

Initial radiation of jaws demonstrated stability despite faunal and environmental change

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More than 99 per cent of the roughly 58,000 living vertebrate species have jaws¹. This major clade, whose members are collectively known as gnathostomes ('jawed mouths'), made its earliest definitive appearance in the Silurian period, 444–416 million years (Myr) ago, with both the origin of the modern (crown-group) radiation and the presumptive invasion of land occurring by the end of the Devonian period² (359 Myr ago). These events coincided with a major faunal shift that remains apparent today: the transition from Silurian ecosystems dominated by jawless fishes (agnathans) to younger assemblages composed almost exclusively of gnathostomes^{2,3}. This pattern has inspired several qualitative descriptions of the trophic radiation and ecological ascendancy of the earliest jawed vertebrates^{3–7}. Here we present a quantitative analysis of functional variation in early gnathostome mandibular elements, placing constraints on our understanding of evolutionary patterns during this critical interval. We document an initial increase in functional disparity in the Silurian that stabilized by the first stage of the Devonian, before the occurrence of an Emsian (~400 Myr ago) oxygenation event implicated in the trophic radiation of vertebrates⁸. Subsequent taxonomic diversification during the Devonian did not result in increased functional variation; instead, new taxa revisited and elaborated on established mandibular designs. Devonian functional space is dominated by lobe-finned fishes and 'placoderms'; high disparity within the latter implies considerable trophic innovation among jaw-bearing stem gnathostomes. By contrast, the major groups of living vertebrates—ray-finned fishes and tetrapods—show surprisingly conservative mandibular morphologies with little indication of functional diversification or innovation. Devonian gnathostomes reached a point where they ceased to accrue further mandibular functional disparity before becoming taxonomic dominants relative to 'ostracoderm'-grade jawless fishes, providing a new perspective on classic adaptive hypotheses concerning this fundamental shift in vertebrate biodiversity.

Morphological disparity has often been used as a proxy for ecological/functional variety in the fossil record⁹. However, divergent anatomies can be biomechanically similar^{10–12}, leading to decoupling of morphological and functional metrics^{12–14}. To evaluate potential functional diversity, we have devised a measure of variation derived from biomechanical traits. We focus on the mandible because it is well characterized functionally in modern fishes¹⁵ and because it is the key character proposed by adaptive schemes to separate the gnathostomes from their jawless predecessors^{4,6}. We document how functional variation accumulates after the origin of jaws and test the hypothesis that, during their rise to dominance, gnathostomes outcompeted or displaced jawless fishes.

We assembled a data set consisting of 198 Silurian/Devonian gnathostome genera scored for 31 mandibular traits (11 continuous and 20 discrete), many of which have been shown to be functionally relevant in living taxa. These data were analysed using non-metric multidimensional scaling, yielding a multivariate 'function space'. Functional disparity was calculated across eight time bins (the late

Silurian plus the seven stages of the Devonian) using a variety of measures (sum of variances is presented here because it is relatively robust to variation in sample size¹⁶). We tested for differences between successive bins using multiple approaches (likelihood ratios and *t*-tests), and used a jackknifing procedure that pruned exceptional fossil assemblages from our data set to examine the sensitivity of results to 'Lagerstätten effects', biases arising from localities characterized by exceptional preservation or fossil abundance. Full details of our methodology are given in Supplementary Information.

Our results show remarkably stable levels of lower-jaw functional disparity during the Devonian (Fig. 1a). There is a trend of increasing disparity from the late Silurian to the end of the Early Devonian (the Emsian stage); however, by the earliest Devonian (the Lockhovian stage, ~415 Myr ago) functional mandibular disparity attained a level statistically indistinguishable from that found in the Late Devonian. When *P* values are adjusted for multiple comparisons, the only significant disparity shift between successive Devonian stages (corrected *P* value, 0.013) is a decline on entering the Middle Devonian (the Eifelian stage, ~398 Myr ago; Fig. 1a). This seems to reflect a reduction in the number of marine sites sampled in the Eifelian, combined with the Emsian Taemas/Wee Jasper fauna, which contains a series of extensively studied durophagous lungfishes with exceptionally robust jaws. When this site is removed in jackknife analyses, the drop in disparity is no longer significant (corrected *P* value, 0.112). When differences are assessed using likelihood ratios, none exceeds a threshold value of 8 (ref. 17; likelihood ratio range, 1.023–4.34). This pattern of functional stability arises despite an increase both in the number of mandibles sampled per bin over our study interval and in the taxonomic diversity of gnathostomes during the Devonian¹⁸, and is robust to the removal of exceptional Lagerstätten. Details of all analyses are given in Supplementary Information.

A breakdown of morphospace by stage shows that initial functional disparity in the late Silurian was localized in the lower-left and upper-right quadrants (Fig. 2). The former is populated by gnathostomes (for example stem sarcopterygians and ischnacanthid 'acanthodians') with gracile mandibles bearing slender, pointed cusps and characterized by low closing mechanical advantages, whereas the latter contains taxa (for example mesacanthid acanthodians) with toothless jaws. The Lockhovian expansion into the lower-right quadrant reflects the appearance of taxa (for example the lungfish *Diabolepis*) with robust jaws characterized by both high closing mechanical advantage and high second moment of area, two features consistent with durophagy. Subsequent mandibular evolution during the Devonian resulted in novel designs that elaborated existing ones, but did not substantially exceed the boundaries established earlier in the interval (Fig. 2). Specific anatomical correlates of our ordination axes are provided in Supplementary Table 2.

We examined patterns of partial disparity¹⁹ to dissect the contributions to overall functional variation made by major taxonomic assemblages: 'Acanthodii', an extinct assemblage sometimes called spiny sharks; Actinopterygii, or ray-finned fishes, related to most fishes alive today; Chondrichthyes, or cartilaginous fishes, the precursors of rays, sharks and ratfishes; 'Placodermi', armoured stem gnathostomes; and

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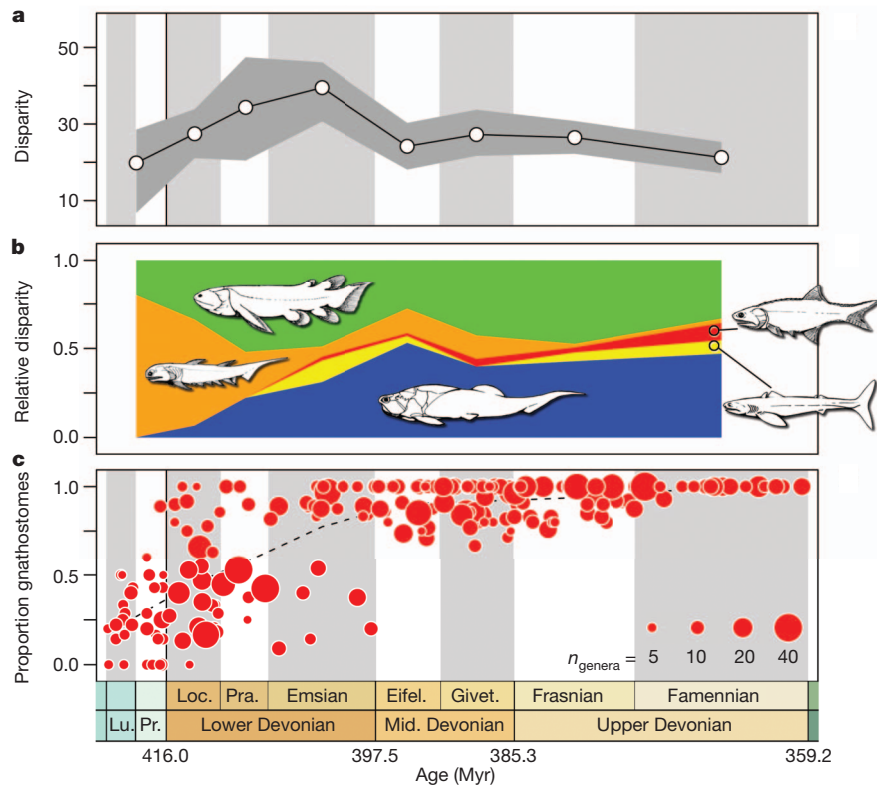


Figure 1 | Functional mandibular disparity among Silurian/Devonian gnathostomes. All horizontal axes show time as indicated at bottom.

a, Disparity (sum of variances) across eight time bins. The dark-grey region spans the 95% confidence intervals based on 1,000 bootstrap pseudoreplicates. **b**, Relative contributions (partial disparity) of major gnathostome groups to overall functional disparity. Orange, 'Acanthodii'; green, Sarcopterygii; blue, 'Placodermi'; yellow, Chondrichthyes; red, Actinopterygii. **c**, Faunal

composition data for the late Silurian and Devonian. Discs represent individual vertebrate assemblages plotted as a function of time and proportion of gnathostomes that comprise those faunas (discs jittered within time bins for clarity). The area of each disc is proportional to the total number of vertebrate genera represented, n_{genera} . Eifel., Eifelian stage; Givet., Givetian stage; Loc., Lockhovian stage; Lu., Ludlow series; Pr., Pridoli series; Pra., Pragian stage.

Sarcopterygii, or lobe-finned fishes, including lungfishes and terrestrial vertebrates. Sarcopterygians make a major and relatively stable contribution to mandibular disparity throughout our study interval (Fig. 1b). The earliest definitive digit-bearing tetrapods (*Acanthostega* and *Ichthyostega*) and their immediate relatives (*Ventastega*, *Elginerpeton*, *Densignathus* and *Metaxygnathus*) show a conservative pattern in mandibular function relative to sarcopterygian 'fishes' (Fig. 2). This is in contrast to studies that report a distinct shift in cranial suture patterns between aquatic taxa and early digit-bearing tetrapods²⁰, suggesting that different parts of the feeding system evolved in separate phases. By contrast, lungfishes are a major source of mandibular innovation among sarcopterygians, colonizing a new region of functional space in the Lockhovian and occupying it exclusively throughout the Devonian (Fig. 2).

'Placoderms' occupy 50% of realized Devonian gnathostome morphospace volume (Fig. 2), indicating that considerable functional differentiation occurred on the gnathostome stem, independently of the origin of modern jawed vertebrates. 'Placoderm' functional variety remains undiminished until their sudden extinction at the Devonian/Carboniferous boundary. A direct reading of our results implies that 'placoderms' were a major contributor to gnathostome disparity only from the Middle Devonian onward. We argue that this is an artefact; many 'placoderms' are known from the Early Devonian and, increasingly, the Silurian^{2,21}, but few preserve mandibular material that can be included in our analysis. This suggests that disparity measures for the Silurian and Early Devonian are probably conservative underestimates, and that the addition of more 'placoderms' of this age would only reinforce the pattern of early functional morphospace saturation.

The remaining three gnathostome assemblages—'acanthodians', chondrichthyans and actinopterygians—make relatively minor

contributions to overall disparity (Fig. 1b). 'Acanthodians' make a major contribution to functional variety during the Silurian, but their relative importance wanes substantially throughout the Devonian, reflecting a decline in functional diversity and apparent richness combined with the taxonomic ascendance of other gnathostome clades²². Actinopterygians, the most speciose group of living jawed fishes¹, contribute little to overall disparity in the Devonian, with their few representatives conservatively clustering within tightly delimited regions of function space (Fig. 2). This is consistent with previous arguments, drawn from taxonomic data, that actinopterygians were not ecologically diverse until the Carboniferous period²². The reliability of low measures of chondrichthyan partial disparity is unclear, however, because the numerous Devonian chondrichthyans known exclusively from dental remains²³ cannot be included in our analysis.

Our results provide a new perspective on debates concerning the Devonian shift from agnathan- to gnathostome-dominated fossil assemblages, a transition that remains apparent in modern vertebrate fauna^{1,22}. A range of schemes, largely derived from anecdotal evidence, have sprung up in response to this pattern of turnover^{3–7}. Faunal data clearly show that gnathostomes shared habitat space evenly with 'ostracoderm'-grade agnathans well into the Early Devonian (Fig. 1c). It is only during and after the Emsian that gnathostomes became taxonomic dominants in most fossil assemblages, several million years after they explored the extremes of realized Devonian mandibular function space. The offset between the trophic radiation of gnathostomes (Fig. 1a) and the taxonomic collapse of 'ostracoderms' (Fig. 1c), combined with the long history of coexistence between these two groups, argues against the direct ecological replacement of jawless fishes by jawed forms⁶. Furthermore, we find no evidence for a significant positive relationship between mandibular disparity within assemblages and the taxonomic

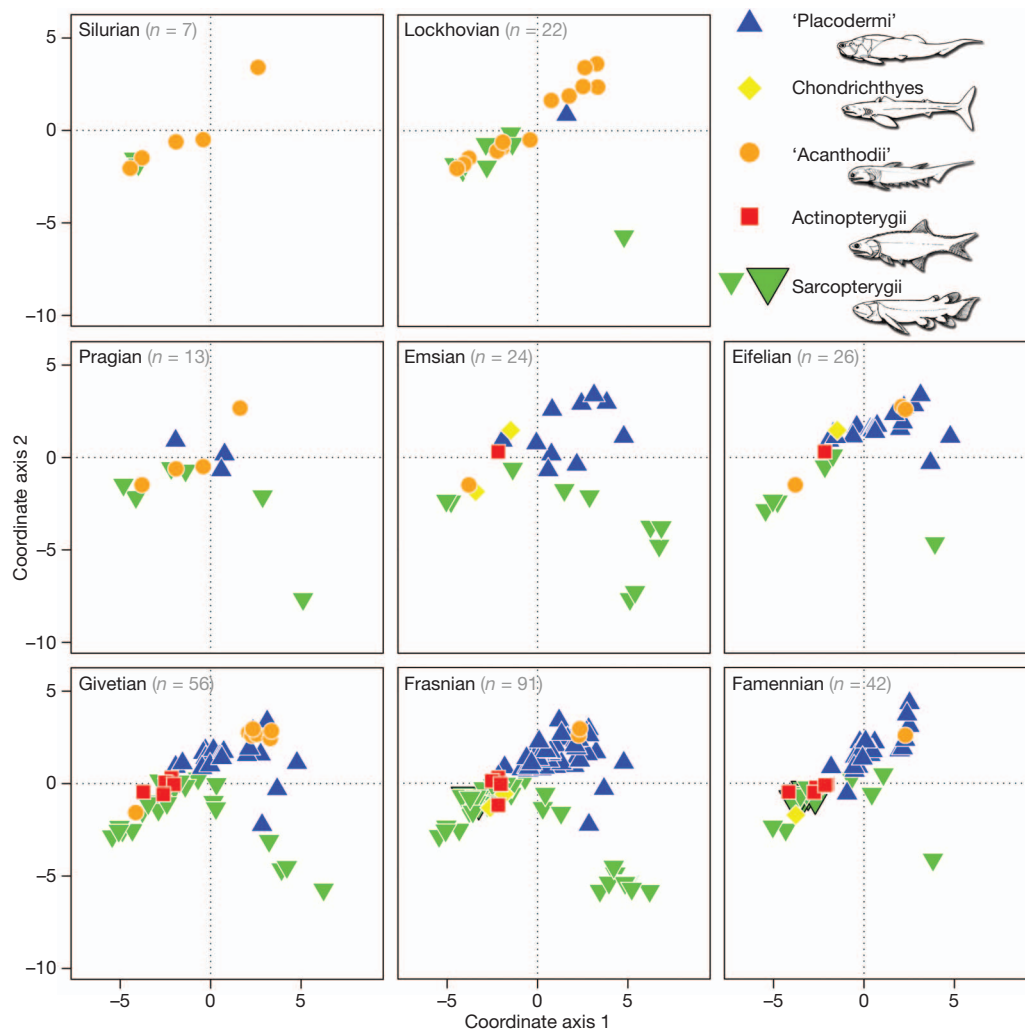


Figure 2 | Patterns of functional morphospace occupation for jawed vertebrates during the late Silurian and Devonian. Points represent averages for genera plotted on coordinate axes 1 and 2 of the non-metric multidimensional scaling ordination. Orange circles, 'Acanthodii'; green down-triangles, Sarcopterygii (tetrapods indicated by larger symbols outlined in

black); blue up-triangles, 'Placodermi'; yellow diamonds, Chondrichthyes; red squares, Actinopterygii. The area in the lower-right corner of the functional morphospace is occupied solely by lungfishes. See text and Supplementary Information for further details.

dominance of jawed vertebrates within those faunas (measured as the proportion of gnathostomes; Pearson and Kendall rank-order correlations, $P = 0.90\text{--}0.94$; weighted least-squares regression, $P = 0.40\text{--}0.44$). This pattern is inconsistent with the assertion⁶ that gnathostome diversification primarily reflects the ecological displacement of agnathans and subsequent refilling of their functional roles. Indeed, few of the feeding strategies apparently taken up by early gnathostomes, such as macropredation and durophagy, have any clear analogue among jawless taxa³. Instead, the proliferation of gnathostomes probably reflects new ecological opportunities associated with the origin of jaws and, perhaps just as importantly, the shift from benthic lifestyles to pelagic ones²⁴.

The Devonian radiation of gnathostomes is marked by an early plateau of functional disparity and a consistent range of mandibular variation in the face of major environmental perturbations, including fluctuating global temperatures²⁵, shifting continental weathering patterns²⁶, sea level changes²⁶ and a major extinction event²⁷. Various proposals have linked patterns of early vertebrate evolution to changes in atmospheric composition, with parallel claims that gnathostome diversification was driven by increases in oxygen levels during the Silurian²⁸ or the Devonian⁸. Silurian data are too scant to comment on the first proposal, but we note that gnathostomes achieved stable levels of functional diversity before the occurrence of an Emsian oxygenation event (~400 Myr ago) implicated in the trophic radiation

of vertebrates⁸. There is no significant shift in functional disparity between the Frasnian and Famennian stages (~375 Myr ago; Fig. 1) correlating with the Kellwasser event, which is classically identified as one of the 'Big Five' Phanerozoic extinctions²⁷. This event resulted in a global reef collapse²⁹; however, jawed vertebrates seem to be unaffected in terms of diversity²², functional disparity and potentially ecological variation. More broadly, our results imply constraints on the functional diversity of the gnathostome mandibular system, with early functional saturation and subsequent refilling of established biomechanical roles by new taxonomic actors.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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