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# Fossil Focus: Acanthodians

by Richard Dearden[*1]

## Introduction:

The acanthodians are a mysterious extinct group of fishes, which lived in the waters of the Palaeozoic era (541 million to 252 million years ago). They are characterized by a superficially shark-like coating of tiny scales, and spines in front of their fins (Fig. 1). The acanthodians' heyday was during the Devonian period, about 419 million to 359 million years ago, but their fossil record stretches back to the Silurian period (around 440 million years ago). One specialized filter-feeding group, the Acanthodiformes, persisted until the end of the Permian period (about 252 million years ago), disappearing in the end-Permian mass extinction. Acanthodian fossils were first described by the eminent Swiss palaeontologist Louis Agassiz during the nineteenth century, and are today known worldwide; acanthodians from the Lower Devonian Old Red Sandstone of the United Kingdom have been particularly well described (Fig. 2a–d), with extremely well-preserved fossil fishes found in places such as Wayne Herbert Quarry in the Welsh Borders. More recently, many spectacularly preserved fossils have also been described from northwestern Canada, in the Man on the Hill (MOTH) locality; these fossils have had a profound impact on our understanding of vertebrate evolution.

Acanthodians are of particular interest to palaeontologists because of the insight they provide into the early stages of evolution of the jawed vertebrates. Today, all vertebrates with jaws are separated into two groups: the osteichthyans and the chondrichthyans. Osteichthyans include fishes with a bony skeleton, like trout and tuna, as well as the tetrapods, such as humans. Chondrichthyans are fishes with a skeleton made of cartilage, like sharks, rays and chimaeras. Jawed vertebrates were more diverse in the past, however, and there are several extinct groups known only from the fossil record, including acanthodians. Studying these fossils helps us to build up a more complete picture of how the jawed vertebrates came to be so successful, as well as revealing how the body plan of modern forms was assembled during their early evolution.

Here, we will examine the general anatomy of acanthodians and discuss where they fit into the vertebrate family tree. We will also consider in more detail why they are so important for understanding the evolution of jawed vertebrates. Throughout this article, the word 'acanthodian' will be used to refer to this collection of fishes. However, as we will see, the acanthodians probably do not form a true group at all.

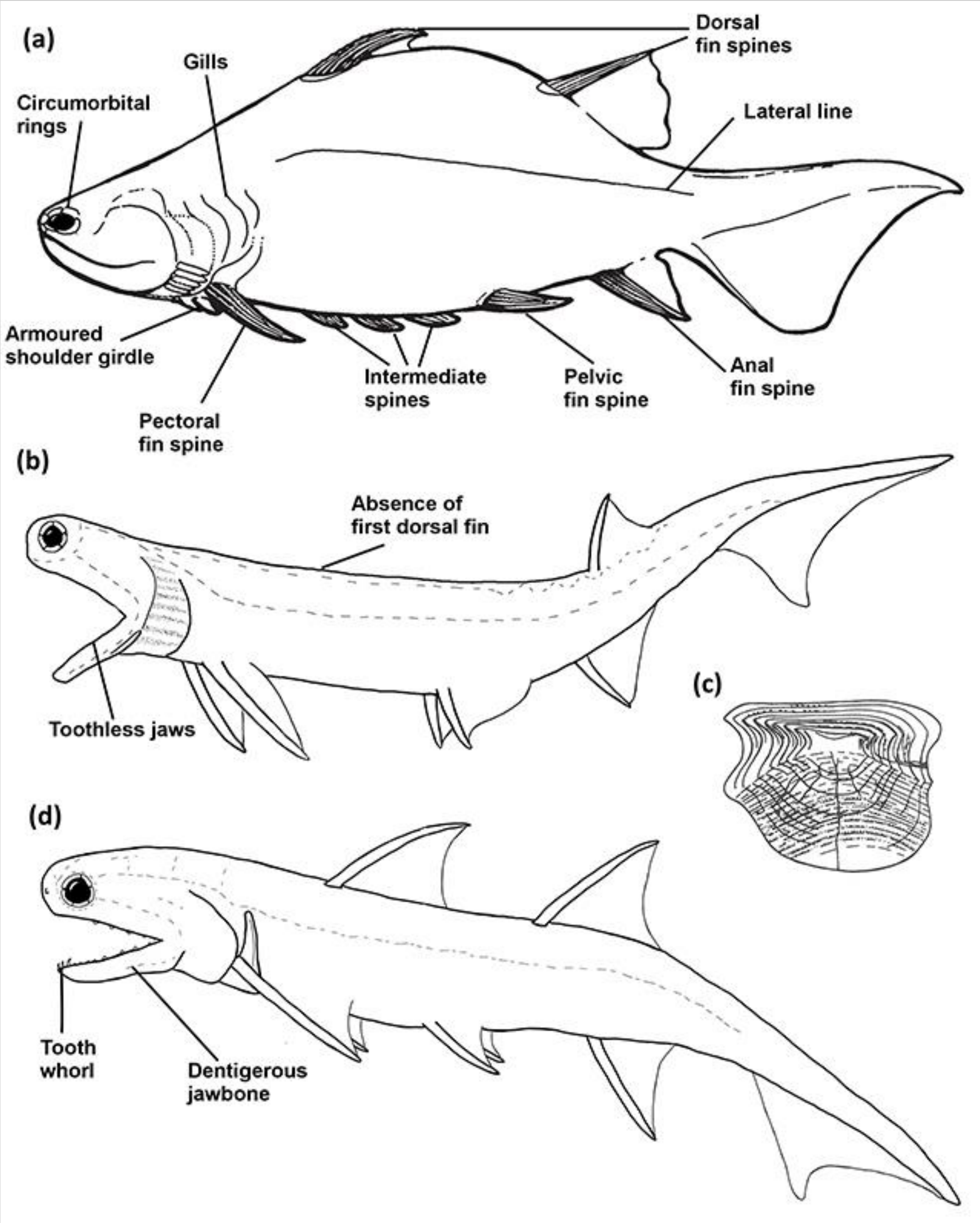


Figure 1 — Reconstructions of three different acanthodians, showing 'typical' anatomy: (a) *Ptomacanthus*, a climatiiform from the Devonian of the United Kingdom; (b) *Howittacanthus*, an acanthodiform from the Devonian of Australia; (c) the scale of the acanthodiform *Acanthodes bronni*, showing 'typical' acanthodian onion-like scale growth; and (d) *Ischnacanthus*, an ischnacanthiform from the Devonian of the United Kingdom. (a) modified from Brazeau (2012); (b) and (d) redrawn from Long (1986) and Watson (1937) respectively; (c) modified from Denison (1979).

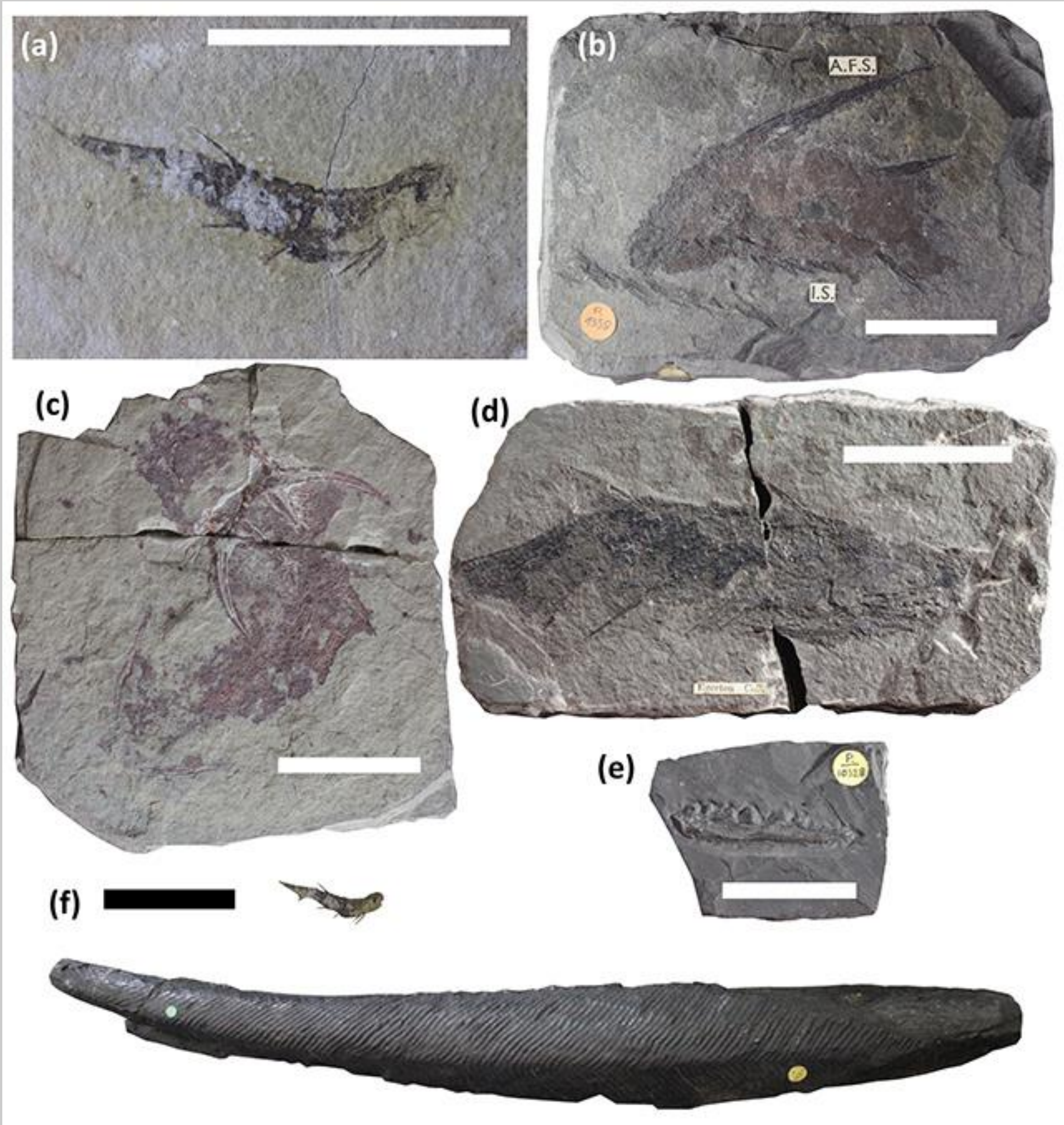


Figure 2 — Acanthodians from the United Kingdom. (a) *Mesacanthus mitchelli*, an acanthodiform; (b) *Parexus recurvus*, a climatiiform; (c) *Diplacanthus striatus*, a climatiiform, viewed from the bottom to show armoured pectoral girdle; (d) *Ischnacanthus gracilis*, an ischnacanthiform; (e) the lower jaw of *Acanthodopsis*, which has a dentigerous jaw bone; (f) the pectoral spine of *Gyracanthus formosus*, with *M. mitchelli* from (a) included for size comparison. Scale bars are 30 mm in (a), (b), (c) and (e), and 50 mm in (d) and (f). Pictures courtesy of the Natural History Museum, London.

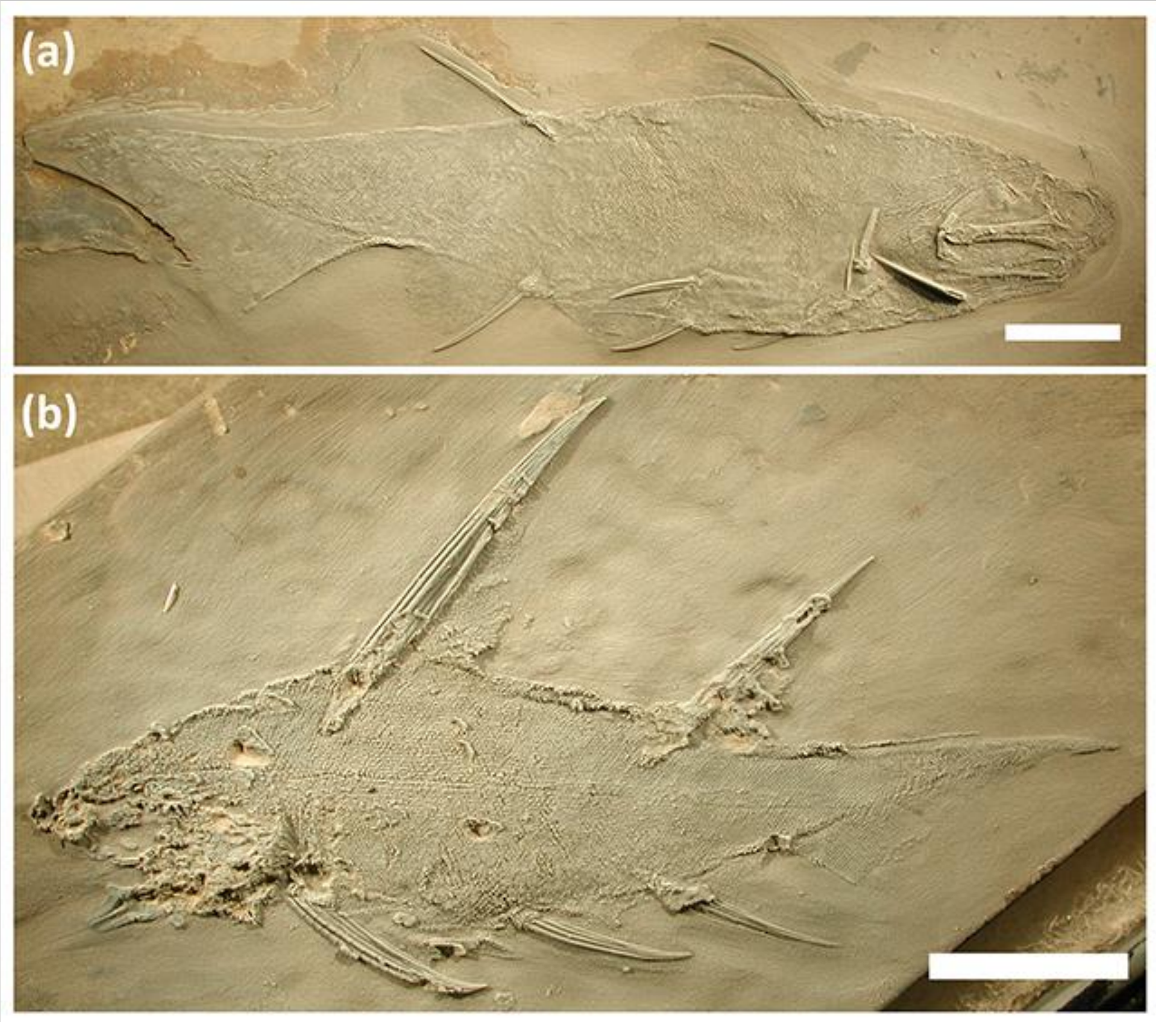


Figure 3 — MOTH acanthodians. (a) Ischnacanthiform; (b) *Uraniacanthus probaton*. Scale bars are 10 mm. Photos by G. Hanke, Victoria, British Columbia.

## Anatomy:

The most striking characteristic of acanthodians is the set of bony spines that sits in front of their fins, and it is from these that the group draws its name: the Greek *akanthos* means spine. Although most were fairly small, these spines (and the acanthodians to which they were attached) could grow to imposing sizes: compare the *Gyracanthus* spine in Fig. 2f to the *Mesacanthus* in Fig. 2a! Like modern sharks, acanthodians had bodies covered in micromeric dermal armour (tiny scales), as opposed to the larger scales of osteichthyan fishes. In many (but not all) acanthodians, these scales also show a characteristic onion-like growth pattern, building up in concentric layers (Fig. 1c). The internal skeleton of most acanthodians is made of cartilage rather than bone, similar to that of modern sharks. The combination of tiny scales and a weakly mineralized cartilaginous skeleton means that acanthodians tend to fossilize poorly, with even good acanthodian fossils looking at first like vaguely fish-shaped 'splats' of scales and spines.

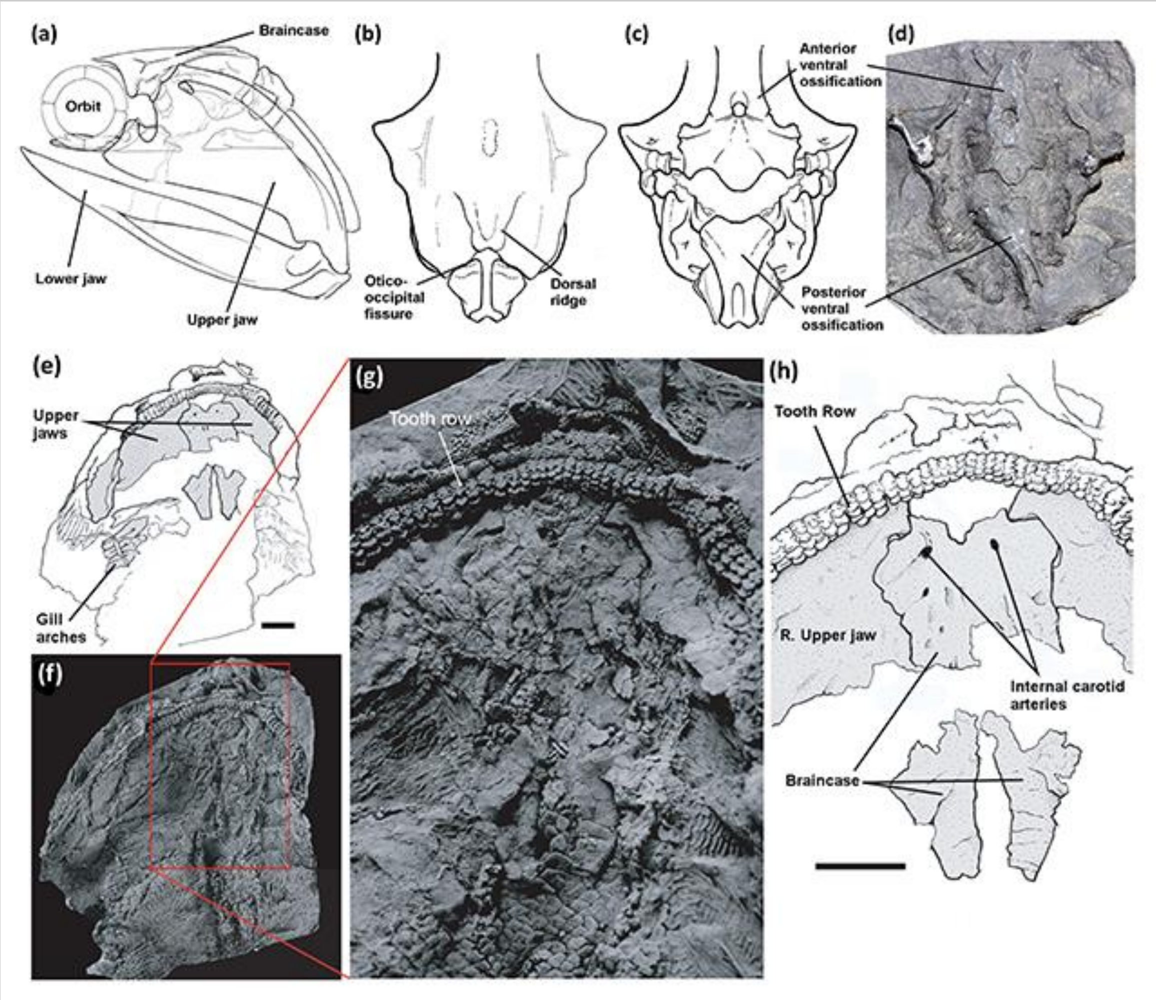


Figure 4 — Acanthodian braincases: (a–d) *Acanthodes bronni*, an acanthodiform from the Permian of Germany. Braincase is shown reconstructed in (a) lateral (side), (b) dorsal (from above) and (c) ventral (as if looking upwards into the roof of the mouth) view, with (d) a photograph of the cast of the braincase in ventral view. (e–h) *Ptomacanthus anglicus*, a climatiiform from the United Kingdom, in a ventral view of the head. (e) and (f) are a drawing and a photograph respectively of the whole specimen; (g) and (h) are a photograph and drawing respectively of the area of preserved braincase. Scale bar in (e) and (h) is 10 mm. (a–c) modified from Davis *et al.* (2012), (d) courtesy of the Natural History Museum, London; (g–h) modified from Brazeau (2009).

Traditionally, the acanthodians have been split into three groups: the Climatiiformes, the Ischnacanthiformes and the Acanthodiformes. The Climatiiformes (Fig. 1a) comprise the oldest of these groups, and are particularly well known from the Lower Devonian of the United Kingdom. They have heavy armour surrounding the pectoral fins (see Fig. 2c) and teeth arranged in a whorl-like series like those of modern sharks, as well as a series of intermediate spines stretching between the pectoral and pelvic fins. The most notable character of the Ischnacanthiformes (Fig. 1d) is their dentigerous jawbone — a bony lower jaw with teeth fused to it (Fig. 2e), which they possessed in addition to tooth whorls. Some spectacular ischnacanthiform fossils have been described from the MOTH locality in northwestern Canada (Fig. 3a), which show how these jaws and teeth were adapted to different feeding styles in different species. Finally, the Acanthodiformes (Fig. 1b) seem to have been specialized for filter-feeding, possessing no teeth, rakers on their gill arches and only one dorsal fin. They were the latest-surviving of the acanthodian groups, existing from the Early Devonian to the Late Permian.

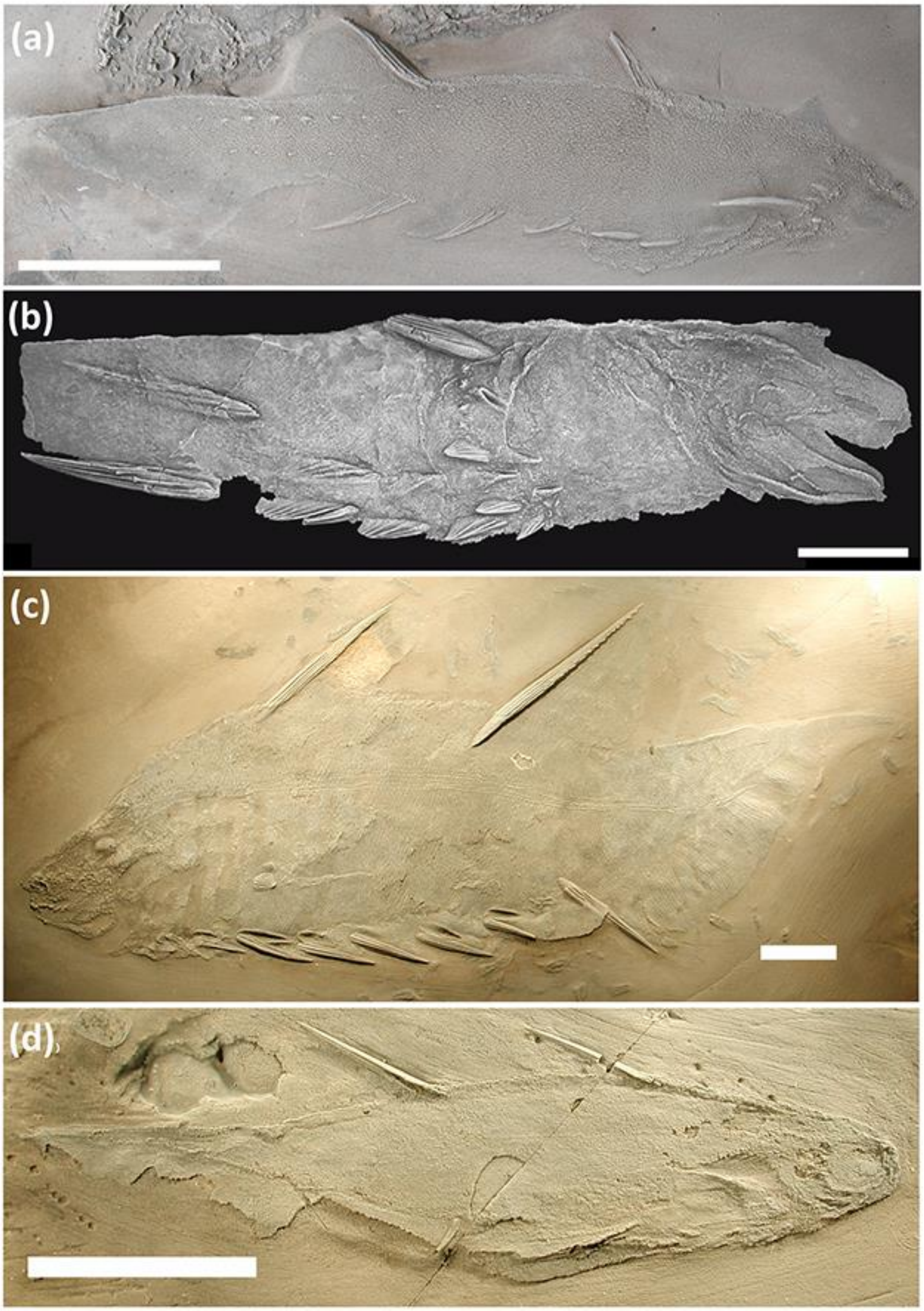


Figure 5 — MOTH acanthodians with odd morphologies. (a) *Lupopsyrus pygmaeus*; (b) *Kathemacanthus rosulentus*; (c) *Brochoadmones milesi*; (d) *Paucicanthus vanelsti*. Scale bars are 10 mm. Photos (a), (c) and (d) by G. Hanke, Victoria, British Columbia; photo (b) from Hanke and Wilson (2010).

Because of their generally poor fossilization, the internal anatomy of acanthodians is known chiefly from a single fossil species of acanthodiform, *Acanthodes bronni*, which has a skeleton that was at least partly made from bone. Acanthodes preserves details of the backbone, the fin skeleton and the braincase (the part of the skull housing the brain). The last of these features is perhaps the most interesting, because it reveals a great many anatomical characters that can be compared to those of other groups of early vertebrates. Indeed, the braincase of *Acanthodes* displays an unusual combination of traditionally chondrichthyan and osteichthyan characteristics (Fig. 4a–d). Features such as a dorsal (top) ridge at the rear of the braincase are shared with chondrichthyans, whereas the braincase's overall shape and bony nature are more typical of osteichthyans. Still other features, such as the otico-occipital fissure separating the rear of the braincase from the main part, are shared with both early chondrichthyans and osteichthyans. The only other acanthodian braincase that is known in any detail is that of *Ptomacanthus anglicus*, an Early Devonian acanthodian from the Welsh Borders (Fig. 4e–h). It shows a very different anatomical makeup to that of *Acanthodes*, sharing some features, such as the arrangement of the entrances for the internal carotid arteries, with placoderms — extinct, heavily armoured fishes that lived during the Silurian and Devonian. The disparity in the two known acanthodian braincases hints at a more complex pattern of relationships than superficial similarities in spines and scales would suggest.

Further muddying the waters are a number of other acanthodian-like fishes that cannot easily be placed into one of the three traditional groups on the basis of their external appearance. Some acanthodians from the MOTH locality are remarkably similar to the familiar acanthodian groups we've already seen (for example, ischnacanthiforms and *Uraniacanthus*; Fig. 3a,b), but others are less easily understood. Fossils such as *Lupopsyrus* (Fig. 5a) and *Kathemacanthus* (Fig. 5b) have acanthodian-like spines but scales with similarities to those of chondrichthyans. *Broachoadmones* (Fig. 5c) is climatiiform-like, but lacks armour around the pectoral fins. *Paucicanthus* (Fig. 5d) is broadly acanthodian-like, but has no paired fin spines. All of these fossils combine external features of different groups of fishes, 'acanthodian' and otherwise. Together with what we know of acanthodian internal morphology, this suggests that the relationships of acanthodians are not as clear cut as the traditional grouping might make it seem.

## Why is this important?

Acanthodians are important to evolutionary biologists and palaeontologists because they can shed light on the early evolution of jawed vertebrates. The jawed vertebrates make up the vast majority of vertebrates alive today; their jawless cousins, the hagfishes and lampreys, are much less diverse and have highly specialized lifestyles. Consequently, the evolution of jawed vertebrates is particularly intriguing: how and why did the jawed vertebrates become so successful? It seems likely that their success was built on key evolutionary innovations such as jaws, a bony skeleton and paired fins: all features that are unique to the jawed vertebrates. So, to understand their success, we first need to get to grips with how these innovations arose.

The difficulty with studying the evolution of the jawed-vertebrate body plan is that the two modern groups, chondrichthyans and osteichthyans, are separated by at least 420 million years of evolution. This has proved to be plenty of time for each group to become so specialized that it is no longer of much use for working out the early stages of its own evolutionary history. Fortunately, the fossil record provides windows into the past, showing us the morphologies of organisms spanning this critical period, and allowing us to work out how the body plans of modern groups were assembled. This makes the anatomy of groups such as the acanthodians, and other early jawed fishes like the placoderms, crucial to reconstructing the evolution of jawed vertebrates. However, to be able to interpret the information that these groups provide, we must first understand their evolutionary relationships to the other jawed vertebrates: we need to fit the acanthodians into the vertebrate family tree.

## What, if anything, is an acanthodian?

Phylogenetic analyses of the genes of living vertebrates tell us that the osteichthyans and chondrichthyans are sister groups; that is, they are more closely related to each other (share a more recent common ancestor) than either is to the next most closely related living group, the jawless vertebrates (Fig. 6). The acanthodians, with jaws and paired fins, clearly fit into this scheme somewhere around the jawed vertebrates, but finding out exactly where is problematic. Because we have no genetic data for fossil forms, we have to base our ideas about their relationships on their preserved morphology, and this is used to generate hypotheses about evolutionary relationships, also known as phylogenetic trees.

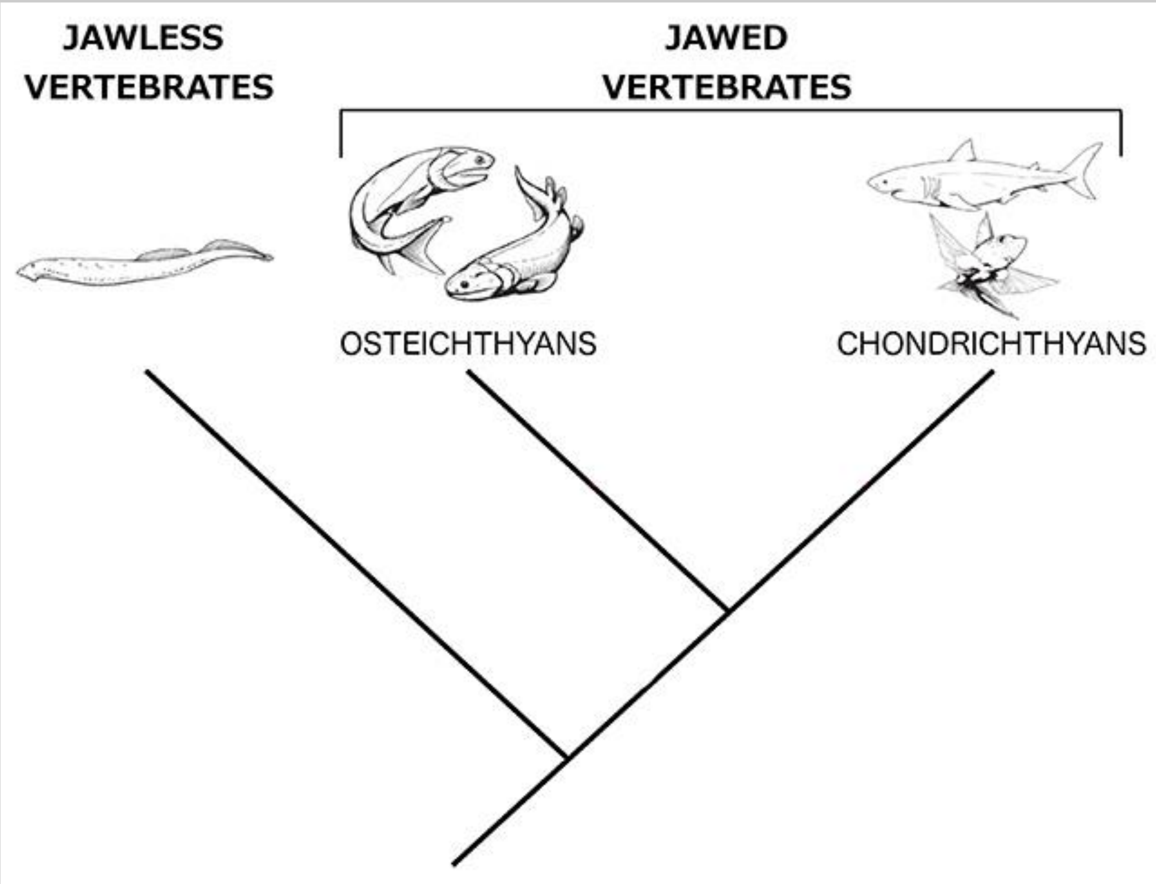


Figure 6 — Phylogenetic relationships of living vertebrates. Images from Brazeau and Friedman (2014).

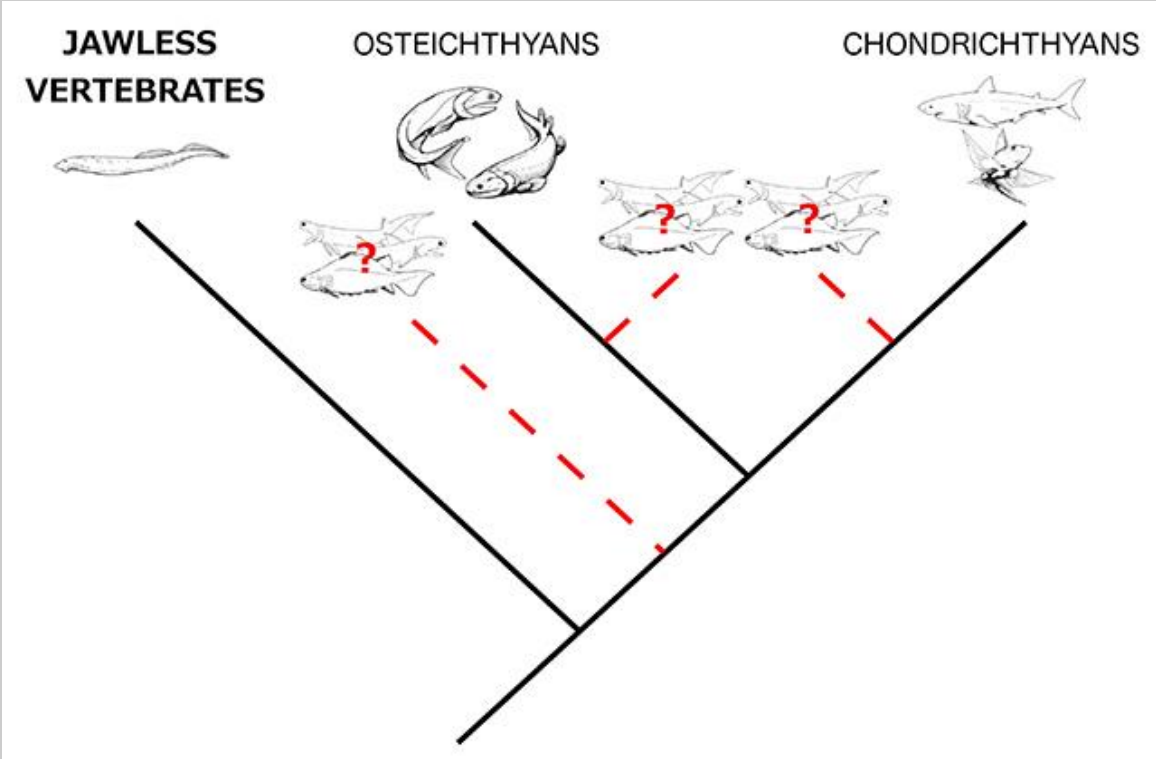


Figure 7 — Possible positions of acanthodians within vertebrate phylogeny. Note that the positions do not necessarily indicate monophyletic groups, and are not mutually exclusive, so acanthodians could form a paraphyly with some acanthodians more closely related to osteichthyans and others more closely related to chondrichthyans. Images from Brazeau and Friedman (2014), modified from Brazeau (2012), and redrawn from Long (1986) and Watson (1937).

Our idea of exactly where acanthodians fit into the phylogenetic tree of jawed vertebrates has varied ever since the group was first described, with competing ideas placing them with the chondrichthyans, with the osteichthyans and sometimes with extinct groups such as the placoderms (Fig. 7). One thing that united all of these past ideas was the more or less unchallenged assumption that acanthodians formed a monophyletic group: a group made up of all the descendants of a common ancestor (like today's jawed vertebrates as a whole; osteichthyans and chondrichthyans). In recent years, however, this assumption has repeatedly been tested in phylogenetic analyses, and acanthodians have been repeatedly found to be paraphyletic — that is, a series of monophyletic subgroups that are spread throughout the jawed-vertebrate tree (Fig. 7).

Evidence has been building that these smaller groups of acanthodians are most closely related to the chondrichthyans. Redescription of important acanthodian fossils, including *Ptomacanthus* and *Acanthodes*, demonstrates that acanthodians have a less osteichthyan-like braincase than was previously thought. Fossils are also being described that blur the line between what we know about the anatomy of chondrichthyans and acanthodians, such as *Kathemacanthus* with its chondrichthyan-like scales, as well as early sharks such as *Doliodus* that have acanthodian-like paired fin spines. Furthermore, there is building evidence suggesting that the common ancestor of bony and cartilaginous fishes had large dermal plates rather than small, acanthodian-like scales. This would make micromeric dermal armour a shared character that unites traditional chondrichthyans and acanthodians.

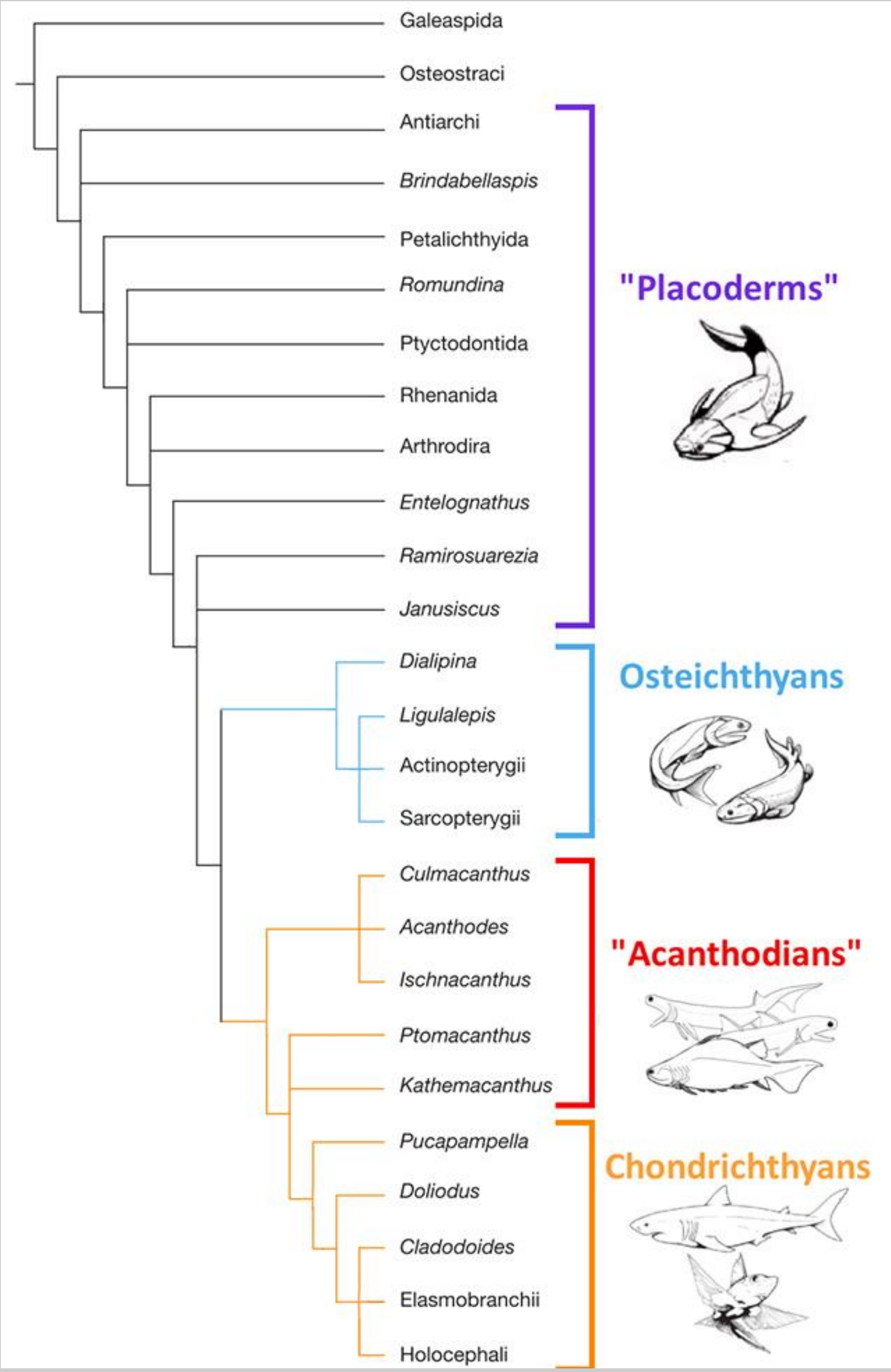


Figure 8 — The tree recovered in the most recent major phylogenetic analysis of fossil jawed vertebrates, Giles *et al.* (2015). Acanthodians are placed as a paraphyly along the chondrichthyan stem. If correct, this means that for all intents and purposes, acanthodians are chondrichthyans. Images taken from Brazeau and Friedman (2014), and Brazeau and Friedman (2015).

The upshot of all this is that it now seems likely that what have been called acanthodians are actually a series of smaller groups that branched off during the early evolution of cartilaginous fishes, and this has been borne out in phylogenetic analyses (Fig. 8). Historically, the cartilaginous fishes have been seen as the more ‘primitive’ of the two groups of modern jawed vertebrates, and so have often been taken as a model of what the ancestral jawed vertebrate would have looked like. We now know that this is not the case: acanthodians (and other early jawed vertebrates) show us that the common ancestor of today’s jawed fishes would not actually have looked particularly chondrichthyan-like, but was instead a morphological hotchpotch, displaying a mixture of chondrichthyan and osteichthyan characters. By placing the acanthodians into a phylogenetic context, we gain insight that we would otherwise have missed into the early evolution of jawed fishes.

## Future prospects:

Despite these advances, there remains a lot to learn about the enigmatic acanthodians. Our knowledge of their internal anatomy is still mainly based on a single animal, *Acanthodes*; this is problematic because *Acanthodes* was a very late-occurring acanthodian, which had doubtless evolved many adaptations to its specialized filter-feeding lifestyle. Furthermore, we still have no clear idea of how the groups that make up the acanthodians are related to one another and to the chondrichthyans, and so exactly how the chondrichthyan body plan was assembled remains ambiguous. Indeed, it is not impossible that acanthodians could turn out to be a monophyletic group after all. Currently, an effort is under way to redescribe many species of well-preserved acanthodian in greater detail, with the ultimate aim of improving our understanding of their relationship to other jawed vertebrates. Alongside the discovery of new taxa fossils from key localities such as MOTH, this will hopefully lead to a clearer picture of exactly what acanthodians are, with further implications for our knowledge of early jawed-vertebrate evolution.

## Acknowledgements:

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## Suggestions for further reading:

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