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Introduction

Zerina Johanson, Martha Richter and Charlie Underwood

Fishes, or lower vertebrates, occupy the basal nodes of the vertebrate phylogeny, and are therefore crucial in interpreting almost every feature of more derived vertebrates, including amphibians, reptiles, birds and mammals. Fishes have a longer fossil record than other vertebrates and constitute about half of all living vertebrate species. Recent research has focused on combining evolutionary observations, primarily from the fish fossil record, with developmental data from living fishes to better interpret the evolutionary history of this extensive region of vertebrate phylogeny.

This fish 'evo-devo' research programme has grown exponentially in the last two decades due to several factors: the growing numbers of researchers in the field making new discoveries worldwide; important new fossils (e.g., China, Australia, South America) and a better understanding of their evolutionary relationships; the rapid development of new, non-destructive 3D imaging techniques; and a new focus on an increasing range of 'non-model' fishes such as lampreys, hagfish, chondrichthyans and primitive bony fish.

Fishes are a particularly favourable vertebrate group to utilize in evolutionary and developmental studies, with a rich fossil record extending from the Cambrian geological period (540 MYA) to the recent. Although many extinct fossil fishes bear little resemblance to those living today, they nevertheless provide the only hard data to understand how lower vertebrates evolved through time. Alongside this, the unprecedented bulk of new knowledge made available by molecular and experimental biology, embryology, developmental morphology, genetics and epigenetics have permitted researchers to interpret fossils in an entirely new light. New concepts like 'molecular clocks' help make predictions about when in the deep time a particular lineage might have arisen, allowing the evolutionary timing of various characters to be more firmly established.

Covering each of these topics fully would require a series of volumes; our aim with this single book is to bring together world-class fish biologists and palaeontologists to illuminate state-of-the-art research in key areas of evolutionary development of non-tetrapod vertebrates, the history of which was written over the last 500 million years. A general introduction to fish taxa and the evolution of fishes through time is given in Chapter 1. Chapter 2 discusses the development of the cyclostomes – lampreys and hagfish – with embryos from the latter only recently available, and the implication for the evolution of vertebrate characters. Chapter 3 describes the Ordovician origins of fishes as part of the Great Ordovician Biodiversification Event, along with new phylogenies that place these enigmatic taxa within crown group gnathostomes (chondrichthyans and osteichthyans). The next chapter, Chapter 4, discusses the implications of important new placoderm taxa from the Silurian of China, playing a crucial role in a reinterpretation of the evolution of bony jaws, previously thought to be an exclusive osteichthyan character. Chapter 5 investigates problems involved in resolving phylogenies of stem chondrichthyans, focusing on two highly informative taxa, which possess very different morphologies. An extended (and long-overdue!) list of crown group chondrichthyan characters is also included.

Following this, the next chapters focus more on relevant morphological or anatomical components of fishes, and notably, on 'new model' animals such as sharks and rays. For example, Chapter 6 investigates the evolution and development of the cartilaginous skeleton in chondrichthyans, and in particular genetic networks involved in skeletal mineralization. Chapter 7 reviews the concept of plasticity and its relevance to the skeleton of bony fishes and the tissues responsible for the formation of this skeleton. Chapter 8 presents a review of some key evolutionary and developmental studies of the skull of agnathan and gnathostome fishes, including an assessment of Cambrian fish-like chordates and images generating from computed tomography (CT) scans of a range of representative taxa. Chapter 9 discusses molecular and genetic networks involved in the development of teeth in sharks and bony fishes, and how these regenerate, as an evolutionarily critical component of the dentition in these major groups. Chapter 10 focuses on head musculature, the developmental relationship between head and heart muscles, as well as the ontogenetic and phylogenetic links among the head muscles. Chapter 11 moves to the postcranial skeleton, reviewing the axial (vertebral) and appendicular skeleton in fishes (paired fins), both fossil and extant, including features such as regionalization of the axial skeleton and reproductive structures such as claspers and gonopodia.

This segues into Chapter 12, which reviews the evolution of reproduction in a range of fish taxa, including recent research establishing that reproductive structures in the phylogenetically basal group, the placoderms, are separate structures along the body and homologous to the appendicular skeleton. Chapter 13 investigates a modified region of the axial skeleton characteristic of a group of teleost fishes, the Weberian apparatus of the Otophysi, and how these modifications are related to thyroid hormone signalling affecting rates of development in the fish skeleton. Chapter 14 reviews the evolution of the pharyngeal region, and how remodelling of the individual arches in this region into structures, such as the parathyroid glands, in the transition from fish to tetrapods. Our final chapter, Chapter 15, examines the evolution of air breathing and lungs among fishes, and the skeletal structures involved.

These chapters, covering a range of taxa and topics on the evolution and development of fishes, will serve to highlight one of the most interesting and vibrant fields of ‘evo-devo’ research today. This modern ‘total evidence’ approach, combining anatomical characters of living and fossil taxa, has major implications for the understanding of key evolutionary events among vertebrates, as well as for the identification of deep time homologies and unique adaptations, and for our increased understanding of certain human pathologies.

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1 The Evolution of Fishes through Geological Time

John A. Long, Brian Choo and Alice Clement

Abstract

Fishes, here defined as ‘non-digitate aquatic vertebrates’, first appear in the Cambrian Period at least 520 million years ago (Ma). They are first represented by fusiform taxa lacking well-developed fins and dermal bone covering. The first fishes to bear external dermal bones forming a protective and supporting framework appear in the mid-Ordovician, about 460 Ma, represented by fusiform heterostracans and other associated taxa, found in Australia and South America. By the late Ordovician, fishes were widespread across the globe and the first jawed vertebrates, gnathostomes, had possibly appeared. The oldest gnathostome remains are enigmatic small placoid-like scales with chondrichthyan affinity, but cannot be resolved without more complete material. The oldest jawed vertebrates, both placoderms and stem chondrichthyans (‘acanthodians’), come from what is today China, with articulated diverse remains of placoderms and the first osteichthyans in the upper Silurian (Ludlow) of Yunnan. These forms include maxillate placoderms like *Entelognathus* and *Qilinyu* as well as heavily spined sarcopterygian (osteichthyan) fishes like *Guiyu*. At the start of the Early Devonian we see a new placoderm fish fauna emerging globally which has little resemblance to the late Silurian taxa of China, with some five main clades of placoderms and a few smaller groups of uncertain affinity. Osteichthyans diversified into two major clades, one of which, the Actinopterygii, or ray-fins, were represented by early forms with rhombic scales and fixed cheek-mouth complexes, loosely termed ‘paleoniscoids’. The Sarcopterygii, which include Actinistia (coelacanths), Dipnomorpha (dipnoans and porolepiforms), Onychodontiformes, and stem tetrapods (Tetrapodomorpha), had all appeared by the end of the early Devonian. Since the end of the Palaeozoic the non-tetrapod sarcopterygians are represented only by lungfishes and coelacanths. Chondrichthyans are known from isolated teeth, scales, and spines in the early Devonian with one articulated fish from the Emsian. By the late Devonian chondrichthyans had radiated into many families, including the first stem holocephalans, like *Cladoselache*. The Carboniferous saw a huge radiation of chondrichthyans and actinopterygians. Neopterygians appeared by the late Carboniferous with the first teleosteans by the late Triassic. Since the Mesozoic percomorphans especially have diversified to comprise the great majority of all fish families extant today, represented by some 29,000 spp. of teleosteans. Chondrichthyans also underwent a secondary radiation when batoids and modern sharks appeared in the Jurassic. Today there are some 1,200 species of living chondrichthyans.

1.1 Introduction

‘Fish’ in common parlance are vertebrates with a well-developed notochord, gill slits, well-formed paired sensory organs, a lateral line system, and a mineralised skeleton comprising either cartilage and bone, or both. The skeleton can be either external bony plates formed in the dermis (dermal bone), or internally ossified bony or cartilage units formed from cartilage precursors (endochondral bone) or laminated bone surrounding cartilage blocks (perichondral bone: Hall, 2015). Bone is the key to understanding fish evolution and diversity. It provides a solid support for attachment of muscles, and this gives a greater efficiency for using a muscular tail to propel the animal through water. Faster speeds give escape from predators and the ability to catch slower-moving prey. Bone also acts as a storehouse for phosphates and other chemicals required in daily metabolism. Furthermore, it gives protection to more vulnerable parts of the anatomy, such as the brain and heart. Typical fish bone has cell-spaces for osteocytes (bone-producing cells), and the external layers of the dermal bone of basal forms (many agnathans and stem gnathostomes) have an ornament covered by thin enameloid layer over a dentine layer. Certain early fossil jawless forms have bone formed of layers of non-cellular bone, called aspidin.

The earliest fishes had only external dermal bone, formed in the dermis of the skin. Internal bony skeletons made of cartilage with perichondral bone layers appeared first in jawless fishes and placoderms, with endochondral bone evolving later in osteichthyans, and this development drove the next great event in fish evolution when jaws and

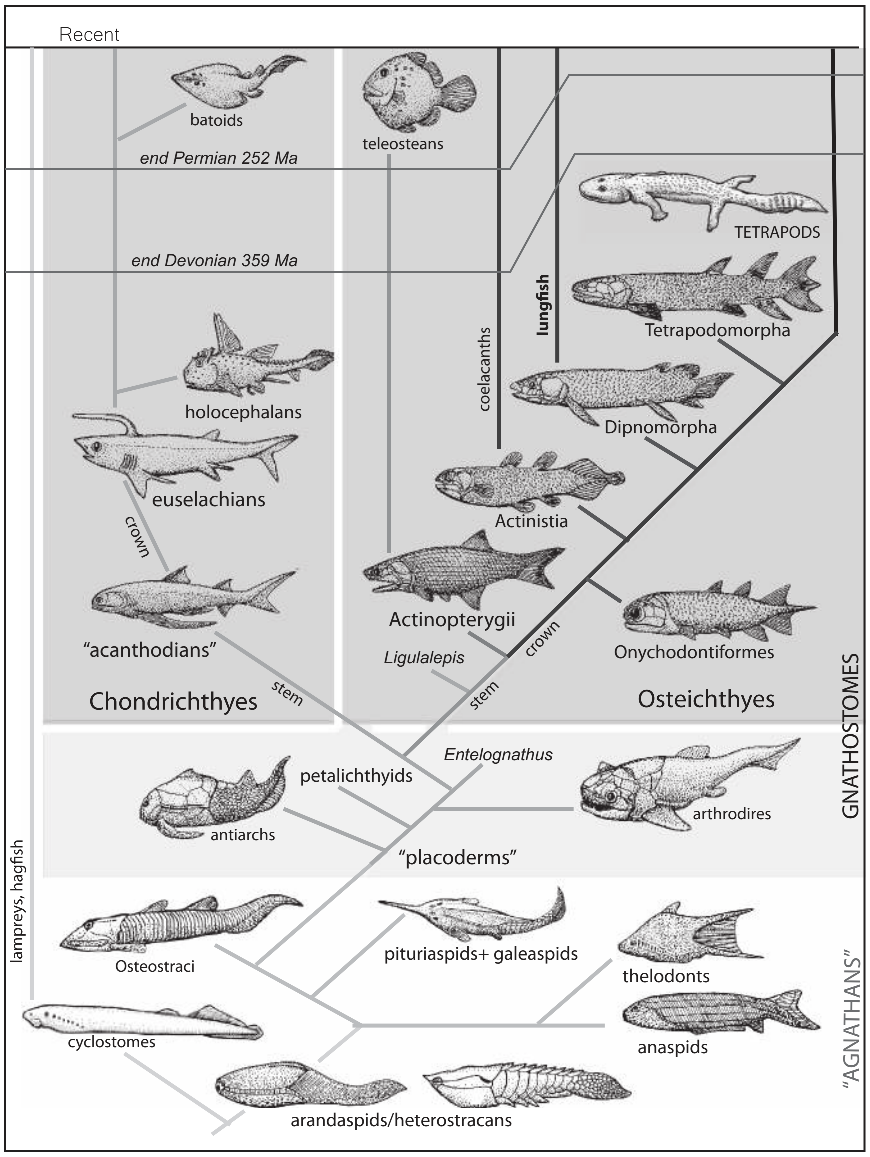

Fig. 1.1. Relationships of major groups of fishes, based on recent analyses by Qiao et al. (2016) and King et al. (2016); the latter argues that placoderms might be monophyletic.

teeth appeared ('gnathostomes'). The origins of large bony plates in fishes were thought to have formed from small centres, or plates of bone called odontodes, which later joined up to make large bony sheets.

The term 'agnathan' is here used in an informal sense, as the group represents the radiation of all jawless fishes, and as such are a paraphyletic collection of groups, mostly extinct clades that lived in the Palaeozoic (Fig. 1.1). Lampreys and hagfishes are the only extant representatives of the jawless fishes which first appeared in the Cambrian, about 525 million years ago, and peaked in diversity in the Early Devonian, about 400 million years ago. The study of fossil agnathans is vital to understanding important anatomical transformations that took place early in vertebrate evolution.

1.2 The Oldest Fishes

The Chengjiang fauna of Yunnan, South China, demonstrates that stem vertebrates (craniates) were already in existence in Asia by the Early Cambrian. *Haikouichthys* and *Myllokunmingia* had a head with olfactory, optic and otic sensory organs, filamentous gills in a distinct branchial region, chevron-shaped myomeres, and possible arcualia, etc. (see Shu et al., 1999, 2003; Janvier, 2003). *Metaspriggina* from the Mid Cambrian Burgess Shale of Canada may have lacked bony vertebrae but had a well-formed head with paired eyes and nasal sacs (Conway Morris and Caron, 2014). More significantly, it had seven pairs of well-developed gill-arches that were external, as in jawed fishes, not internally positioned, as in modern

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jawless forms, such as lampreys and hagfishes, suggesting that the latter condition is specialised. *Metaspriggina* is described as having well-formed anteriormost gill bars that were the precursors to the origin of jaws.

Phosphatic fragments called *Anatolepis* from the Late Cambrian and Early Ordovician of North America and Greenland, previously reported as vertebrate remains (Repetski, 1978), are now regarded not to be of vertebrate origin (Janvier, 2003), but could be arthropod cuticle (Smith et al., 2001). Possible late Cambrian bone described by Young et al. (1996) from central Australia is contentious, also possibly belonging to arthropod cuticle (Sansom et al., 2001) and will rely on further finds to resolve its vertebrate affinity.

1.3 The Lower Palaeozoic Radiation of Jawless Fishes

The extinct fossil agnathans include eight major types of armoured and some non-armoured forms, most of which had evolved by the start of the Silurian Period, about 430 million years ago (Fig. 1.1): Arandaspida, Astraspida, Osteostraci, Heterostraci, Anaspida, Thelodonti, Galeaspida and Pituriaspida. Only three of these groups – the Arandaspida, Thelodonti and the Pituriaspida – are recorded in Australia and other eastern Gondwanan regions. The Osteostraci and Heterostraci are unique to the ancient Old Red Continent Euramerica (Europe, Greenland, western Russia and North America), and fossils of the Galeaspida are unique to the North and South China terranes (South China, Vietnam; Young, 1981).

In the Early-Middle Ordovician (Arenig-Llanvirn) in central Australia the arandaspids were fusiform armoured jawless fishes with headlight-facing eyes and anterior open mouths and possessed many rectangular branchial plates. These include *Arandaspis*, *Porophoraspis* (Ritchie and Gilbert-Tomlinson, 1977) and *Sacabambaspis* (Young, 1997) with the latter represented by complete specimens of slightly younger Caradoc age in Bolivia (Gagnier et al., 1986). Like *Arandaspis*, *Sacabambaspis* has a large dorsal and ventral shield with numerous rectangular branchial plates, small eyes at the front of the skull and paired pineal openings (opening for the pineal organ or ‘third eye’ on top of the head). It also has a rounded plate on each side near the front of the head. The body is covered with many fine elongated scales, but lacks paired or median fins. The tail is well developed with a long ventral lobe. The dermal exoskeleton has three layers of acellular bone with superficial dentine and enameloid (Sansom et al., 2005). The late Ordovician Harding Sandstone of Colorado, United States, has yielded fragmentary bits of heterostracans, including *Astraspis*, and rare complete remains of *Astraspis* (Elliott, 1987). These all share the primitive feature of having numerous paired openings for the gills, these being reduced in number in all subsequent jawless fishes except for some anaspids. The bone making up the shields of the North American *Astraspis* is composed of four layers of phosphatic minerals, including fluorapatite and hydroxyapatite. This suggests a close relationship to the heterostracans, a diverse group that had similar shields to these Ordovician forms but which possessed only one branchial opening over the gills.

The heterostracans underwent their major radiation early in the Silurian Period, and were common in Euramerica (including Siberia) throughout the Devonian, reaching a peak of diversity in the Early Devonian (Blieck, 1984). The largest heterostracans were the largest armoured agnathans, reaching estimated lengths of around 1 m, while most were small fishes about 10–20 cm in total length. Heterostracans occupied the niche of microphagous filter-feeders (Purnell, 2001).

The small traquairaspids and cyathaspids from Arctic Canada and Britain are distinguished by their relatively simple shields, with highly elaborate surface ornament. They are basal heterostracans that lack the elaborate spines developed in later lineages, such as the pteraspidiforms, and the tail has only a few large scales. *Aethenaegis* from the Delorme Group of the Northwest Territories of Canada (Soehn and Wilson, 1990) was a small fish about 5 cm long, which had a V-shaped leading edge on the lower lip of the mouth that may have been used for plankton or detrital feeding. Other cyathaspids, such as *Traquairaspis*, *Corvaspis*, *Tolypelepis* and *Lepidaspis*, have very distinctive surface ornament, consisting of many polygonal units of elaborately sculptured bony ridges (Blieck et al., 2002). The cyathaspids flourished during the later half of the Silurian Period but were extinct by the early part of the Devonian.

One of the most diverse groups of Devonian heterostracans was the pteraspidiforms, so-named because of their winglike pointed spines at the sides of the armour. Pteraspidiforms have a complex shield with separate rostral, pineal and dorsal discs forming the upper part of the armour (Blieck, 1984). Some forms, such as *Doryaspis* from Spitzbergen, evolved rostral processes (Blieck and Heintz, 1979). Some of the well-known pteraspidiforms include *Errivaspis* from Britain and France; *Rhinopteraspis* from Europe and North America, which has a long, elongated rostrum; and the large flattened form, *Drepanaspis*, from the Hunsrück Shales of the Rhineland, Germany. Other heterostracans include a group unique to the Russian terranes, the amphiaspids (Novitskaya, 1986). These had wide, rounded armour, made of a single piece of bone. Most had shields about 10–18 cm long, the largest forms being as long as 40 cm. *Lecaniaspis* and *Elgonaspis* had bony feeding tubes or scoops at the front of the head that may have functioned as a pump to suck in small organisms from the mud. Some of them have traces of healed bites on them, suggesting that they regularly survived attacks from the larger jawed fishes.

The anaspids were simple, laterally compressed eel-like jawless fishes that may or may not have had a covering of thin elongated scales on the body. They were mostly small, rarely exceeding 15 cm, although there are some very large anaspid scales from the early Silurian of Canada (Blom and Miller, 2002). The group flourished during the Silurian and early part of the Devonian (Blom and Märss, 2010). They had simple fins, developed along the dorsal and ventral ridges of the body, and some forms, such as *Jamoytius* and *Pharyngolepis*, had well-formed lateral fins which are supported by radials. *Euphanerops*, from the Late Devonian of Miguashua, Quebec, bore paired intromittent elements made of cartilage for internal fertilisation, and had the axial skeleton differentiated into different components (Chevrinais et al., 2018).

Thelodonts were scale-covered jawless fishes whose scales bear a distinctive crown of dentine on a bony base, perforated ventrally by a large pulp cavity (Marss et al., 2007). Rare whole thelodont fossils show that most were flattened fishes with broad winglike pectoral fin fold, lacking radials as seen in anaspids. They also feature large heads with ventral rows of gill openings (e.g., *Turinia*; Turner, 1982). Thelodonts ranged in size up to nearly 1 m in length, but most were small fishes, generally less than 15 cm long. Thelodont scales vary in morphology, according to which part of the fish they come from; short, squat head scales give way to elongate trunk scales, plus there are fin scales and internal pharyngeal scales (Van der Brughen and Janvier, 1993). Recently it has been discovered that the morphological diversity of thelodont scales correlates closely with functional types established for sharks, suggesting thelodonts occupied a much wider variety of niches than previously thought (Ferrón and Botella, 2017). The oldest fossil thelodonts, known from scales in Siberia, are of Late Ordovician age, and the group became extinct by the end of the Famennian stage (Late Devonian) in Iran and Australia (Harapetian et al., 2015). Well-preserved thelodonts from the Silurian-Early Devonian of the Northwest Territories of Canada (Wilson and Caldwell, 1993) include deep-bodied fork-tailed forms such as the Furcacaudiformes, exemplified by *Sphenonectris*. Some of them, such as *Furcacauda*, show the suggested presence of a large stomach (Wilson and Caldwell, 1993), an organ thought to be absent in jawless fishes, as it is lacking in the living forms such as lampreys.

Galeaspids were a group of jawless fishes unique to the ancient terranes of Southern China and northern Vietnam (Halstead, 1979; Janvier, 1996; Zhu and Gai, 2006). The armour is formed of a single bony shield without separate plates, except on the ventral side of the head, as in osteostracans and pituriaspids. The unique feature of galeaspids is that the armour has a large median hole in front of the paired orbits, the median dorsal fenestra. This is very large in most galeaspids, opening directly below to the paired nasal cavities. Some, like *Dongfangaspis*, had up to 45 pairs of gill openings. Galeaspids were a diverse group, with more than 80 known species (Long, 2011), with fine preservation of tubes of laminar perichondral bone around soft tissues of the head. They had a complex brain and a well-developed inner ear with two vertical semicircular canals. *Shuyu* revealed paired nasal capsules close to the orbits, inside the head, a feature seen in some basal gnathostomes like *Romundina* (Gai et al., 2011).

The pituriaspids are known by two forms, both of which come from the Toko Range in south-western Queensland, Australia. They represent the only body fossils of agnathans of Devonian age from Australia, close to the Emsian-Eifelian boundary. They have long bony armour, forming a tube around the head and trunk region, with a large opening below the orbits, and a long, forward-projecting rostrum (Young, 1991). Two forms are known, *Pituriaspis* and *Neeyambaspis*, the latter having a broader, shorter armour shape. The pituriaspids possibly possessed pectoral fins, as evinced by large paired openings on each side of the armour, and a strong ridge that would have protected the front edge of the fin. We know little about the anatomy of pituriaspids but the presence of pectoral fins suggests they are closely related to the osteostracans.

The osteostracans were a diverse group of solid-shielded agnathans restricted to the ancient Euramerican continent, with fossil remains well known from Britain, Europe, western Russia, Spitsbergen, and North America (Stensiö, 1927; Janvier 1985, 1996). They have a single bony shield with two round orbits, a smaller, key-shaped opening for nasohypohyseal organ, and a tiny pineal opening between the eyes. The sides of the shield have large areas of sensory function and a dorsal sensory field. The shield grew from tesserated smaller plates that fused to form a solid shield at maturity. The pectoral fins are well developed in osteostracans and were attached on simple internally ossified shoulder girdle bones (scapulocoracoid), on which articulated a simple, paddle-shaped, cartilage was supported (Wilson et al., 2010).

In some osteostracans (e.g. *Tremataspis*), the paired fins have secondarily disappeared. They had one, or sometimes two, dorsal fins on the body, as shown in *Ateleaspis* from Scotland (Ritchie, 1967). In some osteostracan fossils, like *Boreaspis*, impressions of the brain cavity are well preserved, with pathways of nerves, arteries and veins preserved by thin perichondral bone (Janvier, 1985). They had just two semicircular canals forming the inner ear, as opposed to the three found in higher vertebrates, and the

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general plan of the cranial nerves and vascular supply to the head was similar to that of the larvae of lampreys. Osteostracans also had well-developed sclerotic bones around the eyes, and some had small tuberculated oral areas at the front of the mouth. The lifestyle of osteostracans has been reconstructed by Afanassieva (1992): many were largely bottom-dwelling forms that were heavy shielded without paired fins, and hence less mobile swimmers. All the osteostracan fossils that have the tail preserved show the presence of thick scales, often arranged as a series of vertically oriented rectangular units, capped by a series of smaller ridge scales along the back and meeting another series underneath on the belly. The osteostracans underwent a major radiation during the Early Devonian resulting in a great diversity of forms (at least 214 species; Sansom, 2009), ranging from those with simple semicircular headshields (such as *Cephalaspis*) to others with prominent dorsal spines (*Machairaspis*), or elongated shields that cover much of the trunk of the fish (*Thyestes*, *Dartmuthia*, *Nectaspis*).

1.4 The Origins of Gnathostomes

The earliest possible gnathostomes are known only from scales which have a close resemblance to the placoid scales of sharks, hence suggesting they are of gnathostome origin. Putative gnathostomes from the Middle Ordovician of Australia include scales of *Areyongalepis*, a possible chondrichthyan (Young, 1997), and a second scale type (*Apedolepis*) combining dentine and an enamel-like surface tissue that also lines ampulla-shaped spaces of the pore canal system, which was compared by Young (1997) with osteostracans, heterostracans, and primitive gnathostomes. Possible gnathostomes of Late Ordovician age are represented by microremains from the Harding Sandstone of North America. One taxon known is only from cartilage – *Skiichthys* (Smith and Sansom, 1997). Various scales from the Harding Sandstone are thought to include chondrichthyan placoid scales, possible acanthodians, and possible other gnathostomes (Sansom et al., 2001). By the early Silurian, the ‘*Tesakoviaspis* fauna’ in Siberia includes gnathostome microremains comprising acanthodians and mongolepid chondrichthyans (Andreev et al., 2016); at the same time, there are remains attributed to placoderms and *Sinacanthus* found in South China.

The taxon favoured by most palaeontologists as being the sister group to jawed vertebrates is the Osteostraci (Janvier, 1996). Janvier (2001) summarised the shared characters of osteostracans with jawed fishes as follows: development of paired fins (including pectoral fins with an ossified scapulocoracoid and a cartilaginous fin skeleton), open endolymphatic duct on the head, ossified bones around the eye (sclerotic bones), perichondrally ossified sclera, cellular bone in both the external and internal ossifications, two dorsal fins, an epicercal tail, and slit-shaped gill openings. The Galeaspida also share with osteostracans and gnathostomes a perichondrally ossified (or calcified) endoskeleton, externally open endolymphatic ducts, a large dorsal jugular vein, and an occipital region developed on the braincase which encloses the exit for the vagus nerve. As noted above, galeaspids share paired, laterally separated nasal capsules with the gnathostomes (Gai et al., 2011).

1.5 Placoderms

The placoderms were armour-plated jawed fishes which first appeared in the mid-late Silurian Period about 430 million years ago and dominated the seas, rivers and lakes of the Devonian Period, becoming extinct at the end of the Devonian (Fig. 1.2). Placoderms are regarded by some researchers as a paraphyletic cluster of clades (e.g. Johanson, 2002; Brazeau, 2009; Qiao et al., 2016). However, rates of placoderm evolution using Bayesian tip-dated clock methods show how that placoderm monophyly is more statistically likely for the group when more balanced rates of evolution are considered, as compared to the paraphyly hypothesis (King et al., 2016). Phylogenetically, placoderms are resolved on most recent trees as more crownward than the jawless osteostracans and galeaspids, but still on the gnathostome stem, i.e., basal to the crown group gnathostomes (Chondrichthyes and Osteichthyes; Brazeau and Friedman, 2014; Dupret et al., 2014; Brazeau and Friedman, 2015; Long et al., 2015; King et al., 2016; Qiao et al., 2016; Fig. 1.3). Their rapid evolution and diversification meant that species generally occupied short timespans, and their fossils can often be used to relatively determine the ages of Devonian rocks.

Most placoderms are characterised by their peculiar armour made up of an overlapping series of bony plates with extensive flat overlap surfaces which form a protective cover around the head (headshield) and enclosing an immobile ring of bone around the anterior of the body (trunkshield). These shields articulate by bony knobs and grooves, or in rare cases may be fused (e.g. *Synauchenia*). Originally classified in seven major orders, each characterised by its own pattern of the bony plate morphology, recent phylogenetic analyses are seeing the coalescence of some of these traditional groups (e.g. Dupret et al., 2014; Brazeau and Friedman, 2015; Long et al., 2015; King et al., 2016; Qiao et al., 2016). Phyllolepids are now regarded as a group nested within arthrodires, and ptyctodontids appear to be nested within petalichthyids. Some acanthothoracids are widely separated from others within some phylogenies (e.g. the placement of *Brindabellaspis* and *Romundina*: Brazeau and Friedman, 2015; King et al., 2016; Qiao et al., 2016). These show that much

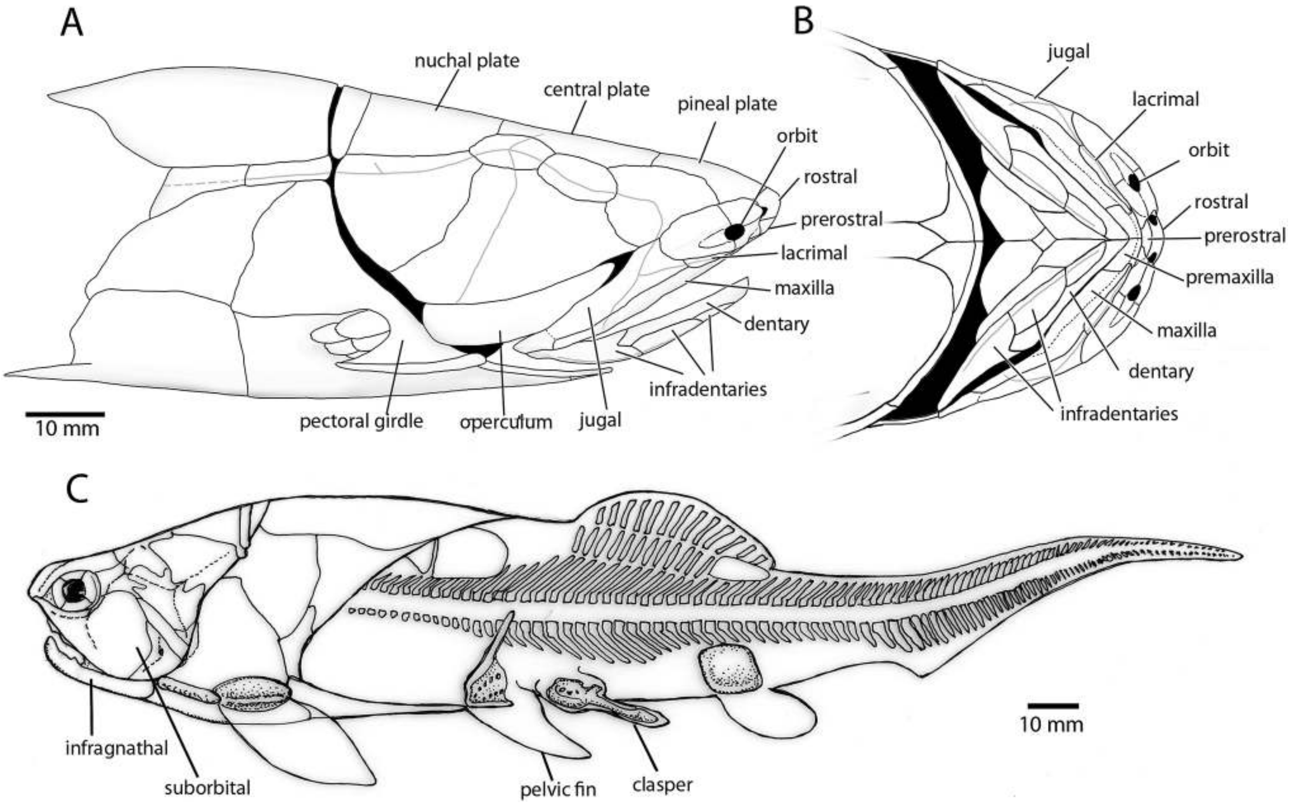

Fig. 1.2. Placoderms, stem gnathostomes. **A, B)** Late Silurian maxillate placoderm *Entelognathus*, showing dermal armour (**A**, lateral view), and jaw structures (**B**, ventral view from Zhu et al., 2013). **C)** Typical Devonian arthrodire *Coccosteus*, skeleton with male intromittent organs developed as separate pair of limb-like structures. (from Trinajstic et al., 2015)

further work is required, describing – and redescribing – the detailed anatomy of various placoderms in order to resolve such issues (Fig. 1.3).

Generalised placoderms show an external ornament of simple tubercles, whereas others such as the phyllolepids, may develop complex linear or reticulate network patterns. The braincase of all early placoderms (except antiarchs) was well ossified with layers of laminar perichondral bone (Young, 1979), but in later species, such as those from the Late Devonian Gogo Formation, Western Australia, it was entirely cartilage. The body is primitively covered with thick bony platelets which resemble miniature versions of dermal bones, often having similar ornament on each scale. In advanced lineages of placoderms, the body scales may be reduced or absent.

The earliest complete placoderms come from the late Silurian (Ludlow) Kuanti Formation of Yunnan, China. These include 'maxillate forms' possessing a dermal upper jaw bone, the maxilla, and a premaxilla, such as *Entelognathus* (Zhu et al., 2013; Fig. 1.4A, L) and *Qilinyu* (Zhu et al., 2016). While *Entelognathus* has a lower jaw with a set of dermal bones resembling that of a basal osteichthyan (with dentary and infradentary series present, and gulars under the jaw), *Qilinyu* has lost the outer dermal covering and the jaw is approaching the typical shape of the infragnathals seen in most other placoderms. The Chinese forms suggest that the two arthrodiran upper tooth plates (the supragnathals) be homologised to the premaxilla and maxilla of osteichthyans, with the infragnathal being the dentary equivalent (Long, 2016; Zhu et al., 2016).

Very well-preserved three-dimensional placoderms are known from the Early Devonian limestones of south-eastern Australia. Forms like *Parabuchanosteus* (Young, 1979; White, 1978; Long et al., 2014) show extraordinary detail of the anatomy of these primitive jawed fishes. A great diversity of advanced placoderms, perfectly three-dimensionally preserved from the Gogo Formation, show the complex adaptations evolved by these fishes for life in a reef ecosystem (Long and Trinajstic, 2010; Fig. 1.4M). Some of these Gogo placoderms have revealed the presence of embryos, showing that many reproduced by copulation using bony intromittent organs, and gave

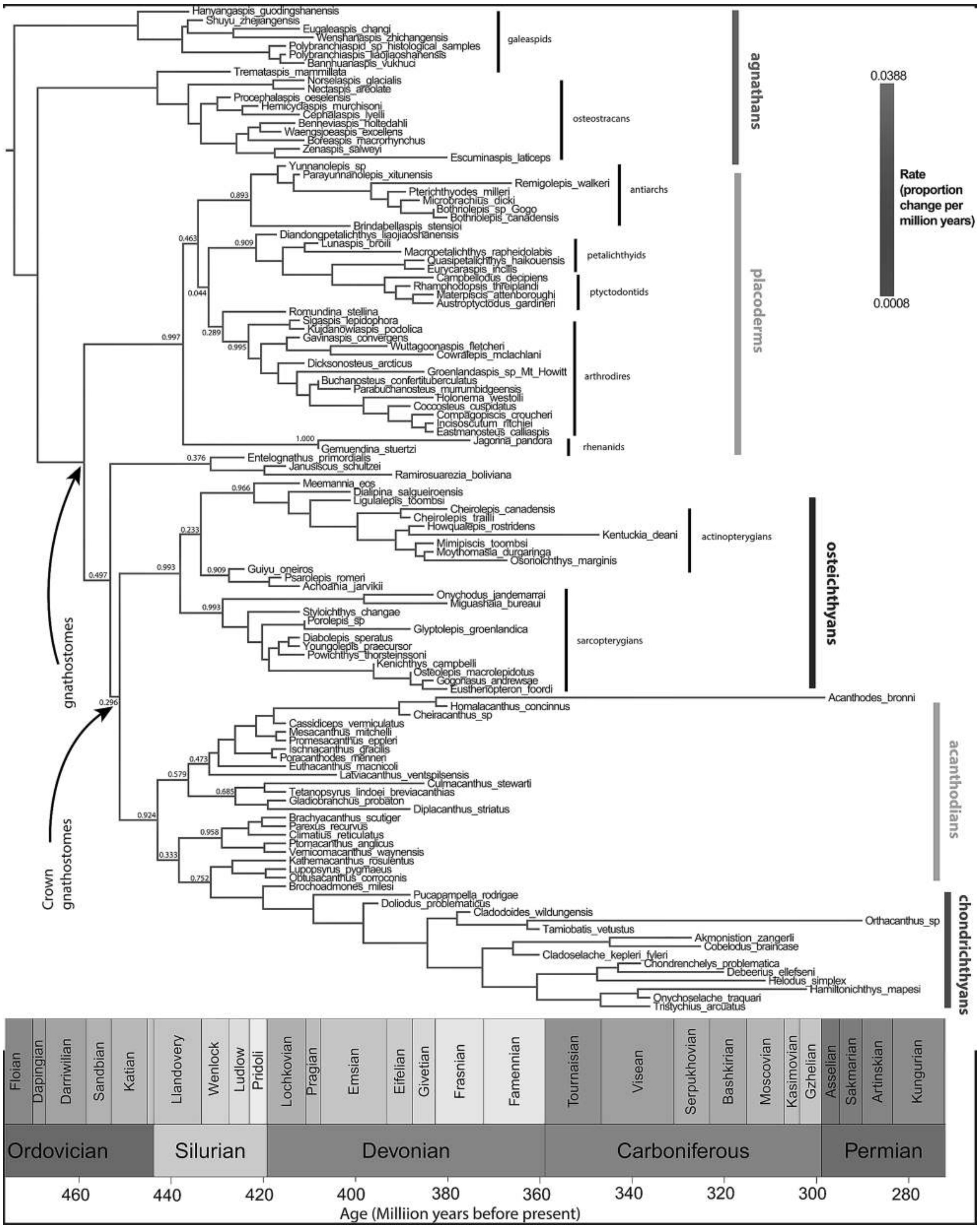

Fig. 1.3. Gnathostome rates of evolution, from King et al. (2016). With permission of the author.

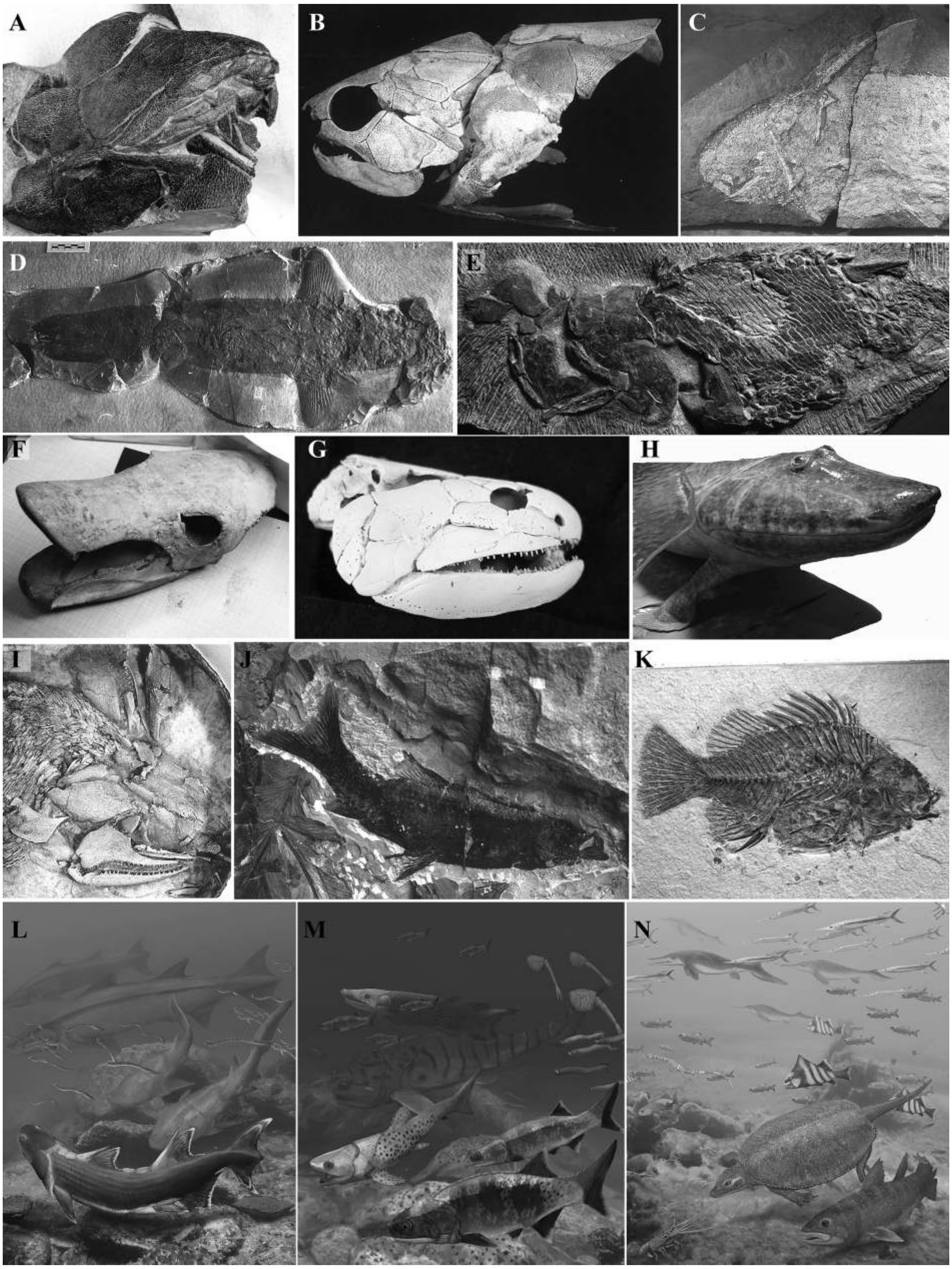

Fig. 1.4. **A)** Holotype of the maxillate placoderm *Entelognathus primordialis*, late Silurian Kuanti Formation, Yunnan, China. **B)** Holotype of *Mcnamaraspis kaprios*, an arthrodire placoderm, Late Devonian Gogo Formation, Western Australia. **C)** *Milesacanthus antarctica*, an