early crown gnathostomes (see Rokas et al., 2005; Rokas and Carroll, 2006; Whitfield and Lockhart, 2007 and Townsend et al., 2011).

The matter is further complicated by the possibility that periods of such rapid diversification can be characterized, and even promoted, by reticulate evolutionary processes, such as hybridization, introgression and gene flow (Seehousen, 2004; Mallet et al., 2015; Chan et al., 2020; Cai et al., 2021), and this has been demonstrated for the early radiation of jawed vertebrates (Simakov et al., 2020). This can result in patterns of divergence that are more complicated to reconstruct, and which may require more complicated frameworks and tools than phylogenetic trees only (see Caparros and Prat, 2021).

Ancient rapid radiations are often detected and discussed in molecular studies (Fishbein et al., 2001; Whitfield and Kjer, 2008; Larridon et al., 2024) but have rarely been properly explored in a strictly morphological context (but see Shaffer et al., 1997). We can expect these areas of phylogenetic topologies to display low support values or to be completely unresolved. Further, we can expect them to be the future objects of debates around relationships of fossil taxa, because relationship instabilities, depending on taxon sampling and models used, are characteristic of short ancient internodes (Whitfield and Kjer, 2008). This could, in part, explain uncertainties regarding relationships of major acanthodian clades.

Divergence age estimates recovered in this study receive little support from the fossil record and are considerably older than previous ones. Nonetheless, a model of diversification where taxonomic diversity of stem-group chondrichthyans remained relatively low in the Middle-Late Ordovician and Silurian could help explain the very limited fossil evidence of the group in these time periods.

## Data availability

All the original files used to conduct the phylogenetic analyses are included in nexus format as supplementary files and all the computed cladograms, together with a complete character list, are present in the Supplementary Material.

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## Author contributions

L.M.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing of the original draft and editing.

## Competing interests

The author declares no conflicts of interests.

## Ethics and AI use

No AI was used for this research. This work did not require any ethical approval.

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## References

Agassiz, L. 1844. Monographie des poissons fossiles des Vieux Grès Rouges ou Système Dévonien (Old Red Sandstone) des Îles Britanniques et de Russie. *Imprimerie de Petitpierre et Prince, Neuchâtel.*

Andreev, P.S., Sansom, I.J., Li, Q., Zhao, W., Wang, J., Wang, C.-C., Peng, L., Jia, L., Qiao, T. and Zhu, M. 2022a. The oldest gnathostome teeth. *Nature*, 609, 964–968. https://doi.org/10.1038/s41586-022-05166-2

Andreev, P.S., Sansom, I.J., Li, Q., Zhao, W., Wang, J., Wang, C.-C., Peng, L., Jia, L., Qiao, T. and Zhu, M. 2022b. Spiny chondrichthyan from the lower Silurian of South China. *Nature*, 609, 969–974. https://doi.org/10.1038/s41586-022- 05233-8

Bapst, D.W. 2013. When can clades be potentially resolved with morphology? *PLoS ONE* 8:4, e62312. https://doi.org/10.1371/journal.pone.0062312

Barido-Sottani, J., Aguirre-Fernández, G., Hopkins, M.J., Stadler, T. and Warnock, R. 2019. Ignoring stratigraphic age uncertainty leads to erroneous estimates of species divergence times under the fossilized birth–death process. *Proceedings of the Royal Society B: Biological Sciences*, 286:1902, 20190685. https://doi.org/10.1098/rspb.2019.0685

Beznosov, P. 2009. A redescription of the Early Carboniferous acanthodian *Acanthodes lopatini* Rohon, 1889. — *Acta Zoologica* 90:s1, 183–193 https://doi.org/10.1111/j.1463-6395.2008.00352.x

Blais, S.A., 2017. Precise occlusion and trophic niche differentiation indicate specialized feeding in Early Devonian jawed vertebrates. *FACETS* 2, 513-530. https://doi.org/10.1139/facets-2016-0030

Blais, S.A., Hermus, C. R., and Wilson, M. V. H. 2015. Four new Early Devonian ischnacanthid acanthodians from the Mackenzie Mountains, Northwest Territories, Canada: An early experiment in dental diversity. *Journal of Vertebrate Paleontology* 35:1, e948546. https://doi.org/10.1080/02724634.2014.948546

Brazeau, M.D., Castiello, M., El Fassi El Fehri, A., Hamilton, L., Ivanov, A.O., Johanson, Z., Friedman, M. 2023. Fossil evidence for a pharyngeal origin of the vertebrate pectoral girdle. *Nature* 623, 550–554. https://doi.org/10.1038/s41586-023-06702-4

Brito, P.M. and Ferreira, P.L.N. 1989. The first Hybodont shark, *Tribodus limae* n. gen., n. sp., from the Lower Cretaceous of Chapada do Araripe (North-East Brazil). *Anais da Academia Brasileira de Ciências*, 61:1, 53–57

Burrow, C.J., den Blaauwen, J., Newman, M., and Davidson, R. 2016. The diplacanthid fishes (Acanthodii, Diplacanthiformes, Diplacanthidae) from the Middle Devonian of Scotland. *Palaeontologia Electronica* 19.1.10A: 1-83. https://doi.org/10.26879/601

Burrow, C.J. and Rudkin D. 2014. Oldest near-complete acanthodian: The first vertebrate from the Silurian Bertie Formation Konservat-Lagerstätte, Ontario. *PLoS ONE* 9:8, e104171. https://doi.org/10.1371/journal.pone.0104171

Caetano, D.S. and Quental, T. B. 2023. How important is budding speciation for comparative studies? *Systematic Biology* 72:6, 1443–1453, https://doi.org/10.1093/sysbio/syad050

Cai, L., Xi, Z., Lemmon, E.M., Lemmon, A.R., Mast, A., Buddenhagen, C. E., Liu, L., and Davis, C.C. 2021. The perfect storm: Gene tree estimation error, incomplete lineage sorting, and ancient gene flow explain the most recalcitrant ancient angiosperm clade, Malpighiales. *Systematic Biology* 70:3, 491–507. https://doi.org/10.1093/sysbio/syaa083.

Caparros, M., and Prat, S. 2021. A phylogenetic networks perspective on reticulate human evolution. *iScience* 24:4, 102359. https://doi.org/10.1016/j.isci.2021. 102359

Chan, K.O., Hutter, C.R., Wood, P.L., Grismer, L.L., and Brown, R.M. 2020. Target-capture phylogenomics provide insights on gene and species tree discordances in Old World tree frogs (Anura: Rhacophoridae). *Proceedings of the Royal Society B*. 287, 20202102. https://doi.org/10.1098/rspb.2020.2102.

Chevrinais M., Sire J.-Y. and Cloutier R. 2017. From body scale ontogeny to species ontogeny: Histological and morphological assessment of the Late Devonian acanthodian *Triazeugacanthus affinis* from Miguasha, Canada. *PLoS ONE* 12:4, e0174655. https://doi.org/10.1371/journal.pone.0174655

Cui, X., Friedman, M., Yu, Y., Zhu, Y. an, Zhu, M. 2023. Bony-fish-like scales in a Silurian maxillate placoderm. *Nature Communications* 14, 7622. https://doi.org/10.1038/s41467-023-43557-9

Cui, X., Qiao, T., Peng, L. and Zhu, M. 2025. New material of the Early Devonian sarcopterygian *Styloichthys changae* illuminates the origin of cosmine. *Journal of Systematic Palaeontology* 23:1. https://doi.org/10.1080/14772019.2024.2432273

Davis, S.P., Finarelli, J.A. and Coates, M.I. 2012. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature*, 486, 247–250. https://doi.org/10.1038/nature11080

Denison, R. 1979. Acanthodii. *Handbook of paleoichthyology*, Vol. 5. Verlag Dr Friedrich Pfeil, 62 pp.

Duff, P. 1842. Sketch of the Geology of Moray. Forsyth and Young, Elgin.

Fishbein, M., Hibsch-Jetter, C., Soltis, D.E., and Hufford, L. 2001. Phylogeny of saxifragales (Angiosperms, Eudicots): analysis of a rapid, ancient radiation. *Systematic Biology* 50, 817–847. https://doi.org/10.1080/106351501753462821

Frey, L., Coates, M., Ginter, M., Hairapetian, V., Rücklin, M., Jerjen, I. and Klug, C. 2019. The early elasmobranch *Phoebodus*: Phylogenetic relationships, ecomorphology, and a new time-scale for shark evolution. *Proceedings of the Royal Society B* 286, 20191336. http://dx.doi.org/10.1098/rspb.2019.1336

Fonseca, A.O., Reid, I.J., Venner, A., Duncan, R.J., Garcia, M.S., and Müller, R.T. 2024. A comprehensive phylogenetic analysis on early ornithischian evolution. *Journal of Systematic Palaeontology* 22:1, 2346577. https://doi.org/10.1080/14772019.2024.2346577

Gavryushkina, A., Welch, D., Stadler, T., and Drummond, A.J. 2014. Bayesian inference of sampled ancestor trees for epidemiology and fossil calibration. *PLoS Computational Biology* 10:12, e1003919. https://doi.org/10.1371/journal.pcbi.1003919

Goujet, D. 1975. *Dicksonosteus*, un nouvel arthrodire du Dévonien du Spitsberg — Remarques sur le squelette viscéral des Dolichothoraci. *Colloques internationaux du Centre National de la Recherche Scientifique* 218, 81–99.

Harper, D.A.T., Cascales-Miñana, B. and Servais, T. 2019. Early Palaeozoic diversifications and extinctions in the marine biosphere: A continuum of change. *Geological Magazine* 157:1, 5–21. https://doi.org/10.1017/S0016756819001298. hdl:20.500.12210/34267

Heath, T.A., Huelsenbeck, J.P. and Stadler, T. 2014. The fossilized birth–death process for coherent calibration of divergence-time estimates. *Proceedings of the National Academy of Sciences* 111:29, E2957–E2966. https://doi.org/10.1073/pnas.1319091111

Holland, B. and Moulton, V. 2003. Consensus networks: a method for visualising incompatibilities in collections of trees. Pp. 165–176. In G. Benson and R. Page (Eds.) *Algorithms in bioinformatics*. Volume 2812. Springer, Berlin, 270 pp.

Huson, D.H., and Bryant, D. 2006. Application of phylogenetic networks in evolutionary studies. *Molecular Biology and Evolution* 23:2, 254–267. https://doi.org/10.1093/molbev/msj030

Inoue, J.G., Miya, M., Lam, K., Tay, B.H., Danks, J.A., Bell, J., Walker, T.I. and Venkatesh, B. 2010. Evolutionary origin and phylogeny of the modern holocephalans (Chondrichthyes: Chimaeriformes): a mitogenomic perspective. *Molecular Biology and Evolution* 27:11, 2576–2586. https://doi.org/10.1093/molbev/msq147

Janvier, P. 1996. *Early vertebrates*. Clarendon Press, 393 pp.

King, B. 2021. Bayesian tip-dated phylogenetics in paleontology: Topological effects and stratigraphic fit, *Systematic Biology* 70:2, 283–294. https://doi.org/10.1093/sysbio/syaa057

King, B., Qiao, T., Lee, M.S.Y., Zhu, M. and Long, J.A. 2017. Bayesian morphological clock methods resurrect placoderm monophyly and reveal rapid early evolution in jawed vertebrates. *Systematic Biology* 66:4, 499-516. https://doi.org/10.1093/sysbio/syw107

King, B. and Rücklin, M. 2020. A Bayesian approach to dynamic homology of morphological characters and the ancestral phenotype of jawed vertebrates. *eLife* 9:e62374. https://doi.org/10.7554/eLife.62374

Klug, C., Coates, M., Frey, L., Greif, M., Jobbins, M., Pohle, A., Lagnaoui, A., Bel Haouz, W. and Ginter, M. 2023. Broad snouted cladoselachian with sensory specialization at the base of modern chondrichthyans. *Swiss Journal of Palaeontology* 142, 2. https://doi.org/10.1186/s13358-023-00266-6

Laing, A.M., Doyle, S., Gold, M.E.L., Nesbitt, S.J., O'Leary, M.A., Turner, A.H., Wilberg, E.W. and Poole, K.E. 2018. Giant taxon-character matrices: The future of morphological systematics. *Cladistics* 34: 333-335. https://doi.org/10.1111/cla.12197

Larridon, I., Villaverde, T., Zuntini, A.R., Pokorny, L., Brewer, G.E., Epitawalage, N., Fairlie, I., Hahn, M., Kim, J., Maguilla, E., Maurin, O., Xanthos, M., Hipp. A.L., Forest, F. and Baker, W.J. 2020. Tackling rapid radiations with targeted sequencing. *Frontiers in Plant Science* 10:1655. https://doi.org/10.3389/fpls.2019.01655

Lewis, P.O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology* 50:6, 913–925. https://doi.org/10.1080/106351501753462876

Li, Q., Zhu, Y-A., Lu, J., Chen, Y., Wang, J., Peng, L., Wei, G. and Zhu, M. 2021. A new Silurian fish close to the common ancestor of modern gnathostomes. *Current Biology* 31:16, 3613 - 3620.e2. https://doi.org/10.1016/j.cub.2021.05.053

Long, J.A. 1986. A new Late Devonian acanthodian fish from Mt. Howitt, Victoria, Australia, with remarks on acanthodian biogeography. *Proceedings of the Royal Society of Victoria* 98: 1-17.

López-Antoñanzas, R. and Peláez-Campomanes, P. 2022. Bayesian morphological clock versus Parsimony: an insight into the relationships and dispersal events of postvacuum Cricetidae (Rodentia, Mammalia). *Systematic Biology* 71:3, 512–525. https://doi.org/10.1093/sysbio/syab059

Mallet, J., Besansky, N. and Hahn, M.W. 2016. How reticulated are species?. *BioEssays* 38: 140-149. https://doi.org/10.1002/bies.201500149

Marjanović, D. 2021. The making of calibration sausage exemplified by recalibrating the transcriptomic timetree of jawed vertebrates. *Frontiers in Genetics* 12:521693. https://doi.org/10.3389/fgene.2021.521693

Matzke, N.J. and Irmis, R.B. 2018. Including autapomorphies is important for paleontological tip-dating with clocklike data, but not with non-clock data. *PeerJ* 6, e4553. https://doi.org/10.7717/peerj.4553

Moon, B.C. 2017. A new phylogeny of ichthyosaurs (Reptilia: Diapsida). *Journal of Systematic Palaeontology* 17:2, 129–155. https://doi.org/10.1080/14772019.2017.1394922

Moy-Thomas, J.A. 1971. Subclass Acanthodii. 61–78. In Moy-Thomas, J. A. and Miles, R. S. (eds). *Palaeozoic fishes*. Springer, 260 pp.

Nelson, G.J. 1969. Gill arches and the phylogeny of fishes, with notes on the classification of vertebrates. *Bulletin of the American Museum of Natural History* 141, 475–552.

Newman, M.J., den Blaauwen, J.L. and Burrow, C.J. 2020. Two newly identified cheiracanthid acanthodians from the Mey Flagstone Formation (Givetian, Middle Devonian) of the Orcadian Basin, Scotland. *Scottish Journal of Geology* 57:1, sjg2020–009. doi: https://doi.org/10.1144/sjg2020-009

Newman, M.J., den Blaauwen, J.L., Burrow, C.J., Jones, R. and Davidson, R.G. 2023. The Middle Devonian acanthodian *Orcadacanthus* n. gen. from the Orcadian Basin of Scotland. *Palaeontologia Electronica* 26:1, a5. https://doi.org/10.26879/1070

Paleobiology Database. 2024. Accessed: November 2024. https://paleobiodb.org/

Pradel, A., Maisey, J.G., Tafforeau, P. and Janvier, P. 2009. An enigmatic gnathostome vertebrate skull from the Middle Devonian of Bolivia. *Acta Zoologica* 90: 123-133. https://doi.org/10.1111/j.1463-6395.2008.00350.x

Qiao, T., King, B., Long. J.A., Ahlberg, P.E. and Zhu, M. 2016. Early gnathostome phylogeny revisited: Multiple method consensus. *PLoS ONE* 11:9, e0163157. https://doi.org/10.1371/journal.pone.0163157

Rambaut, A., Drummond, A.J., Xie, D., Baele, G. and Suchard, M.A. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67, 901– 904. https://doi.org/10.1093/sysbio/syy032

Renz, A.J., Meyer, A. and Kuraku, S. 2013. Revealing less derived nature of cartilaginous fish genomes with their evolutionary time scale inferred with nuclear genes. *PLoS ONE* 8:6, e66400. https://doi.org/10.1371/journal.pone.0066400

Rohon, J.V. 1889. Über fossile Fische vom oberen Jenissei. *Memoires de L'Académie Impériale des Sciences de St-Pétersbourg* VII Séri 36: 1–17.

Rokas, A. and Carroll, S.B. 2006. Bushes in the tree of life. *PLoS Biology* 4:11 899–904 https://doi.org/10.1371/journal.pbio.0040352

Rokas, A., Kruger, D. and Carroll, S.B. 2005. Animal evolution and the molecular signature of radiations compressed in time. *Science* 310, 1933–1938 https://doi.org/10.1126/science.1116759

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Hohna, S., Larget, B., Liu, L., Suchard, M. A., and Huelsenbeck, J. P. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61, 539–542. https://doi.org/10.1093/sysbio/sys029

Sansom, R. S. 2009. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). *Journal of Systematic Palaeontology* 7:1, 95–115. https://doi.org/10.1017/S1477201908002551

Sansom, I.J. and Andreev, P.S. 2018. The Ordovician enigma. Fish, first appearances and phylogenetic controversies. In: Johanson, Z., Underwood, C. and Richter, M. (eds.) *Evolution and Development of Fishes*. Cambridge: Cambridge University Press. 59–70.

Sanson, I.J., Davies, N.S., Coates, M.I., Nicoll, R.S. and Ritchie, A. 2012. Chondrichthyan-like scales from the Middle Ordovician of Australia. *Palaeontology* 55: 243-247. https://doi.org/10.1111/j.1475-4983.2012.01127.x

Schnetz, L., Butler, R.J., Coates, M.I. and Sansom, I.J. 2022. Skeletal and soft tissue completeness of the acanthodian fossil record. *Palaeontology* 65: e12616. https://doi.org/10.1111/pala.12616

Schultze, H.P. 1985. Marine to onshore vertebrates in the Lower Permian of Kansas and their paleoenvironmental omplications. *University of Kansas Paleontological Contributions* 113:1-18

Schultze, H.P. 1990. A new acanthodian from the Pennsylvanian of Utah, U.S.A., and the distribution of otoliths in gnathostomes. *Journal of Vertebrate Paleontology* 10:1, 49–58. https://doi.org/10.1080/02724634.1990.10011789

Seehausen, O. 2004. Hybridization and adaptive radiation. *Trends in Ecology and Evolution* 19:4, 198–207. https://doi.org/10.1016/j.tree.2004.01.003

Serra Silva, A. 2024. Extended Lissamphibia: a tale of character non-independence, analytical parameters and islands of trees. *Journal of Systematic Palaeontology* 22:1, 2321620, https://doi.org/10.1080/14772019.2024.2321620

Servais, T., Lehnert, O., Li, J., Mullins, G. L., Munnecke, A., Nützel, A. and Vecoli, M. 2008. The Ordovician biodiversification: revolution in the oceanic trophic chain. *Lethaia* 41:2, 99–109. https://doi.org/10.1111/j.1502-3931.2008.00115.x

Shaffer, H.B., Meylan, P. and McKnight, M.L. 1997. Tests of turtle phylogeny: Molecular, morphological, and paleontological approaches. *Systematic Biology* 46:2, 235–268. https://doi.org/10.1093/sysbio/46.2.235

Simakov, O., Marlétaz, F., Yue, J.X., O'Connell, B., Jenkins, J., Brandt, A., Calef, R., Tung, C.H., Huang, T.K., Schmutz. J., et al. 2020. Deeply conserved synteny resolves early events in vertebrate evolution. *Nature Ecology and Evolution* 4, 820–830. https://doi.org/10.1038/s41559-020-1156-z

Swofford, D.L. 2002. PAUP:Phylogenetic Analysis Using Parsimony* and other methods. ver. 4.0a169

Townsend, T.M., Mulcahy, D.G., Noonan, B.P., Sites Jr, J.W., Kuczynski, C.A., Wiens, J. J. and Reeder, T.W. 2011. Phylogeny of iguanian lizards inferred from 29 nuclear loci, and a comparison of concatenated and species-tree approaches for an ancient, rapid radiation. *Molecular Phylogenetics and Evolution* 61: 363–380. https://doi.org/10.1016/j.ympev.2011.07.008.

Upeniece, I. 1996. *Lodeacanthus gaujicus* n. g. et sp. (Acanthodii: Mesacanthidae) from the Late Devonian of Latvia. *Modern Geology*20, 383–398.

Whitfield, J.B. and Kjer. K.M. 2008. Ancient rapid radiations of insects: challenges for phylogenetic analysis. *Annual Review of Entomology* 53, 449-472. https://doi.org/10.1146/annurev.ento.53.103106.093304.

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

Zhu, M., Ahlberg, P.E., Pan, Z.-H., Zhu, Y.-A., Qiao, T., Zhao, W.-J., Jia, L.-T. and Lu, J., 2016. A Silurian maxillate placoderm illuminates jaw evolution. *Science* 354, 334–336. https://doi.org/10.1126/science.aah3764

Zhu, M., Yu, X.-B., Ahlberg, P. E., Choo, B., Lu, J., Qiao, T., Qu, Q.-M., Zhao, W.-J., Jia, L.-T., Blom, H. and Zhu, Y.-A., 2013. A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* 502, 188–193. https://doi.org/10.1038/nature12617

Zhu, Y.A., Li, Q., Lu, J., Chen, Y., Wang, J., Gai, Z., Zhao, W., Wei, G., Yu, Y., and Zhu, M. (2022). The oldest complete jawed vertebrates from the early Silurian of China. *Nature* 609:7929, 954–958. https://doi.org/10.1038/s41586-022-05136-8