

The origin and early phylogenetic history of jawed vertebrates

Martin D. Brazeau¹ & Matt Friedman²

Fossils of early gnathostomes (or jawed vertebrates) have been the focus of study for nearly two centuries. They yield key clues about the evolutionary assembly of the group's common body plan, as well the divergence of the two living gnathostome lineages: the cartilaginous and bony vertebrates. A series of remarkable new palaeontological discoveries, analytical advances and innovative reinterpretations of existing fossil archives have fundamentally altered a decades-old consensus on the relationships of extinct gnathostomes, delivering a new evolutionary framework for exploring major questions that remain unanswered, including the origin of jaws.

Jawed vertebrates (gnathostomes) comprise more than 99% of living vertebrate species, including humans. This diversity is built on features including jaws, teeth, paired appendages, and specialized embryonic and skeletal tissues (Box 1); centuries of research have attempted to explain their origins^{1–7}. In particular, jaws and paired appendages have become flagship systems in the study of evolutionary novelty^{5,7} — a key research programme in evolutionary biology⁸.

The deepest split in the modern gnathostome tree is that between the chondrichthyans (sharks, rays and chimaeras) and the osteichthyans (bony fishes and tetrapods). This divergence occurred in the Palaeozoic era, at least 423 million years ago (Ma)⁹, leaving a vast temporal and evolutionary gulf between modern lineages, with ample time for new innovations to overwrite primitive conditions. These complexities compel researchers to turn to the Palaeozoic fossil record to elucidate the origin of jawed vertebrates. A few well-preserved fossil taxa from a handful of Silurian–Permian sites in Europe and North America¹⁰ shaped late nineteenth- and early twentieth-century hypotheses of gnathostome evolution^{1,11,12} (Fig. 1). Many of these narratives persist to this day, either implicitly or explicitly. However, fossils once hailed as avatars for scenarios of jaw^{12,13} or fin^{1,14} origins often turn out to be specialized rather than primitive after phylogenetic investigation^{15,16}. Until they are placed in a evolutionary tree, Palaeozoic fossils are mute on the question of gnathostome origins.

In this Review, we examine the progress made in the past two decades on the study of early gnathostome interrelationships, focusing on key fossil discoveries that have prompted a renewed intensity of phylogenetic investigation. Although tremendous advances have been made, much work remains before this research can deliver finely atomized transformational hypotheses such as those available for mammals¹⁷, birds¹⁸ and early tetrapods¹⁹.

Phylogeny of extant gnathostomes

From the perspective of modern lineages alone, deep vertebrate phylogeny is well resolved and there is little disagreement about the branching patterns surrounding the gnathostome crown node (Box 1). Morphological²⁰ and molecular²¹ data unambiguously indicate that chondrichthyans and osteichthyans are reciprocally monophyletic sister taxa. Together, they form a clade to the exclusion of the jawless cyclostomes: hagfishes and lampreys (Box 1). Molecular evidence strongly supports the monophyly of living agnathans with respect to jawed vertebrates. The

long-standing morphological hypothesis indicated the union of lampreys and gnathostomes to the exclusion of hagfishes^{10,22}, but re-appraisal of traits in living species^{23–25} and reconsideration of existing data sets²⁶ have exposed its weaknesses.

These established relationships put the study of early gnathostome evolution at an advantage. Modern taxa can be organized into a set of crown groups delimiting three stem lineages: the respective branches subtending Osteichthyes and Chondrichthyes, and the branch subtending their last common ancestor (Box 1). The palaeontological problem is reduced to phylogenetic placement of Palaeozoic fossils within this three-branch framework.

Palaeozoic jawed vertebrates and their phylogeny

In this section we outline the range of early gnathostome diversity and review the recent history of progress on their phylogenetic relationships.

Diversity of Palaeozoic jawed vertebrates

Putative examples of jawed vertebrates date to the Ordovician period^{27–29}, but the first definitive remains are of early Silurian age³⁰. Early Devonian (419 Ma) mandibulate gnathostomes were already ecologically diverse³¹ and, by the close of the Devonian (360 Ma), the first tetrapods and many of their adaptations for terrestriality had emerged¹⁹.

Early jawed fishes are divided into four broad categories: ancient representatives of chondrichthyans and osteichthyans, along with two exclusively extinct assemblages: acanthodians and placoderms. The early chondrichthyan record is dominated by isolated denticles (scales), teeth and spines. The oldest records of scales attributed to chondrichthyans are from the earliest Silurian (around 443 Ma)²⁷, such as *mongolepids*³². Sina-canthis, represented by isolated spines that share histological similarities with chondrichthyans³³, are also known from the early Silurian (about 438 Ma)³⁰. The oldest universally accepted chondrichthyans are substantially younger, represented by Early Devonian body fossils (around 400 Ma; Fig. 2e). Some of these specimens derive from the 'Malvinokaffric Realm', a cold-water Southern Hemisphere palaeobiogeographic province that yields distinctive jawed vertebrate faunas almost exclusively composed of acanthodians and chondrichthyans³⁴. Articulated chondrichthyans remain rare throughout the Devonian, with most specimens known from the exceptional Late Devonian Cleveland Shale Lagerstätte (Fig. 1).

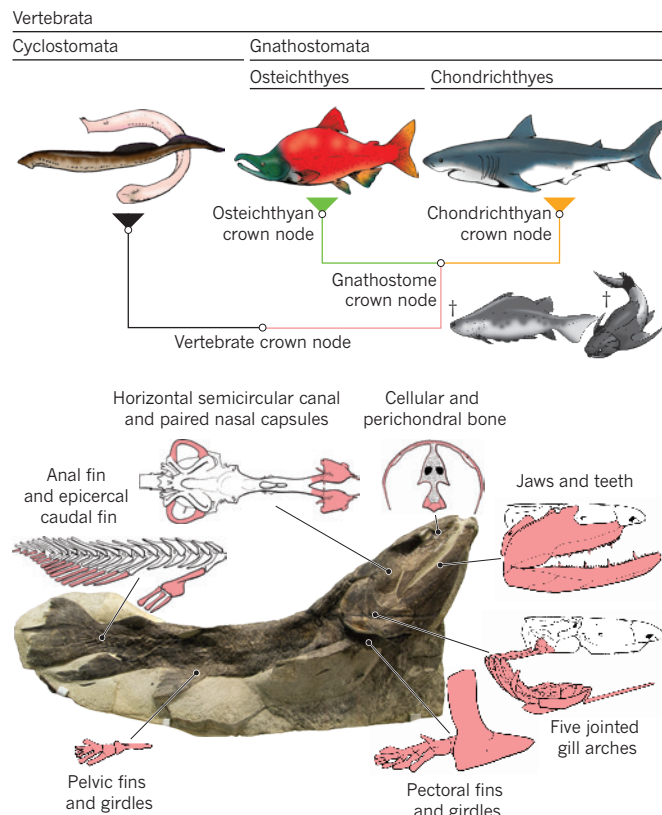
The late Silurian–Devonian osteichthyan record is considerably better than that of chondrichthyans owing to the armour of dermal plates and

¹Department of Life Sciences, Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot SL5 7PY, UK. ²Department of Earth Sciences, University of Oxford, South Parks Road, Oxford OX1 3AN, UK.

BOX 1

Crowns, stems and the characters of jawed vertebrates

Crown-, total- and stem-group concepts provide a useful framework for navigating evolutionary trees that include fossils. The tree shown in the figure reflects the most basic splits among living vertebrates. Crown groups comprise the last common ancestor of a group of living species plus all of its descendants, both fossil and modern. The gnathostome crown group includes the last common ancestor of osteichthyans (represented by a salmon) and chondrichthyans (represented by a shark) plus all of its descendants, and comprises all the green and orange parts of the tree. Total groups include the crown group of interest plus all extinct forms more closely related to that lineage than to any other living species. Here, the gnathostome total group is represented by all coloured parts of the tree. Stem groups are equal to a clade's total group minus its crown group, shown here by the pink lineage connecting the vertebrate and gnathostome crown nodes. Jawed vertebrates include all of the gnathostome crown, and the upper reaches of the gnathostome stem. The lower part of the gnathostome stem is populated by jawless ostracoderms, which are more closely related to jawed vertebrates than they are to modern jawless fishes. The principal task faced by palaeontologists is to fit fossil groups (such as acanthodians and placoderms; the dagger symbol indicates that they are extinct) within the genealogical framework for modern species. Monophyly of jawed vertebrates is evidenced by a series of shared morphological specializations including, but not limited to, jaws. Key gnathostome features are illustrated here for *Eusthenopteron* (Cleveland Museum of Natural History CMNH 8158, image courtesy of D. Chapman), an osteichthyan and relative of land vertebrates. These traits must have evolved along the gnathostome stem lineage, but without fossils it is impossible to determine the order in which — or when — they arose.



ossified endoskeleton typical of bony fishes. Consequently, osteichthyans have been intensively studied, with particular emphasis on sarcopterygians (lobe-finned fishes), reflecting their importance in reconstructing early stages of tetrapod evolution^{19,35,36}. Lobe fins are known from the late Silurian (about 423 Ma)⁹, but the earliest definitive remains of the other division of modern bony fish radiation — actinopterygians — are from the late Early or the earliest Middle Devonian, some 30 million years later³⁷. Some scales and other skeletal detritus of late Silurian–Early Devonian age (about 427–400 Ma) are conventionally aligned with actinopterygians^{38,39}. However, many — or perhaps all — of these taxa could represent stem osteichthyans^{40,41} or even stem gnathostomes⁴² (Fig. 3). As with chondrichthyans, early osteichthyans show some striking distributional patterns, including the conspicuous concentration of early members of major lobe-fin lineages in the latest Silurian and earliest Devonian of the South China Block³⁰ (Fig. 1). Outside of this restricted area, coeval bony fishes are limited to a handful of mostly fragmentary examples.

Several extinct groups join the familiar modern jawed vertebrate lineages. Armoured jawless fishes (ostracoderms) that are most often implicated as a jawed vertebrate sister group include: Middle Ordovician–Late Devonian (467–370 Ma) thelodonts, encompassing dorsoventrally flattened to cigar-shaped to deep-bodied forms⁴³ and bearing a shark-like shagreen of tiny scales; galeaspid, which are bottom-dwelling early Silurian–Late Devonian (439–370 Ma) fishes with flattened headshields that assume a bewildering variety of shapes and are found only in Chinese and Vietnamese deposits^{44,45}; and osteostracans, which are another benthic group with spade-shaped headshields and are restricted to the middle Silurian–Late Devonian (433–372 Ma) of today's northern landmasses^{45,46}. Two extinct jawed groups join this ostracoderm parade: placoderms, which are a species-rich and anatomically heterogeneous early Silurian–Late Devonian (435–360 Ma) assemblage characterized by

heavy head and trunk armour and bony jaw plates⁴⁷; and acanthodians, which are covered in tiny scales and bear well-developed spines along the leading edges of nearly all of their fins¹⁰ that together inspire the moniker 'spiny sharks'. The earliest fossils associated with acanthodians are isolated scales from the latest Ordovician (around 444 Ma)²⁷. More reliable remains are Silurian in age, with the group's record extending to early Permian deposits (about 295 Ma) that yield the best-known and last-surviving genus *Acanthodes*^{48,49}.

The evolution of gnathostome phylogeny

The current picture of Palaeozoic gnathostome relationships is the product of three phases of study. Throughout, researchers have benefitted from high-quality data, thanks to the early application of physical tomography by Stensiö and the 'Stockholm school'^{50–52}, followed by the maturation of acid-preparation techniques in the middle of the twentieth century^{53–56} and the non-destructive computed tomography of the past 15 years^{42,57–60}.

The modern phase of research into gnathostome relationships began with the introduction of phylogenetic systematics to vertebrate palaeontology, which had previously focused on linking species from successive geological strata as an approximate ancestor–descendant chain. Monophyly of the major taxonomic divisions of early gnathostomes was assumed, and their relative relationships were largely inferred using evidence from European and North American fossils. Within a decade of the initial application of cladistics to early vertebrates, an imperfect consensus emerged that acanthodians were a clade of stem osteichthyans⁴⁸ and that placoderms were the immediate sister group of crown gnathostomes⁶¹. This framework would persist for more than 30 years¹⁰, despite the intervening discovery and detailed description of fossils from Australia^{53,56,62}, China^{30,63} and northern Canada⁶⁴ that provided fresh morphological information beyond the stagnating stable of classic Euramerican taxa.

The second phase began in the 1980s with a cladistic reinterpretation of the ostracoderms. Detailed anatomical reinvestigations of ostracoderm sublineages and numerical phylogenetic analysis resulted in the recognition of this assemblage as a paraphyletic gnathostome stem group^{65–69}. Reconfiguration of the agnathan menagerie permitted reconstructions of evolutionary patterns in fin morphology and skeletal hard tissues, and identified the extinct jawless sister group of jawed vertebrates. Although many ostracoderm lineages have been considered contenders for this position, anatomical evidence overwhelmingly supports osteostracans. Like jawed vertebrates, but unlike other agnathans, osteostracans bear well-developed pectoral fins with associated girdles, a epicercal tail, and perichondral and cellular bone (Box 1).

The third and ongoing phase is the detailed scrutiny of the pioneering cladistic framework relating acanthodians and placoderms to modern jawed vertebrate lineages. Traction on this problem arose indirectly, beginning around the turn of the century with the development of expanded numerical phylogenetic analyses targeting relationships within osteichthyans^{70–73} and chondrichthyans^{74–76}, but employing acanthodian and placoderm outgroups. These studies introduced the use of increasingly larger data sets, and provided the character information that would seed analyses targeting not individual lineages, but early jawed vertebrates

as a whole. At the same time, a series of new fossil discoveries (outlined later) revealed unexpected anatomical combinations that raised serious questions about the coherence of acanthodians and placoderms. This set in motion a series of refined analyses of early jawed vertebrates bent on testing the supposed monophyly of these groups^{42,49,58,77,78}. This final phase is a current debate and the setting for the following discussion.

New fossil discoveries and their importance

In this section, we highlight key finds since the 1980s that have challenged embedded perceptions and explain their importance in light of what is or was known about early jawed vertebrate evolution. Presented in approximate phylogenetic order, ascending from jawless members of the stem lineage, to placoderms, to members of the gnathostome crown, these discoveries provide a broad summary of the emerging picture of major evolutionary patterns in early gnathostomes. Detailed accounts of character transformation are provided elsewhere²⁰.

Shuyu and *Romundina* and their noses for success

The neurocranium, or braincase, is a primitively cartilaginous structure that houses the brain and paired sensory organs in vertebrates. When coated with a mineralized rind, structurally complex braincases can be

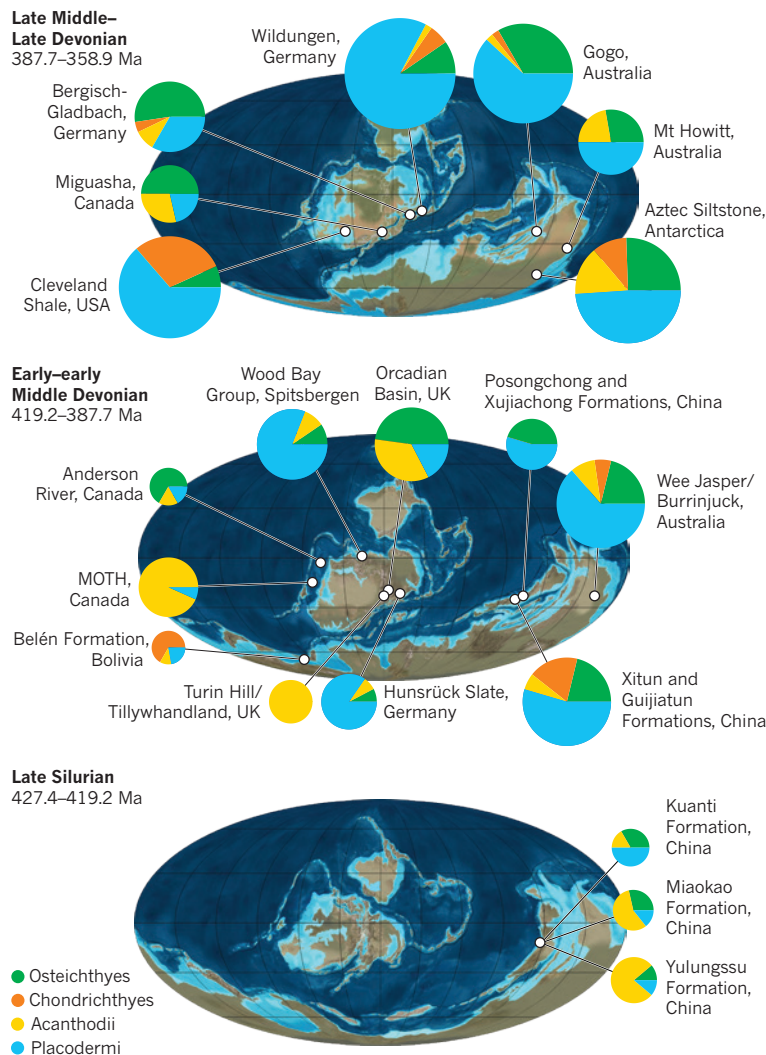


Figure 1 | Fossils relevant to early jawed-vertebrate evolution derive from major fossil sites in North America and Europe, and increasingly China and Australia. Palaeogeographic positions of localities bearing early jawed vertebrates and characterized by abundant fossils, high-fidelity preservation or both. Taxonomic breakdown of gnathostome diversity within sites is indicated by the associated pie charts and size-scaled to reported species richness.

MOTH, Man on the Hill. The vignettes depict scenes based on key fossil sites: Gogo, Australia (left) and Cleveland Shale, USA (right) in the late Middle–Late Devonian; the Xitun Formation, China (left) and Orcadian Basin, UK (right) in the Early–early Middle Devonian; and the late Silurian Kuantu Formation, China (left and right). Illustrations by B. Choo, Flinders University. Palaeogeographic reconstructions by R. Blakey, Colorado Plateau Geosystems.

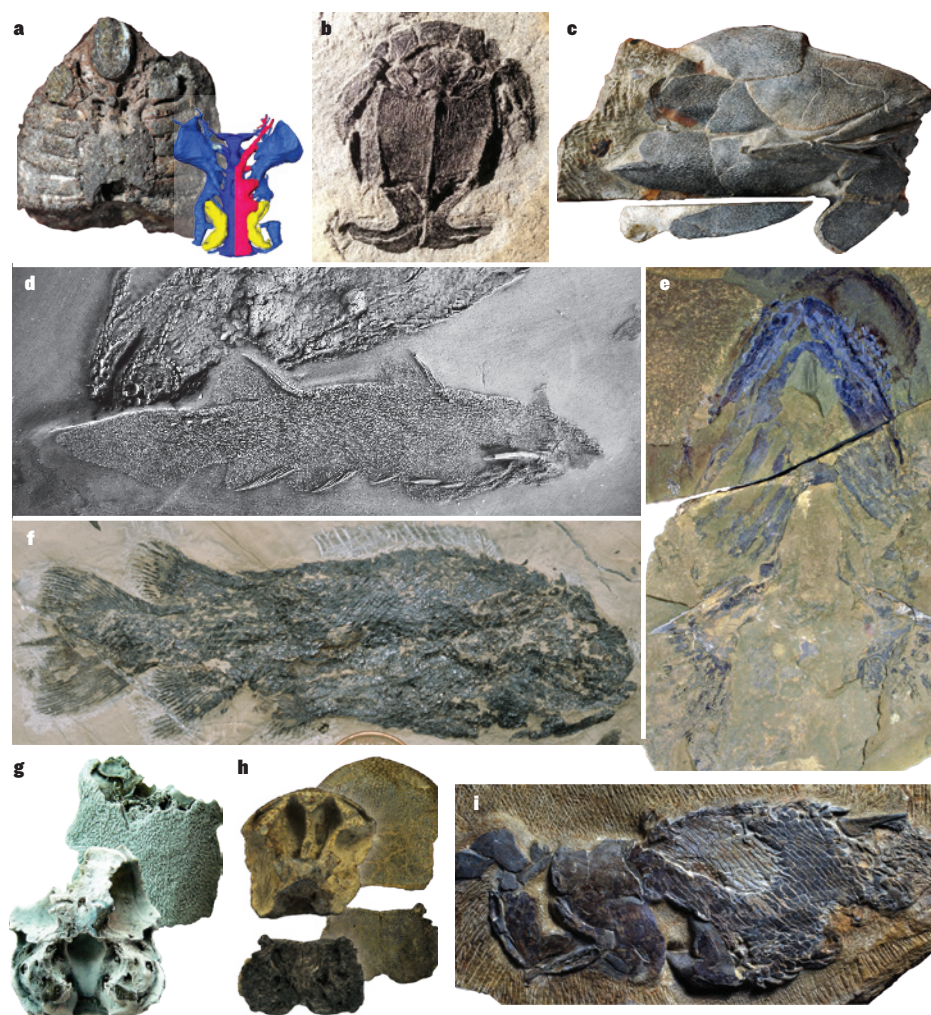


Figure 2 | Discoveries over the past two decades provide new clues about the evolution of early jawed vertebrates and their kin. **a**, High-fidelity virtual models of the Silurian galeaspid *Shuyu* reveal cranial architecture in jawless relatives of jawed vertebrates. **b**, Claspers in most placoderm groups, including antiarchs like *Microbrachius* shown here, raise questions about placoderm relationships and the evolution of vertebrate reproductive strategies. **c**, Osteichthyan-like pattern of bones in the Silurian placoderm *Entelognathus* suggest that the last common ancestor of all modern jawed vertebrates was clad in a bony-fish-like skeleton. **d**, Stunningly preserved fossils from the Early Devonian Man on the Hill (MOTH) locality of Canada challenges acanthodian monophyly, suggesting affinities with chondrichthyans. **e**, Pectoral-fin spines and tooth whorls with fused bases in the Early Devonian chondrichthyan *Doliodus* are features typically associated with acanthodians. **f**, The Early Devonian osteichthyan *Dialipina* shows a puzzling combination of traits despite being initially identified as a ray-finned fish based on isolated scales. **g**, An Early Devonian braincase attributed to the osteichthyan *Ligulalepis* shows features generally associated with placoderms and chondrichthyans. **h**, Braincase of *Psarolepis*, an Early Devonian lobe-finned osteichthyan from China represented by isolated bones, including spines of the kind associated with chondrichthyans, placoderms and acanthodians. **i**, The surprising reconstruction of *Psarolepis* was corroborated by the discovery of the more complete and even more ancient *Guiyu*, from the late Silurian of China. Images courtesy of **a**, Z. Gai; **b**, **g**, J. Long; **c**, **i**, M. Zhu; **e**, R. Miller; **f**, S. Cumbaa.

preserved as fossils and are a key source of phylogenetic information. Discriminating between specialized and primitive features in jawed vertebrates demands comparison with jawless fishes, but knowledge of the internal anatomy in ostracoderm lineages that lack endoskeletal mineralization is rudimentary^{10,65}. By contrast, a thin coat of bone surrounds the cartilage forming the consolidated braincase and supports for the gills and pectoral fins of osteostracans. This permitted the first detailed reconstructions of osteostracan brains, cranial vessels and nerves nearly a century ago^{50,51}. Galeaspid also bear a mineralized endoskeleton, but interpretations of their neurocranial structure have long been sketchy. High-resolution synchrotron scanning of the early galeaspid *Shuyu*⁵⁷ reinforced past identifications of widely separated, anterolaterally placed nasal capsules^{68,79} that open medially into a central, dorsally directed duct that is also joined by the hypophysis (Fig. 2a). Thus, galeaspid show a tantalizing mosaic of cyclostome-like (nasal capsules located well behind the front of the head and opening into a common nasohypophyseal duct) and crown gnathostome-like (broad separation of nasal capsules) traits in the anterior region of the skull, and suggest that the cyclostome-like geometry of the better known osteostracans might be secondary. These features are more than just anatomical arcana — broad separation of nasal capsules is interpreted as a developmental necessity for the origin of jaws because the median nasohypophyseal placode of cyclostomes obstructs anterior growth of neural crest cells that contribute substantially to mandibles^{24,57,80}. It seems that restructuring of the anterior portion of the head continued after the origin of jaws. Posteriorly placed, separate nasal capsules resembling those of galeaspid characterize the least crownward placoderms such as antiarchs, *Brindabellaspis* and *Romundina*, but these share with other jawed vertebrates a hypophysis that opens into the mouth, rather than a common nasohypophyseal duct as in agnathans⁵⁸.

By contrast, more crownward placoderms such as arthrodires, with their anteriorly placed nasal capsules, broadly resemble crown gnathostomes. These major architectural changes reflect a key piece of evidence for placoderm paraphyly^{49,58,73,77,78}, but ambiguities in the relationships among placoderms do not provide a consistent picture for the evolution of skull geometry in this crownward segment of the gnathostome stem.

Claspers and their evolutionary implications

The ptyctodontid placoderms have long been known to possess claspers⁸¹, intromittent organs associated with the pelvic fins and evidence of internal fertilization. This trait factored in early cladistic investigations of placoderm intra- and interrelationships, tying placoderms to chondrichthyans⁵² and fuelling arguments that ptyctodonts are the sister group of all other placoderms¹⁰. The discovery of arthrodire embryos within adult specimens prompted renewed investigation of this group in which long-overlooked evidence of claspers was finally discovered^{82–84}, followed by the realization that antiarchs also possessed these structures⁸⁵ (Fig. 2b). The palaeobiological and reproductive importance of claspers has been well considered^{83,85}, but their full phylogenetic importance is unresolved. Current phylogenetic consensus does not regard placoderm and chondrichthyan claspers to be homologous²⁰, but the homology of claspers within placoderms seems likely. Placoderm paraphyly demands the loss of internal fertilization before the origin of crown gnathostomes, signalling an unprecedented shift in reproductive biology within vertebrates⁸⁵. Thus, we face two problematic alternatives: either internal fertilization was lost in a crownward segment of the gnathostome stem, defying observational data on the reproductive biology of living vertebrates⁸⁵, or placoderms with claspers form a clade, contradicting the apparent signal of other traits⁵⁸.

Entelognathus reframes ancestral conditions

The perceived 'primitiveness' of chondrichthyan anatomy entrenched in many general introductions to vertebrate biology has deep pre-Darwinian roots. Faced only with living species, this view seems reasonable enough: with their shagreen of tiny scales and cartilaginous internal skeletons, chondrichthyans seem to be tailor-made morphological intermediates between the naked hagfishes and lampreys on the one hand and the internally and externally bony osteichthyans on the other. The fossil record subverts this tidy picture by showing that both large dermal plates and a bony internal skeleton are innovations that arose long before the divergence of osteichthyans and chondrichthyans^{22,66,67,69,86}. However, the condition of the skeleton in the last common ancestor of jawed vertebrates has remained controversial thanks to two mutually reinforcing phenomena: a reluctance to make explicit comparisons between the bony plates of osteichthyans and placoderms, and repeated interpretations of at least some acanthodians as early osteichthyan relatives^{41,48,49,73,77}. Together these factors paint a picture of an ancestral crown gnathostome covered in a 'micromeric' outer skeleton of tiny scales, with a 'macromeric' skeleton composed of large plates reappearing in the osteichthyan lineage. This view was turned on its head by the discovery of the late Silurian *Entelognathus* in China⁷⁸ (about 423 Ma; Fig. 2c). Although *Entelognathus* broadly resembles a standard-issue placoderm, its cheek and upper and lower jaws are covered with bones that match the pattern seen in osteichthyans, rather than other placoderms. This remarkable correspondence suggests that there is evolutionary continuity between the large dermal plates of placoderms and those of bony fishes^{42,58,78}.

Man on the Hill brings acanthodians into the light

The Man on the Hill (MOTH) locality in the Northwest Territories of Canada is an Early Devonian (about 419 Ma) Konservat Lagerstätte yielding articulated early vertebrates. Originally discovered in the 1970s⁶⁴, new collections and advances in chemical preparation have since revealed exquisitely preserved fossils (Fig. 2d). Jawed vertebrates from MOTH are mostly acanthodians (Fig. 1), providing important anatomical detail on this enigmatic assemblage. Previously, the record of complete acanthodian fossils was mostly restricted to crudely prepared specimens from low-diversity, fluvial-lacustrine Early Devonian deposits of the United Kingdom¹². By contrast, acid-prepared acanthodians from the species-rich marine MOTH locality reveal crisp anatomical details. In particular, a host of these species have umbellate and denticle-like scales such as those found in chondrichthyans^{87–90}. Perhaps more importantly, the MOTH fauna include examples of acanthodian-like fishes covered in scales with growth patterns and structure previously known only from isolated fragments, but conventionally assigned to chondrichthyans⁸⁹. This simultaneously suggests a position for acanthodians in the jawed vertebrate tree, while undermining confidence that they comprise a natural group.

The inside story on acanthodian morphology

Several early placoderms, osteichthyans and chondrichthyans yield detailed braincases^{10,52,91}, but acanthodian examples are rare. Subject to many re-interpretations over the past 100 years^{12,48,49}, the neurocranium of the Permian *Acanthodes* is central to debates on the evolutionary affinities of acanthodians. Various authors have been impressed by what they perceived as either particularly osteichthyan-like^{41,48,77} or chondrichthyan-like^{49,52} features of *Acanthodes*, triggering contrasting views on the placement of acanthodians as a whole. The Early Devonian (around 419 Ma) *Ptomacanthus* also preserves a braincase, although detail is obscure to the degree that this structure was initially ignored. Re-examination of *Ptomacanthus* revealed a neurocranium with a gross architecture that is more similar to that of placoderms or chondrichthyans than that of *Acanthodes* and osteichthyans, providing evidence in the first explicit argument for acanthodian paraphyly⁷⁷.

A sneak peek at early shark anatomy

With a sparse early record, interpretation of primitive chondrichthyan conditions drew heavily on body fossils from the latest Devonian¹¹ and

even younger braincases⁹¹, all of which are probably highly specialized. This changed with two stunning finds in the early 2000s. First was the discovery of more complete neurocrania of *Pucapampella* from the Early Devonian of Bolivia⁷⁶ and a similar South African form⁹². Previously named on the basis of an isolated neurocranial base, *Pucapampella* bears a chondrichthyan-specific hard tissue (prismatic calcified cartilage) in combination with a ventral fissure: a persistent division between two embryonic braincase components. Absent in ostracoderms, placoderms and other chondrichthyans, but present in *Acanthodes* and bony fishes, the ventral fissure was long considered key evidence for a close relationship between acanthodians and osteichthyans⁴⁸. *Pucapampella* suggests that this trait is a general feature of crown-group gnathostomes. Subsequent discoveries provided additional anatomical details for *Pucapampella*, revealing peculiar teeth and jaws to accompany its unanticipated neurocranial architecture³⁴. Hot on the heels of *Pucapampella* came the discovery of the oldest articulated chondrichthyan, *Doliodus*, from the Early Devonian of New Brunswick⁹³, was known for more than a century only by isolated teeth, and assigned to acanthodians. Recovery of an articulated head and forequarters revealed the signature chondrichthyan trait of prismatic calcified cartilage occurring in a fish with stubby spines along the leading edges of its pectoral fins (Fig. 2e), casting further doubt on acanthodian monophyly. Subsequent analysis of the braincase⁵⁹ and dentition^{60,94} of *Doliodus* revealed primitive character states, such as fused tooth bases, not widely seen in crown chondrichthyans and certainly absent in modern sharks and rays, but common to acanthodians and early osteichthyans.

Rosetta stones for fragmentary bony fish remains

Fossil bony fishes have conventionally been deposited in one of the two living divisions: actinopterygians or sarcopterygians. This leaves the osteichthyan stem bereft of fossils that document the origin of this enormously successful clade. A series of isolated scales of late Silurian–Early Devonian age were loosely tethered to actinopterygians as their representatives^{38,39}, but the discovery of more complete material attributed to *Dialipina*⁹⁵ (Fig. 2f) and *Ligulalepis*^{54,55} (Fig. 2g) raised questions about their actinopterygian affinities, and the importance of scale-based characters used to identify ray-finned fishes^{41,73}. The braincase aligned with the scale-taxon *Ligulalepis* shows evidence of an eyestalk^{54,55}, a cartilaginous plinth that supports the eye in chondrichthyans and placoderms, but that is absent in modern osteichthyans. This might suggest *Ligulalepis* is a stem osteichthyan, but reports of eyestalks in early sarcopterygians⁷² argue for parallel loss in the two bony fish divisions. Complete specimens of *Dialipina* are even more puzzling, marrying a tail geometry found only in lobe-finned fishes with a cheek comprising tiny bones that bear no clear resemblance to the large plates of other osteichthyans or even *Entelognathus*. *Ligulalepis* and *Dialipina* vacillate between Actinopterygii and the osteichthyan stem in many analyses^{42,78}, and solid placements are likely to be elusive until these taxa are more completely documented.

Psarolepis and *Guiyu* encapsulate the revolution

Perhaps more than any other discovery, *Psarolepis* represents the principal instigator of the current revolution in early jawed-vertebrate systematics. Recovered from late Silurian and earliest Devonian rocks of China, it is one of the earliest bony fishes (Fig. 1). First identified as a stem lungfish on the basis of jaw and braincase material⁹⁶, subsequent investigation of *Psarolepis* and the discovery of isolated cheek and shoulder bones highlighted more interesting affinities⁷⁰. *Psarolepis* exhibits two hallmarks of the lobe-finned fishes: a braincase divided into front and hind units by an articulating joint and a pore-canal complex in its dermal bones (Fig. 2h). However, the cleaver-shaped cheek and maxilla (upper external jaw bone) bear an uncanny resemblance to those of early ray-finned fishes, suggestive of a shared primitive condition for bony fishes. More surprisingly, *Psarolepis* bristled with spines: the shoulder girdle bears a pronounced spine over the fin articulation area, reminiscent of acanthodians and some placoderms, whereas the dorsal fins were preceded by spines like those of chondrichthyans and acanthodians. *Psarolepis* is most reasonably interpreted as a

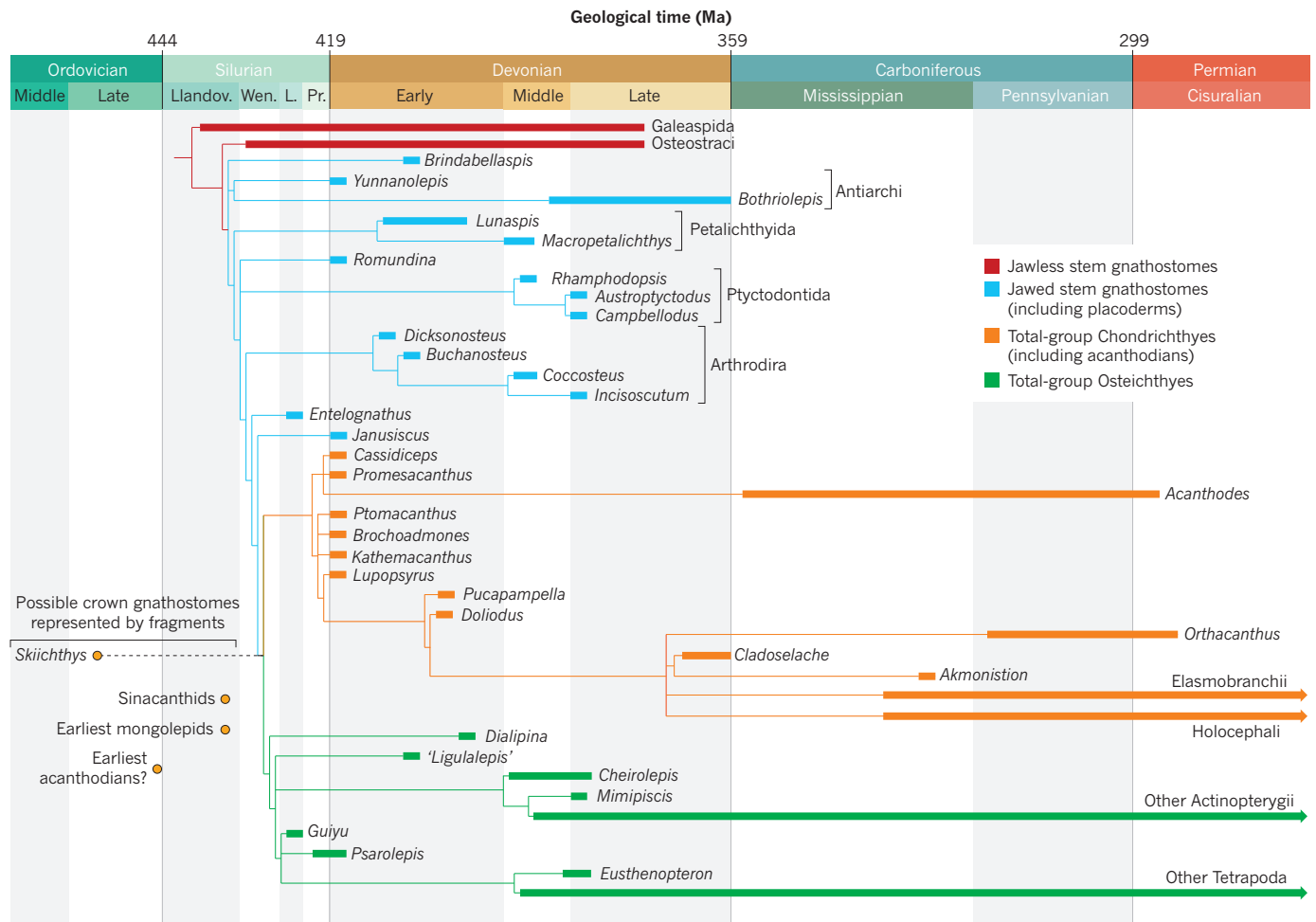


Figure 3 | Time-calibrated phylogeny of early jawed vertebrates and their immediate jawless relatives, showing minimum times of divergence based on fossil evidence. Topology based on ref. 42, with some taxa omitted for clarity and modifications showing presumed phylogenetic positions of key extant lineages. Also shown are key early jawed vertebrates or putative jawed

vertebrates with uncertain affinities to the crown group. The minimum age of the gnathostome crown could be profoundly recalibrated if *Skiichthys*²⁸ is confirmed as a crown-group gnathostome. Dotted line indicates possible range extension for the gnathostome crown node. Llandov., Llandovery; Wen. Wenlock; L., Ludlow; Pr., Přídolí.

stem-group sarcopterygian^{9,72,73}, and thus an early example of the bony fish lineage that would give rise to tetrapods. However, it is held in this position by such a small number of traits, and retains so many plesiomorphies, that some analyses have recovered it as a stem-group osteichthyan^{70,71}. This shook confidence in the seemingly stable, decades-old sets of attributes that characterize major early vertebrate groups¹⁰. However, the disarticulated nature of these fossils raised the troubling possibility that the combination of characters in *Psarolepis* was chimaeric: parts of different species misattributed to a single one. This concern was rejected, albeit indirectly, by the discovery of *Guiyu*⁹ (Fig. 2j). Broadly similar to *Psarolepis*, but from even older Silurian rocks in China (about 423 Ma), *Guiyu* provides exceptional corroboration that traits such as a jointed braincase occurred in the same animal as pectoral- and dorsal-fin spines, and delivers further surprises, including the presence of placoderm-like external pelvic girdles⁹⁷. Interpreted as an early sarcopterygian, *Guiyu* also shows that the last common ancestor of all modern osteichthyans arose no later than the Silurian, before the Devonian 'Age of Fishes'.

The re-shaping of early jawed vertebrate phylogeny

This panoply of new taxa and unexpected character distributions fuelled doubts about the status of classic early jawed vertebrate categories^{93,98}, but early studies did not match these queries with cladistic tests. In the past five years, the field has witnessed a spate of numerical analyses giving rise to rapidly shifting perspectives on phylogenetic relationships^{9,42,49,58,77,85}. However, some stable patterns are apparent and key areas of ongoing

debate are now coming into focus.

The monophyly of fossil osteichthyans and chondrichthyans is universally supported. Placoderms are repeatedly recovered as stem-group gnathostomes and acanthodians are generally agreed to be members of the gnathostome crown, with some noteworthy exceptions⁴⁹. Major differences with previous hypotheses stem from important shifts in approach, such as abandoning earlier assumptions of placoderm and acanthodian monophyly. In all cases so far, the monophyly of placoderms has been rejected and, in all but one⁵⁸, acanthodian monophyly has also been rejected.

In the earliest iterations, acanthodians were inferred to be massively paraphyletic, with some members associated with chondrichthyan, osteichthyan and gnathostome stem branches^{49,58}. This configuration helped to explain the odd conjunction of osteichthyan, chondrichthyan and more primitive characters found in acanthodians. Furthermore, it implied an acanthodian-like appearance of the ancestral crown gnathostome: a small fusiform fish, covered in a denticle shagreen, a skull composed of mostly undifferentiated plates, with spines preceding the fins. The unfortunate complication of this hypothesis was that it implied non-homology of osteichthyan and placoderm armoured exoskeletons. Similarities between osteichthyan and placoderm skulls and shoulder girdles had not gone unnoticed^{70,71,99}, but were matched by dismissals citing 'fundamental differences' in construction¹⁰⁰. The discovery of *Entelognathus* (already discussed) deals a blow to the latter perspective. Phylogenetic analysis accompanying the discovery⁷⁸ unsurprisingly led to a wholesale

shift of acanthodian-type taxa to the chondrichthyan total group. Every subsequent analysis has corroborated this outcome^{42,58,85}. This key rearrangement eliminates the need to invoke convergence between placoderm and osteichthyan exoskeletons. By viewing the fragmented dermal skeletons of chondrichthyans and acanthodians as a derived condition, no special sister group relationship between osteichthyans and placoderms is implied, as had been assumed in the past⁹⁹.

Current analyses universally reject placoderm monophyly, with arthrodires (and similar forms such as *Entelognathus*) resolved closest to the gnathostome crown (Fig. 3). This arrangement suggests that resemblances between arthrodires and modern gnathostomes are homologous — a point reinforced by the arthrodire gestalt of *Entelognathus*. Likewise, it suggests that the similarities between the more flat-headed and presumably benthic placoderms, such as antiarchs and petalichthyids, and jawless outgroups reflect a shared primitive condition^{10,20,77}. This has the convenient effect of stretching the placoderms into an array of jaw-bearing stem gnathostomes, although mandibles remain unknown in forms such as *Brindabellaspis* and petalichthyids.

The consistency of placoderm paraphyly across recent analyses^{20,42,49,58,73,77,78,85} suggests that this is well supported. However, available solutions are not wholly independent, with each data set incrementally updated from a core original study⁷⁷. Perhaps notably, the addition of taxa and characters has not increased support for the paraphyletic placoderm backbone. Instead, successive analyses have seen a winnowing of branch support for the deepest divergences among jaw-bearing stem gnathostomes, coupled with inconsistent arrangements of major placoderm lineages crownward of antiarchs and *Brindabellaspis*. This instability, combined with potential placoderm synapomorphies such as pelvic claspers⁸⁵ and a persistent fissure between the nasal capsules and the remainder of the braincase²⁰, indicate that the 'placoderm problem' is far from resolved. A satisfactory resolution of the relationships of placoderms will have profound consequences for our understanding of the origin of modern jawed vertebrates.

Future directions

Early jawed vertebrate phylogenetics is in a state of infancy, but rapid progress is being made. Present discourse on early jawed vertebrate phylogenetics is marked by a growth of healthy debate and a relative lack of the kind of dogmatism that held back the field for nearly half a century. The question of the origin of the jaws themselves remains open. So far, the problem has been debated in terms of highly idealized archetypal scenarios, such as the transformation of gill arches into jaws¹. From both palaeontological and neontological perspectives, this scenario has proved deficient^{6,10,80}. Little direct evidence of the visceral skeleton of fossil jawless fishes is known; even the proximate outgroups of the jawed vertebrates — osteostracans and galeaspid — are presumed to have been jawless, but remains of the oral skeleton remain absent. What is known of the oral regions of osteostracans and galeaspid suggests that they possessed mouths that were specialized relative to the branchial arches, a condition consistent with modern jawless fishes¹⁰. Placoderm paraphyly raises some hope that relevant data could be sourced from this assemblage (for example, *Brindabellaspis* or petalichthyids). The discovery of additional fossils will hopefully help to fill these gaps, but they will not be sufficient by themselves. Rigorous phylogenetic analysis must accompany these new finds to avoid simply shoe-horning fossils into appealing narratives¹². ■

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1. Gegenbaur, C., Bell, F. J. & Lankester, E. R. *Elements of Comparative Anatomy* (Macmillan and Co., 1878).
2. Balfour, F. M. On the development of the skeleton of the paired fins of Elasmobranchii, considered in relation to its bearings on the nature of the limbs of the Vertebrata. *Proc. Zool. Soc. Lond.* **49**, 656–670 (1881).
3. de Beer, G. *The Development of the Vertebrate Skull* (Oxford Univ. Press, 1937).
4. Reif, W.-E. Evolution of dermal skeleton and dentition in vertebrates. *Evol. Biol.* **15**, 287–368 (1982).
5. Shubin, N. H. Origin of evolutionary novelty: examples from limbs. *J. Morphol.* **252**, 15–28 (2002).
6. Kuratani, S. Evolution of the vertebrate jaw: comparative embryology and

molecular developmental biology reveal the factors behind evolutionary novelty. *J. Anat.* **205**, 335–347 (2004).

7. Shigetani, Y., Sugahara, F. & Kuratani, S. A new evolutionary scenario for the vertebrate jaw. *Bioessays* **27**, 331–338 (2005).
 8. Wagner, G. P. & Lynch, V. J. Evolutionary novelties. *Curr. Biol.* **20**, R48–R52 (2010).
 9. Zhu, M. *et al.* The oldest articulated osteichthyan reveals mosaic gnathostome characters. *Nature* **458**, 469–474 (2009).
 10. Janvier, P. *Early Vertebrates* (Clarendon, 1996).
- This masterful summary provides a window on the 'state of the art' immediately preceding the major changes to our understanding of relationships among early gnathostomes that took place over the past two decades, and is still an indispensable and accessible resource.**
11. Dean, B. Contributions to the morphology of *Cladoseleche* (*Cladodus*). *J. Morphol.* **9**, 87–114 (1894).
 12. Watson, D. M. S. The acanthodian fishes. *Philos. Trans. R. Soc. Lond.* **228**, 49–146 (1937).
 13. Zangerl, R. & Williams, M. E. New evidence on the nature of the jaw suspension in Palaeozoic anacanthous sharks. *Palaeontology* **18**, 333–341 (1975).
 14. Gregory, W. K. Further observations on the pectoral girdle and fin of *Sauripterus taylori* Hall, a crossopterygian fish from the Upper Devonian of Pennsylvania, with special reference to the origin of the pentadactylate extremities of Tetrapoda. *Proc. Am. Phil. Soc.* **75**, 673–690 (1935).
 15. Miles, R. S. A reinterpretation of the visceral skeleton of *Acanthodes*. *Nature* **204**, 457–459 (1964).
 16. Davis, M. C., Shubin, N. & Daeschler, E. B. A new specimen of *Sauripterus taylori* (Sarcopterygii, Osteichthyes) from the Famennian Catskill Formation of North America. *J. Vertebr. Paleontol.* **24**, 26–40 (2004).
 17. Kemp, T. S. *The Origin and Evolution of Mammals* (Oxford Univ. Press, 2005).
 18. Makovicky, P. J. & Zanno, L. E. In *Living Dinosaurs: The Evolutionary History of Modern Birds* (eds Dyke, G. & Kaiser, G.) 9–29 (Wiley, 2011).
 19. Clack, J. A. *Gaining Ground* (Indiana Univ. Press, 2012).
 20. Brazeau, M. D. & Friedman, M. The characters of Palaeozoic jawed vertebrates. *Zool. J. Linn. Soc.* **170**, 779–821 (2014).
 21. Chen, M., Zou, M., Yang, L. & He, S. Basal jawed vertebrate phylogenomics using transcriptomic data from *Solexa* sequencing. *PLoS ONE* **7**, e36256 (2012).
 22. Donoghue, P. C., Forey, P. L. & Aldridge, R. J. Conodont affinity and chordate phylogeny. *Biol. Rev. Camb. Philos. Soc.* **75**, 191–251 (2000).
 23. Ota, K. G., Fujimoto, S., Oisi, Y. & Kuratani, S. Identification of vertebra-like elements and their possible differentiation from sclerotomes in the hagfish. *Nature Commun.* **2**, 373 (2011).
 24. Oisi, Y., Ota, K. G., Kuraku, S., Fujimoto, S. & Kuratani, S. Craniofacial development of hagfishes and the evolution of vertebrates. *Nature* **493**, 175–180 (2013).
 25. Ota, K. G., Kuraku, S. & Kuratani, S. Hagfish embryology with reference to the evolution of the neural crest. *Nature* **446**, 672–675 (2007).
 26. Heimberg, A. M., Cowper-Sal-lari, R., Semon, M., Donoghue, P. C. & Peterson, K. J. microRNAs reveal the interrelationships of hagfish, lampreys, and gnathostomes and the nature of the ancestral vertebrate. *Proc. Natl Acad. Sci. USA* **107**, 19379–19383 (2010).
 27. Karatajute-Talimaa, V. & Predtechensky, N. The distribution of the vertebrates in the Late Ordovician and Early Silurian palaeobasins of the Siberian Platform. *Bull. Mus. Natl Hist. Nat.* **4**, 39–55 (1995).
 28. Smith, M. M. & Sansom, I. J. Exoskeletal micro-remains of an Ordovician fish from the Harding Sandstone of Colorado. *Palaeontology* **40**, 645–658 (1997).
 29. Sansom, I. J., Davies, N. S., Coates, M. I., Nicoll, R. S. & Ritchie, A. Chondrichthyan-like scales from the Middle Ordovician of Australia. *Palaeontology* **55**, 243–247 (2012).
 30. Zhao, W.-J. & Zhu, M. Siluro-Devonian vertebrate biostratigraphy and biogeography of China. *Palaeoworld* **19**, 4–26 (2010).
 31. Anderson, P. S., Friedman, M., Brazeau, M. D. & Rayfield, E. J. Initial radiation of jaws demonstrated stability despite faunal and environmental change. *Nature* **476**, 206–209 (2011).
 32. Karatajute-Talimaa, V. N., Novitskaya, L. I., Rozman, K. S. & Sodov, J. *Mongolepis*, a new genus of Elasmobranchii from the Lower Silurian of Mongolia. *Paleontologicheskii zhurnal* **1**, 76–86 (1990).
 33. Sansom, I. J., Wang, N.-Z. & Smith, M. The histology and affinities of sinacanthid fishes: primitive gnathostomes from the Silurian of China. *Zool. J. Linn. Soc.* **144**, 379–386 (2005).
 34. Janvier, P. & Maisey, J. G. In *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes* (eds Elliott, D. K., Maisey, J. G., Yu, X. & Miao, D.) 431–459 (Dr Friedrich Pfeil, 2010).
 35. Panchen, A. L. & Smithson, T. R. Character diagnosis, fossils and the origin of tetrapods. *Biol. Rev. Camb. Philos. Soc.* **62**, 341–436 (1987).
 36. Ahlberg, P. E. & Johanson, Z. Osteolepiforms and the ancestry of tetrapods. *Nature* **395**, 792–794 (1998).
 37. Lukševičs, E., Lebedev, O. A. & Zakharenko, G. V. Palaeozoogeographical connections of the Devonian vertebrate communities of the Baltica Province. Part I. Eifelian-Givetian. *Palaeoworld* **19**, 94–107 (2010).
 38. Schultze, H.-P. Palaeoniscoidea-Schuppen aus dem Unterdevon Australiens und Kanadas und aus dem Mitteldevon Spitzbergens [in German]. *British Mus. Nat. Hist. Geol.* **16**, 343–376 (1968).
 39. Gross, W. Fragliche Actinopterygier-Schuppen aus dem Silur Gotlands [in German]. *Lethaia* **1**, 184–218 (1968).
 40. Botella, H., Blom, H., Dorka, M., Ahlberg, P. E. & Janvier, P. Jaws and teeth of the earliest bony fishes. *Nature* **448**, 583–586 (2007).
 41. Friedman, M. & Brazeau, M. D. A reappraisal of the origin and basal radiation of the Osteichthyes. *J. Vertebr. Paleontol.* **30**, 36–56 (2010).

42. Giles, S., Friedman, M. & Brazeau, M. D. Osteichthyan-like cranial conditions in an Early Devonian stem gnathostome. *Nature* <http://dx.doi.org/10.1038/nature14065> (2015).
43. Märss, T., Turner, S. & Karatajute-Talimaa, V. in *Handbook of Paleichthyology* Vol. 1B (ed. Schultze, H.-P.) (Dr Friedrich Pfeil, 2007).
44. Zhu, M. & Gai, Z.-K. Phylogenetic relationships of galeaspids (Agnatha). *Vertebr. Palasiat.* **44**, 1–27 (2006).
45. Sansom, R. S. Endemism and palaeobiogeography of the Osteostraci and Galeaspida: a test of scenarios of gnathostome evolution. *Palaeontology* **52**, 1257–1273 (2009).
46. Sansom, R. S. Phylogeny, classification and character polarity of the Osteostraci (Vertebrata). *J. Syst. Paleontol.* **7**, 95–115 (2009).
47. Young, G. C. Placoderms (armoured fish): dominant vertebrates of the Devonian period. *Annu. Rev. Earth Planet. Sci.* **38**, 523–550 (2010).
48. Miles, R. S. in *Interrelationships of Fishes* (eds Greenwood, P. H., Miles, R. S. & Patterson, C.) 63–103 (Academic, 1973).
- This first-generation application of cladistic methodology to early jawed vertebrates placed the ‘spiny sharks’ as early relatives of bony fishes, a perspective that profoundly influenced perceptions of the ancestral crown gnathostome for more than 40 years.**
49. Davis, S. P., Finarelli, J. A. & Coates, M. I. *Acanthodes* and shark-like conditions in the last common ancestor of modern gnathostomes. *Nature* **486**, 247–250 (2012).
50. Stensjö, E. A. The Devonian and Downtonian vertebrates of Spitsbergen. Part 1. Family Cephalaspididae. *Skr. Svalbard Ishav.* **12**, 1–391 (1927).
51. Stensjö, E. A. *The Cephalaspids of Great Britain* (British Museum (Natural History), 1932).
52. Jarvik, E. *Basic Structure and Evolution of Vertebrates* (Academic, 1980).
53. White, E. I. The larger arthrodontan fishes from the area of the Burrinjuck Dam, N.S.W. *Trans. Zool. Soc. Lond.* **34**, 149–262 (1978).
54. Basden, A. M. & Young, G. C. A primitive actinopterygian neurocranium from the Early Devonian of Southeastern Australia. *J. Vertebr. Paleontol.* **21**, 754–766 (2001).
55. Basden, A. M., Young, G. C., Coates, M. I. & Richtie, A. The most primitive osteichthyan braincase? *Nature* **403**, 185–188 (2000).
56. Young, G. C. A new Early Devonian placoderm from New South Wales, Australia, with a discussion of placoderm phylogeny. *Palaeontogr. A* **167**, 10–76 (1980).
57. Gai, Z., Donoghue, P. C., Zhu, M., Janvier, P. & Stampanoni, M. Fossil jawless fish from China foreshadows early jawed vertebrate anatomy. *Nature* **476**, 324–327 (2011).
58. Dupret, V., Sanchez, S., Goujet, D., Tafforeau, P. & Ahlberg, P. E. A primitive placoderm sheds light on the origin of the jawed vertebrate face. *Nature* **507**, 500–503 (2014).
59. Maisey, J. G., Miller, R. & Turner, S. The braincase of the chondrichthyan *Doliodus* from the Lower Devonian Campbellton Formation of New Brunswick, Canada. *Acta Zool.* **90** (Suppl. 1), 109–122 (2009).
60. Maisey, J. G., Turner, S., Naylor, G. J. & Miller, R. F. Dental patterning in the earliest sharks: implications for tooth evolution. *J. Morphol.* **275**, 586–596 (2014).
61. Schaeffer, B. in *Problèmes Actuels de Paléontologie: Evolution des Vertébrés* Vol. 218 [in French] (ed. Lehman, J.-P.) 101–109 (Colloques internationaux du Centre national de la Recherche scientifique, 1975).
62. Long, J. A. & Trinajstić, K. The Late Devonian Gogo Formation Lagerstätte of Western Australia: exceptional early vertebrate preservation and diversity. *Annu. Rev. Earth Planet. Sci.* **38**, 255–279 (2010).
63. Zhu, M. Catalogue of Devonian vertebrates in China, with notes on bio-events. *Cour. Forsch. Inst. Senckenberg* **223**, 379–390 (2000).
64. Bernacsek, G. M. & Dineley, D. L. New acanthodians from the Delorme Formation (Lower Devonian) of N.W.T. Canada. *Palaeontogr. A* **159**, 1–25 (1977).
65. Janvier, P. & Blicke, A. New data on the internal anatomy of the Heterostraci (Agnatha), with general remarks on the phylogeny of the Craniota. *Zool. Scr.* **8**, 287–296 (1979).
66. Janvier, P. The phylogeny of Craniata, with particular reference to the significance of fossil ‘agnathans’. *J. Vertebr. Paleontol.* **1**, 121–159 (1981).
- This article established osteostracans and galeaspids as successive outgroups to, and thus important comparative models for, jawed vertebrates, an arrangement that has survived intact for more than three decades.**
67. Forey, P. L. Yet more reflections on agnathan-gnathostome relationships. *J. Vertebr. Paleontol.* **4**, 330–343 (1984).
68. Wang, N.-Z. in *Early Vertebrates and Related Problems of Evolutionary Biology* (eds Chang, M.-M., Lui, Y.-H. & Zhang, G.-R.) (Science, 1991).
69. Forey, P. L. & Janvier, P. Agnathans and the origin of jawed vertebrates. *Nature* **361**, 129–134 (1993).
70. Zhu, M., Yu, X. & Janvier, P. A primitive fossil fish sheds light on the origin of bony fishes. *Nature* **397**, 607–610 (1999).
- The bizarre combination of traits for *Psarolepis* reported in this article highlighted weaknesses in existing phylogenies of early jawed vertebrates, and triggered a resurgence in systematic studies.**
71. Zhu, M. & Schultze, H.-P. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 81–84 (Taylor & Francis, 2001).
72. Zhu, M., Yu, X. & Ahlberg, P. E. A primitive sarcopterygian fish with an eyestalk. *Nature* **410**, 81–84 (2001).
73. Friedman, M. *Styloichthys* as the oldest coelacanth: implications for early osteichthyan interrelationships. *J. Syst. Paleontology* **5**, 289–343 (2007).
74. Coates, M. I. & Sequiera, S. E. K. A new stethacanthid chondrichthyan from the Lower Carboniferous of Bearsden, Scotland. *J. Vertebr. Paleontol.* **21**, 438–459 (2001).
75. Coates, M. I. & Sequiera, S. E. K. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 241–262 (Taylor & Francis, 2001).
76. Maisey, J. G. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 263–288 (Taylor & Francis, 2001).
77. Brazeau, M. D. The braincase and jaws of a Devonian ‘acanthodian’ and modern gnathostome origins. *Nature* **457**, 305–308 (2009).
- This study was the first to rigorously test — and, in doing so, to reject — placoderm and acanthodian monophyly, and provides the empirical core for most subsequent phylogenetic investigations of early gnathostomes.**
78. Zhu, M. *et al.* A Silurian placoderm with osteichthyan-like marginal jaw bones. *Nature* **502**, 188–193 (2013).
- Of the many remarkable early gnathostome fossils to emerge from China, few have shifted the evolutionary paradigm as much as *Entelognathus*, a placoderm-like creature with jaw bones resembling those of bony fishes.**
79. Halstead, L. B. Internal anatomy of the polybranchiaspids (Agnatha, Galeaspida). *Nature* **282**, 833–836 (1979).
80. Kuratani, S. Evolution of the vertebrate jaw from developmental perspectives. *Evol. Dev.* **14**, 76–92 (2012).
81. Miles, R. S. Observations on the ptyctodont fish, *Rhamphodopsis* Watson. *Zool. J. Linn. Soc.* **47**, 99–120 (1967).
82. Ahlberg, P., Trinajstić, K., Johanson, Z. & Long, J. Pelvic claspers confirm chondrichthyan-like internal fertilization in arthrodires. *Nature* **460**, 888–889 (2009).
- This direct evidence of claspers in arthrodires renewed the palaeobiological importance of placoderms regarding internal fertilization, but potentially weakens the case for their paraphyly.**
83. Trinajstić, K., Boisvert, C., Long, J., Maksimenko, A. & Johanson, Z. Pelvic and reproductive structures in placoderms (stem gnathostomes). *Biol. Rev. Camb. Philos. Soc.* <http://dx.doi.org/10.1111/brv.12118> (2014).
84. Long, J. A., Trinajstić, K. & Johanson, Z. Devonian arthrodire embryos and the origin of internal fertilization in vertebrates. *Nature* **457**, 1124–1127 (2009).
85. Long, J. A. *et al.* Copulation in antiarch placoderms and the origin of gnathostome internal fertilization. *Nature* **517**, 196–199 (2015).
86. Janvier, P. The relationships of the Osteostraci and Galeaspida. *J. Vertebr. Paleontol.* **4**, 344–358 (1984).
87. Hanke, G. F. & Wilson, M. V. H. in *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds Arratia, G., Wilson, M. V. H. & Cloutier, R.) 189–216 (Dr Friedrich Pfeil, 2004).
88. Hanke, G. F. & Wilson, M. V. H. in *Morphology, Phylogeny and Paleobiogeography of Fossil Fishes* (eds Elliott, D. K., Maisey, J. G., Yu, X. & Miao, D.) 149–182 (Dr Friedrich Pfeil, 2010).
89. Hanke, G. F., Wilson, M. V. H. & Saurette, F. Partial articulated specimen of the Early Devonian putative chondrichthyan *Polymerolepis whitei* Karatajute-Talimaa, 1968, with an anal fin spine. *Geodiversitas* **35**, 529–543 (2013).
90. Hanke, G. F. & Wilson, M. V. H. Anatomy of the Early Devonian acanthodian *Brochodromones milesi* based on nearly complete body fossils, with comments on the evolution and development of paired fins. *J. Vertebr. Paleontol.* **26**, 526–537 (2006).
91. Schaeffer, B. The xenacanth shark neurocranium, with comments on elasmobranch monophyly. *Bull. Am. Mus. Nat. Hist.* **169**, 1–66 (1981).
92. Maisey, J. G. & Anderson, M. E. A primitive chondrichthyan braincase from the Early Devonian of South Africa. *J. Vertebr. Paleontol.* **21**, 702–713 (2001).
93. Miller, R. F., Cloutier, R. & Turner, S. The oldest articulated chondrichthyan from the Early Devonian period. *Nature* **425**, 501–504 (2003).
- This reports the oldest record of an articulated chondrichthyan and the first example with paired fin spines, initiating the dissolution of support for acanthodian monophyly.**
94. Turner, S. in *Recent Advances in the Origin and Early Radiation of Vertebrates* (eds Arratia, G., Wilson, M. V. H. & Cloutier, R.) 67–94 (Dr Friedrich Pfeil, 2004).
95. Schultze, H.-P. & Cumbaa, S. L. in *Major Events in Early Vertebrate Evolution* (ed. Ahlberg, P. E.) 315–332 (Taylor & Francis, 2001).
96. Yu, X. A new porolepiform-like fish, *Psarolepis romeri*, gen. et sp. nov. (Sarcopterygii, Osteichthyes) from the Lower Devonian of Yunnan, China. *J. Vertebr. Paleontol.* **18**, 261–274 (1998).
97. Zhu, M. *et al.* Fossil fishes from China provide first evidence of dermal pelvic girdles in osteichthyans. *PLoS ONE* **7**, e35103 (2012).
98. Coates, M. I. The evolution of paired fins. *Theory Biosci.* **122**, 266–287 (2003).
99. Gardiner, B. G. The relationships of placoderms. *J. Vertebr. Paleontol.* **4**, 375–395 (1984).
100. Young, G. C. The relationships of the placoderm fishes. *Zool. J. Linn. Soc.* **88**, 1–57 (1986).
- This article provided an explicit argument for the status of placoderms as stem gnathostomes that has not been seriously challenged in the following three decades.**

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