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Viewpoint

How did Jawed Vertebrates Originate and Rise?

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99.8% of extant vertebrate species on Earth, including humans, possess jaws (maxilla and mandible). The group which we belong to is accordingly referred to as jawed vertebrates or gnathostomes. The origin and rise of our group is undoubtedly one of the most critical evolutionary milestones in the history of vertebrates from fish to humans. The emergence of the jaw also marked a substantial morphological shift of brains and facial organs in the earliest gnathostomes, leading to significant enhancement of feeding and respiratory efficiency, greatly increasing the evolutionary potential of vertebrates towards larger body sizes and diverse ecological niches. Indeed, many important organs in humans can be traced back to the early evolutionary history of the jawed vertebrates. Therefore, the origin and rise of jawed vertebrates have always been a focal point in paleontology and evolutionary biology (Bi et al., 2021; Brazeau and Friedman, 2015).

Traditionally, jawed vertebrates can be divided into four distinctive groups: placoderms, acanthodians, osteichthyans, and chondrichthyans. Of these, only osteichthyans and chondrichthyans persist to this day. The most recent common ancestor of the latter two groups, and all of its descendants, constitute the crown-group gnathostomes. The discovery of significant transitional fossils has blurred the once distinct boundaries among these four groups. Acanthodians, for instance, have been recognized as stem-group members of the chondrichthyan lineage. Placoderms, on the other hand, are widely accepted as encompassing nearly all the jawed stem-group gnathostomes. Both acanthodians and placoderms are no longer recognized as natural, or monophyletic groups. Additionally, various jawless, armored fishes, such as heterostracans, galeaspids, and osteostracans, bear a closer phylogenetic relationship with jawed vertebrates than with jawless cyclostomes (lampreys and hagfish). These armored jawless fish, together with placoderms, constitute the gnathostome stem-group (Fig. 1). As such, they play pivotal roles in bridging the morphological gap between extant jawless cyclostomes and the crown-group gnathostomes.

When, where, and how did the jawed vertebrates originate and rise? This question encompasses several sub-questions: How did the jaw itself emerge? How did the essential body plans and organs of jawed vertebrates, such as the paired appendages, teeth, nose, ears, tongue, neck, axial skeleton, and lungs, originate? How did the earliest jawed vertebrates evolve? How did the gnathostome crown-group, or modern jawed vertebrates, originate? What was the ancestral body plan of the osteichthyans? How did chondrichthyans lose the macromeric dermal skeleton? The answers to these questions are primarily sought through paleontological studies, often supplemented with insights from evolutionary. molecular and developmental biology.

Molecular biology provides crucial restrictive evidence as to when and how the jaws and jawed vertebrates originated. Molecular clock studies attest to the fact that the last common ancestor of all modern gnathostomes emerged approximately 450 million years ago. Therefore, the emergence of the jaw cannot be later than this date. The genome study of living gnathostomes suggests that the origin of jawed vertebrates might be attributed to a relatively serendipitous event of interspecific hybridization and whole-genome duplication (Simakov et al., 2020). Given the profound evolutionary gap between extant jawless cyclostomes and the gnathostome crown group, the detailed processes and mechanisms of the origin and early diversification of the jaw and jawed vertebrates are still largely to be extrapolated from investigations of early transitional fossils.

Over the past two to three decades, researchers made significant advances in this field. The discovery and detailed studies of the Early Silurian jawed vertebrates, either preserved completely or disarticulated, filled in a 14 million-year gap in the earliest fossil record of jawed vertebrates (Andreev et al., 2022; Zhu et al., 2022). The discovery of Late Silurian (Ludlow) primitive osteichthyans and maxillate placoderms provide hitherto unprecedented transitional fossil evidence for the origins of the gnathostome crown-group (Zhu et al., 2016, 2013). Studies on the new materials of the jawless galeaspids have also yielded useful insights into the origins of the jaw and paired appendages (Gai et al., 2022, 2011). Despite these advances, how the jaw originated remains a persistent conundrum. Traditional theories suggesting a simple transformation from gill arches to jaw arches find little support in both fossil and extant vertebrates. The dermal bone-encased oral regions in various jawless armored fish (collectively known as 'ostracoderms') and the earliest jawed fish, the placoderms, exhibit remarkable similarities despite the former group lacking jaws. Yet, it is challenging to infer from existing fossil evidence how the en-

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doskeletal primary jaw evolved. The jawless galeaspids, which resemble jawed vertebrates in certain aspects such as having separate nasal sacs, provide an intermediate state supporting the heterotopic hypothesis of the jaw origin. However, osteostracans bear paired fins, perichondral ossification of the endoskeleton, and heterocercal tails, all characteristic of jawed vertebrates, but they lack separate nasal sacs, and their pituitary does not communicate with the oral cavity as in lampreys. Therefore, which group of jawless fish is the sister group of the jawed vertebrates, and how the jaw transformed from the jawless condition, remain unresolved.

Consensus has yet to be reached regarding the interrelationships of placoderms, the earliest jawed vertebrates. This lack of agreement primarily arises from the limited anatomical data available on these primitive jawed vertebrates. For example, we know virtually nothing regarding the endoskeleton of antiarchs, possibly the most primitive jawed vertebrates. We also know very little regarding the endoskeleton of all the Silurian placoderms, and most of the body plan of acanthothoracids, another key placoderm group. While the discovery of maxillate placoderms starts to fill in the gap between osteichthyans and placoderms, the gap remains substantial. The traits typically associated with osteichthyans, such as the shedding and replacing teeth, the full set of dermal bones encasing the palate and other parts inside the oral cavity, remain unclear. While potential transitional fossils between chondrichthyans and placoderms have been discovered (Zhu et al., 2022), their anatomical details and how the "armor", or the macromeric dermal skeleton is lost step-wisely in chondrichthyans, await further elucidation.

Future research in the origin and early evolution of jaw and jawed vertebrates is expected to bring significant breakthroughs and point out novel directions. The ever-improving tomographic technologies can extract more exquisite anatomical information from both newly discovered fossils, and those already in the collections. The following analyses will continue to refine the existing phylogenetic framework, and deepen the understanding of how the body plan and key organs of jawed vertebrates arose. Using big data analyses and statistical models to reconstruct the macroevolutionary patterns of major taxonomic groups in this period, could reveal the impact of biotic and environmental factors on the rise, decline and demise of these groups (Sallan et al., 2018).

The evolution of life is intimately linked to Earth's environmental changes. Investigating the taphonomy and sedimentology of the Silurian Lagerstätten can unravel the mystery of why only these fossil troves from South China yield abundant and completely preserved Silurian jawed vertebrates all over the world. Further field works in the three Marine Red Beds of the Silurian of South China, and even in the Ordovician, may lead to the discovery of key fossil material. Multidisciplinary, integrative, and comprehensive research incorporating biostratigraphic, sedimentological, geochemical, and structural geological studies, will refine the spatiotemporal framework of Ordovician–Silurian strata, and reveal the mechanisms of major geological and biological events linked to the rise of jawed

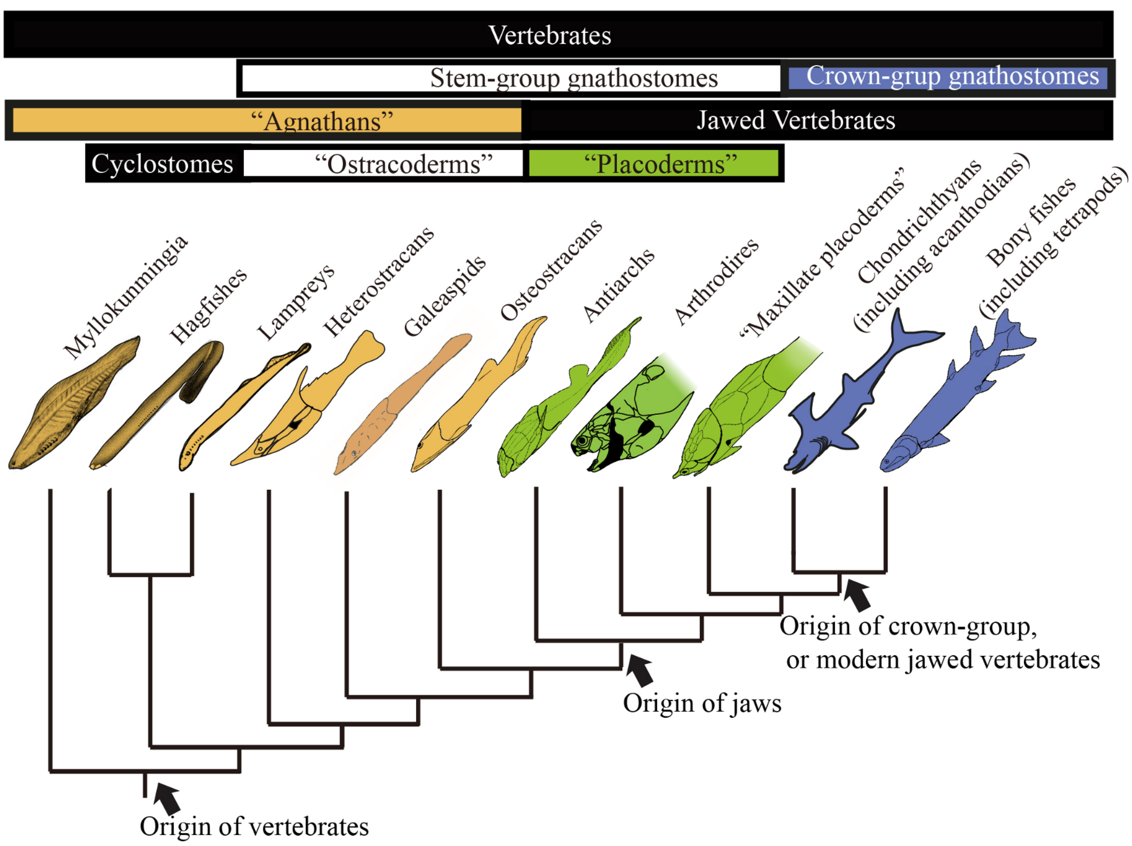

Figure 1. The systematic evolution of jawed vertebrates and the key nodes. Quotation marks indicate paraphyletic groups.

vertebrates. The implementation of these efforts will continue to fill in the gaps in our existing knowledge on the origin and rise of jawed vertebrates.

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Conflict of Interest

The authors declare that they have no conflict of interest.

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