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**Adaptive responses to Ordovician-Silurian environmental changes shaped the morphological diversity and evolution of Osteostraci**

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# Adaptive responses to Ordovician-Silurian environmental changes shaped the morphological diversity and evolution of Osteostraci

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## Abstract

Osteostracans are a Silurian-Devonian clade of jawless stem gnathostomes, and, as the putative sister group to jawed vertebrates, play a fundamental role in the study of the origin of jaws. Despite this, the timing and modality of their early diversification are poorly studied and understood. Here, their early evolutionary radiation is reconstructed using Bayesian tip dating methods. Using a revised and expanded phylogenetic dataset, I estimate that osteostracans originated between 450 and 443 million years ago, in the Late Ordovician. The emergence of Osteostraci is succeeded by a peak in rates of morphological evolution between 443 and 440 million years ago, after the Late Ordovician mass extinction. Following this early burst, major lineages appeared in a relatively rapid time frame, with a particularly rapid radiation taking place between 433 and 429 million years ago, after the Ireviken Biogeochemical event. Results presented in this study show how the Silurian and Devonian morphological diversity of osteostracans was the result of successive and diverse adaptive responses to climate change and extinctions of competing taxa. Further, the condensed pattern of divergences recovered among internal branches possibly explains low support and the different phylogenetic results retrieved in this study compared with previous analyses.

**Keywords:** Osteostracans; Tip-dating; Phylogenetics; Evolutionary rates; Evolutionary radiation.

## Introduction

Adaptive radiations, evolutionary processes in which a single ancestor gives rise to multiple new and ecologically diversified species, are thought to be a major contributor to evolutionary diversification and phenotypic diversity (Schluter 2000; Glor 2010; Wiens and Moen 2025). One of the main drivers of adaptive radiations is ecological opportunity (Stroud and Losos 2016), the abundance of available resources that are not used by competing taxa (Schluter 2000). In turn, mass extinctions can result in new ecological opportunity for some taxa, as environmental changes can render new resources accessible or can liberate previously occupied ecological niches (Friedman 2010; Chen and Benton 2012) and, hence, can favor adaptive radiations (Schluter 2000; Erwin 2001).

Although there is not a direct causal relationship between extinctions and adaptive radiations (Hoyall Cuthill et al. 2020), environmental crises can affect macroevolutionary dynamics and profoundly influence evolutionary trajectories of a clade (Simões et al. 2022).

Osteostraci Lankester, 1868, an exclusively Paleozoic taxon of jawless fish, is generally believed to be the sister taxon to jawed vertebrates (Janvier 1996; Sansom 2009; Ferron et al. 2021; Miyashita et al. 2021). As such, a deeper understanding of the timing and mode of their early diversification becomes necessary, as it would, in turn, provide further insights about the initial radiation of jawed vertebrates. Despite the wealth of anatomical information on Osteostraci (Janvier 1981, 1985a, 1985b, 1996; Miyashita et al. 2025), phylogenetic relationships inside the clade are understudied, with only a handful of computerized phylogenetic analyses carried out in the last 20 years (Sansom 2008, 2009; Scott and Wilson 2012, 2015; Tinn and Märss 2018), all executed using maximum parsimony. In a similar way, macroevolutionary dynamics and patterns of morphological evolution near the root of the clade are poorly studied. Further, new recent information on the earliest unambiguous osteostracan (Tinn and Märss 2018; Tinn et al. 2022) has never been incorporated in a morphological clock-type phylogenetic analysis to infer divergence dates and reconstruct the timing of their early radiation.

A recent study (Hagiwara and Sallan 2026) demonstrated how the Late Ordovician mass extinction (LOME) triggered parallel radiations of jawed vertebrates and their close jawless relatives. Such a scenario is consistent with the age of the earliest osteostracan fossil, which dates back to the Lower Silurian (Tinn and Märss 2018), and would seem to suggest a Late Ordovician to Lower Silurian origin for Osteostraci.

Here I apply Bayesian tip-dating methods to a revised and expanded version of the Sansom (2009) dataset, to infer macroevolutionary dynamics and timing of early osteostracan phylogeny and to investigate the impact the LOME and other Silurian environmental crises had on early osteostracan morphological evolution.

## Materials and Methods

### Matrix choice and revision

The original dataset of Sansom (2009) was used as a starting point. Scores were revised and updated mainly using existing character codings in Yu et al. (2024), Zhu et al. (2022) and Donoghue and Smith (2001). *Cheiracanthus* Agassiz, 1835 and *Guiyu oneiros* Zhu et al., 2009 were added in place of the Acanthodii, Osteichthyes and Chondrichthyes operational taxonomic units (OTUs), as suprageneric taxa are not suitable for time-calibrated analyses. *Cheiracanthus* was scored based on Burrow et al. (2020), while *Guiyu* was scored following Zhu et al. (2009), Zhu et al. (2012) and Qiao and Zhu (2010). Other added taxa are *Xiushanosteus mirabilis* (Zhu et al., 2022), the oldest complete placoderm, *Tujiaaspis vividus* (Gai et al., 2022), the earliest complete galeaspid, and *Kalanaspis delectabilis* (Tinn and Märss 2018), the earliest osteostracan. The resulting matrix is composed of 112 characters scored for 82 OTUs.

All modifications to the original dataset, including other added taxa and sources used to score them, are reported and justified in the Supplementary Materials.

### Phylogenetic analyses

The time-calibrated Bayesian inference analysis was performed in MrBayes ver. 3.2.7 (Ronquist et al. 2012) using the Mkv model of character evolution (Lewis 2001). Rate variation among characters was modeled using a gamma distribution.

The analysis was conducted with a fossilized birth-death (FBD) tree prior (Gavryushkina et al. 2014; Heath et al. 2014) without sampled ancestors ('fossiltip') and using a relaxed clock model. Terminal taxa were calibrated using uniform prior distributions for tip ages, while the age of *Escuminaspis* Traquair, 1893 and *Levesquaspis* Arsenault and Janvier, 1995 was fixed at 377 million years ago (Mya) because MrBayes ver. 3.2.7 requires the age of the most recent taxon to be fixed.

Stratigraphic occurrences for each taxon were obtained from the Paleobiology Database (2025). The tree age was specified using a uniform prior distribution with a minimum age of 461.1 Mya (maximum age of *Sacabambaspis* Gagnier et al., 1986) and a conservative maximum age of 486.85 Mya (corresponding to the start of the Ordovician Period). The dated analysis was run for 15,000,000 generations and the outgroup topology was constrained following results of a previous phylogenetic analysis (Miyashita et al. 2021, i.e. with *Pituriaspis* Young, 1991 stemwards to Osteostraci + jawed vertebrates and crownwards to Galeaspida). The temperature was set at 0.10, the coding was set as variable and all characters were unordered and equally weighted following Sansom (2009).

*Entelognathus* Zhu et al., 2013, *Guiyu* and *Cheiracanthus* were constrained to form a monophyletic group based on previous phylogenetic results (e.g. Li et al. 2021; Zhu et al. 2022) and *Pharyngolepis* Kiaer, 1911 was used as the outgroup instead of *Lampetra* Bonnaterre, 1788 following Tinn and Märss (2018). This was done because *Pharyngolepis* better represents the ancestral condition of the most recent common ancestor of the taxa included in the analysis than *Lampetra*, an extant derived cyclostome.

Convergence was assessed using Tracer ver. 1.7.2 (Rambaut et al. 2018): effective sample size was greater than 200 for all the tested parameters. The FBD analysis results were summarized using a maximum clade credibility tree. The latter was visualized using Figtree ver. 1.4.4 (Rambaut 2018).

To test how and to what extent the modifications made to the Sansom (2009) dataset influenced the recovered topology and divergence dates estimates, a time-calibrated analysis was run using the original matrix. This run used the same parameters and settings as the previous one, but with 10,000,000 Markov Chain Monte Carlo generations.

The nexus files containing the full matrices and the MrBayes scripts used to run the analyses are available as Supplementary Files 1 and 2.

### **Analyses of evolutionary rates and comparison of macroevolutionary parameters**

Data regarding node ages, rates of morphological evolution, branch lengths and posterior support were extracted from the maximum clade credibility tree and were collated, excluding nodes younger than 400 Mya and older than 452.4 Mya. Nodes inside Galeaspida and jawed vertebrates were not considered, and only two nodes outside Osteostraci were included, the node corresponding to the Galeaspida split and the jawed vertebrates-Osteostraci split. The resulting dataset was then analyzed with PAST ver. 5.3 (Hammer et al., 2001), using LOESS regression curves and smoothing splines to visualize evolutionary trends through time.

Variations in rates of morphological evolution and branch lengths through time were further assessed by time-slicing the maximum clade credibility tree and calculating median rates and median branch lengths per million year between 446 and 418 Mya. A similar method was applied in Brocklehurst et al. (2022).

All the generated datasets are available as Supplementary Files 3, 4 and 5.

## Results

### Phylogenetic topology and divergence dates

The topology recovered from the revised dataset analysis is shown in Figure 1 and Supplementary Figure 1 and is in stark contrast with the results presented in Sansom (2009). *Kalanaspis* is recovered as the earliest diverging osteostracan, consistent with results in Tinn and Märss (2018), although such a placement is poorly supported here (posterior probability: 0.64).

Most notably, and differing from results in Sansom (2009), Thyestiida is recovered as sister taxon to a clade comprising Ateleaspididae, Zenaspidida and Benneviaspidida, immediately crownwards to *Kalanaspis*. Such a result is unexpected but consistent with the method of phylogenetic reconstruction used here. As discussed in King (2021) and López-Antoñanzas and Peláez-Campomanes (2022), topologies obtained by time-calibrated Bayesian methods are generally more stratigraphically congruent than trees retrieved by undated Bayesian and parsimony analyses. This, in turn, explains the relatively rootward position of Thyestiida, a clade which contains amongst the oldest occurrences of Osteostraci (Sansom 2008). The monophyly of Thyestiida is very poorly supported (posterior probability: 0.36).

Ateleaspididae is retrieved immediately stemwards to the clade (*Hemicyclaspis* + (Zenaspidida + Benneviaspidida)), with *Ilemoraspis* recovered as sister taxon to a clade formed by the ‘unnamed group D’ of Sansom (2009) and Benneviaspidida. Another unexpected result is the position of *Cephalaspis*, as sister taxon to the clade containing *Pattenaspis*, *Zychaspis*, *Hildenaspis* and *Mimetaspis*.

The inferred age for the most recent common ancestor of Osteostraci (i.e. the *Kalanaspis* + all other included Osteostraci node) is between 450 and 440 Mya, with a median age of 444 Mya, in the Hirnantian, Late Ordovician, 4 million years before the oldest osteostracan fossil. The split between Thyestiida and all other osteostracan clades is placed around 441 Mya, with Thyestiida emerging around 438 Mya. The clade comprising all other Osteostraci is inferred to

originate around 435 Mya, with Ateleaspididae originating 431 Mya, Benneviastidida + ‘unnamed group D’ emerging around 426 Mya and Zenastidida originating around 425 Mya. Divergence dates for jawed vertebrates and galeaspidids are around 437 Mya for both clades, although the taxon sample of the two groups is incomplete as they are not the focus of this study. Moreover, the Osteostraci-jawed vertebrates split is placed at around 448 Mya.

The results of the analysis that used the original dataset are displayed in Supplementary Figure 2 and are in overall agreement with results of the run using the revised dataset. Divergence dates in this case are older, especially those of internal nodes. This is possibly due to the different outgroup used, the presence of suprageneric OTUs and the absence of key taxa such as *Kalanaspis* and *Xiushanosteus*.

### **Rates of morphological evolution and long-term evolutionary trends**

A marked increase in rates of morphological evolution for osteostracans is estimated between 443 and 440 Mya (Fig. 2A and Fig. 3), right after the Late Ordovician mass extinction and the Ordovician-Silurian boundary (Harper 2024; Zhang et al. 2025). Rates then decrease during the Silurian, with a minimum between 425 and 420 Mya. After this minimum, succeeding the Silurian-Devonian boundary, rates increase again in osteostracans overall. Among subclasses, rates are lowest in Zenastidida and Thyestiida between 425 and 420 Mya, whereas rates in Benneviastidida peak in the same time interval. (Fig. 3). Rates increase again after the end of the Silurian in Zenastidida and Thyestiida, and decrease in Benneviastidida.

Branch length values are high in Osteostraci after the Ordovician-Silurian boundary, but decrease to a minimum between 433 and 429 Mya (Fig. 2, Suppl. Fig. 5), after the Ireviken extinction event (Munnecke et al. 2003). This time period corresponds to the initial rapid radiation of non-thyestiidan osteostracans (Fig. 1). Branch length values are also low between 420 and 415 Mya, an age corresponding to the early diversification of boreaspidoids and derived kiaeraspidoids (Figs 1, 2B and Suppl. Fig. 1).

Posterior support trends through time are shown in Figure 4. Notable decreases in posterior support are found between 440 and 435 Mya and between 425 and 418 Mya, with the former corresponding to the initial diversification of Osteostraci and Thyestiida and the latter to the early evolutionary radiations of Benneviastidida and Zenastidida.

## **Discussion**

Here I have provided the first Bayesian tip-dating analysis of Osteostraci and demonstrated that this clade likely originated between 450 and 443 Mya, with a median age placed in the Late Ordovician, 444 Mya. Such an estimate is consistent with the age of the first unambiguous osteostracan (Mid-Llandovery, Lower Silurian) and suggests an Hirnantian origin, between the two pulses of the LOME, for the most recent common ancestor of the clade (Harper 2024; Zhang et al. 2025). Although a post-LOME origin remains entirely possible for Osteostraci, such a scenario would imply even faster rates of morphological evolution and a more compressed pattern of divergences during the early evolutionary history of the group.

Further, a younger origin age for Osteostraci would be less consistent with previous tip-dating analyses of jawed vertebrates (Morra 2026; Zhu et al. 2026), which recovered significantly older ages for the latter group. The fossil record of jawed vertebrates includes occurrences of putative crown-group gnathostomes from as far back as the Middle Ordovician (Sansom et al. 2012; Sansom and Andreev 2018; Hagiwara and Sallan 2026). This seems to corroborate an Ordovician origin for Osteostraci, given their putative sister-group relationship with jawed vertebrates, and makes the older ages reconstructed by the original dataset analysis less improbable. Such a scenario would seem to predict the possible, although seemingly unlikely, presence of Ordovician osteostracans in the fossil record.

Ages inferred herein for Thyestiida, Zenaspidida, Ateleaspididae and Benneviaspidida suggest post-LOME origins for all these groups and indicate that they likely originated within 15 million years after the appearance of the most recent common ancestor of Osteostraci.

Accelerated rates of morphological evolution are reconstructed by the tip-dating analysis during the early diversification of Osteostraci, with a significant peak between 443 and 440 Mya, after the LOME. This suggests new ecological opportunity for osteostracans that lived in the wake of the LOME, possibly due to the liberation of previously occupied morphospace and ecological niches (Friedman 2010; Wright 2017). High evolutionary rates during the early history of the clade are consistent with an early burst model of evolution (Puttick 2018; Moon and Stubbs 2020; Brownstein and Griffin 2026), with the peak in rates preceding the diversification of the major osteostracan groups. An early burst pattern of evolution driven by new ecological opportunity is corroborated also by the relatively rapid appearance of the main osteostracan body plans after the origin of the clade and by the long-term drop in rates of morphological evolution after the initial peak (Moons and Stubbs 2020). A peak in evolutionary rates after the LOME is also consistent with results in Hagiwara and Sallan (2026), which found evidence for postextinction endemic radiations of jawed and jawless vertebrates successive to the LOME.

A rapid radiation of osteostracan taxa, displayed as a marked drop in median branch length (Fig. 2B), is reconstructed by the Bayesian analysis between 433 and 430 Mya, following the Ireviken Biogeochemical Event (Mummecke et al. 2003; Young et al 2019; Stolfus et al. 2023). This relatively minor extinction event, likely triggered by oceans oxygen loss (Young et al. 2019) and changing climatic conditions (Lehnert et al. 2010), affected taxa possibly competing with osteostracans, such as conodonts (Jeppsson 1987; Sallan et al. 2018; Hagiwara and Sallan 2026), and made their ecological niches available. In turn, this could have initiated a rapid osteostracan diversification, although evolutionary rates were already dropping to a plateau in this time period. Indeed, other rapid evolutionary radiations occurring after mass extinctions are known (Brusatte et al. 2010; Ezcurra and Butler 2018; Kear et al. 2023) and support such a scenario for Osteostraci.

Another period of fast diversification of osteostracans is reconstructed around the Silurian-Devonian boundary. This rapid radiation corresponds to a drop in median branch lengths starting towards the end of the Ludlow, with a minimum in the Early Devonian (Fig. 2B). A consequent rise in rates of morphological evolution of kiaeraspidoids and zenaspidids is reconstructed starting in the Pridoli (Fig. 3A). This new drop in median branch lengths follows the Lau and Šilalè extinction events (Calner and Eriksson 2006; Spiridonov et al. 2020). These minor extinctions affected mainly conodont faunas and possibly favored the diversification of kiaeraspidoids and zenaspidids.

The recovered topology is markedly different from previous phylogenetic hypotheses of osteostracan relationships and needs further scrutiny and discussion. The position of Thyestiida as the earliest diverging osteostracan clade is unexpected but not entirely new (Denison 1951; Halstead 1982). This result is possibly due to the method of phylogenetic reconstruction used in this study. Tip-dating Bayesian analyses are known to be able to accommodate large amounts of homoplasy (King et al. 2017) and generally recover more stratigraphically congruent trees than non-dated Bayesian and parsimony analyses (King 2021; López-Antoñanzas and Peláez-Campomanes 2022). The stratigraphic distribution of Thyestiida, which contains some of the oldest occurrences for Osteostraci (Sansom 2008), can thus explain their relatively rootward position compared with previous phylogenetic analyses.

Uncertainty regarding relationships among major osteostracan groups, underscored by low posterior support for internal nodes, can also be due to the relatively compressed pattern of divergences reconstructed between 435 and 430 Mya (Whitfield and Lockhart 2007; Whitfield and Kier 2008; Serra Silva et al. 2025; Morra 2026). Rapid radiations can be particularly

challenging to reconstruct due to the scarce phylogenetic signal of short internal branches (Rokas and Carroll 2006).

Osteostracan relationships, nonetheless, are in need of revision. Further expansion of the present dataset with novel and recent anatomical information is needed (Keating et al. 2012; Miyashita et al. 2025), in order to infer a robust framework of osteostracan evolution and more confidently reconstruct divergence dates for the group.

## Conclusion

Osteostraci probably originated in the Late Ordovician, between 450 and 443 Mya, shortly before their first occurrence in the fossil record. Soon after their appearance, toward the end of the Late Ordovician mass extinction, they underwent a period of accelerated rates of morphological divergence, with a peak between 443 and 440 Mya, consistent with an early burst model of evolution. Following the initial burst, they diversified rapidly into the main clades and body-plans, with a particularly rapid radiation taking place between 433 and 429 Mya. This rapid radiation happened shortly after the Ireviken Biogeochemical event, which likely favored the diversification of osteostracans by freeing up previously occupied ecological niches. Ecological opportunity in the wake of the Late Ordovician mass extinction also appears to have triggered the initial burst of morphological evolution.

The relatively compressed pattern of divergences reconstructed after the Ireviken event could explain uncertainty regarding the relationships of the major osteostracan groups and low support values inferred for internal branches. This is because short internal branches carry a weak phylogenetic signal, which makes the true pattern of divergences difficult to reconstruct. Results presented in this study show how the Silurian and Devonian morphological diversity of Osteostraci was the result of multiple adaptive responses to Ordovician-Silurian climatic shifts and extinctions. Further, they confirm the potential of Bayesian tip-dating analyses to reconstruct and reveal how and to what extent environmental changes influenced the morphological evolution of extinct clades.

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Figure 1. Maximum clade credibility tree recovered by the FBD analysis. Numbers at nodes represent inferred median age values. Silhouettes are from Phylopic and Wikimedia Commons. Credits in the acknowledgements section.

Figure 2. Median rates of morphological evolution and median branch lengths through time. LOESS curves and confidence intervals of (A) median rates of morphological evolution and (B) median branch lengths through time. The thick line represents the median rate per million year, while the narrow lines are LOESS regression curves.

Figure 3. Rates of morphological evolution through time. (A) LOESS curves and confidence intervals of morphological rates by clade through time. (B) Smoothing spline of morphological rates through time. Data points are evolutionary rate node values inferred by the FBD analysis. Silhouettes from Phylopic and Wikimedia commons. Credits can be found in the acknowledgement section.

Figure 4. Posterior support through time. LOESS curve and confidence interval of posterior support data inferred by the FBD analysis.







