When fish wore armour: enter the Placoderms

Armour was all the fashion of the day in the Silurian and Devonian periods and is particularly associated with a group of heavily armoured fish, the Placoderms. This group of highly successful animals lived from early Silurian through to the end of the Devonian (443.8 – 358.9 Ma ago).

In comparison with animals met in previous articles, we are now describing animals with unmistakable vertebrate features: the dorsal nerve cord is surrounded by a calcareous structure forming a vertebral column, the first 3 gill arches have been used by that jobbing builder, Mr Evolution, as a structure to support a jaw complete with hard apatite (real name of material, how appropriate!) containing teeth. Externally, paired fins develop and through time there are internal structures to support them: bony rays in the fins and girdles of bone to attach the fins to the vertebral column. It is interesting that these still primitive animals show evidence of internal fertilisation and live birth. Placoderm males had pelvic fins (that's the ones at the rear of the animal, not visible in the photo below) which were used to transfer sperm into the females and fossils have been found of Placoderm females who apparently died at the time of giving birth.

Bothriolepis panderi: Devonian, Northwest-Russia, Novgorod-Region (also a similar example in Oxford University Museum)

Credit: Haplochromis – Wikipedia Commons

To top it off, Placoderms also had 3 "eyes": two of the usual sort and a third, the Pineal, which may have been used to orientate the animal in relation to the direction of light. The pineal is an interesting appendage of the mid brain and is shared feature amongst nearly all vertebrates including ourselves. Rather than being an organ of sight, an alternative opinion is that it may have secretory significance in the same way as do endocrine glands since in modern vertebrates it secretes Melatonin, a hormone responsible for many cyclic processes such as seasonal breeding and Circadian Rhythm.

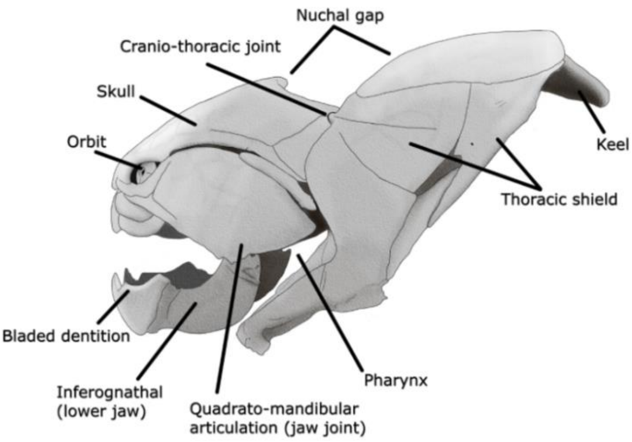
Although Placoderms possessed jaws with teeth, the teeth were positioned medially so that their use appears to have been more holding prey than biting chunks off. However, predation and biting was certainly the order of the day for some Placoderms, let me introduce you to *Dunkleosteus*, 6m long, biting force 7,400N at the blade edge. Contrast this figure with that of modern lions, hyenas and tigers which have bite forces of around 4,450N, however the Salt water Crocodile and Great White Shark take the biscuit with a biting force of around 16,460N. Humans have a puny bite force of around 800N.

What a beauty! Reconstruction of the fossil Placoderm *Dunkleosteus terreli*

Credit: Mateo De Stefano, Science Museum of Trento, Italy. Wikipedia Creative Commons.

The evident “teeth” are bone plates, as you can see in the fossil skull and the diagram

Credit: Zachi Evenor (photo Vienna Natural History Museum), Wikipedia commons



Credit: Steveoc 86 A skull diagram of the placoderm fish *Dunkleosteus*. (Based on figure 1 in Anderson, P.S.L. and Westneat, M.W. (2006) "Feeding mechanics and bite force modelling of the skull of *Dunkleosteus terrelli*, an ancient apex predator", Biology letters, pp 76-79)

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Notice the “Nuchal Gap” in the diagram. It is thought that this allowed the head to flex backwards to open the mouth very wide before the bite. Such behaviour would draw prey into the mouth before the bite.

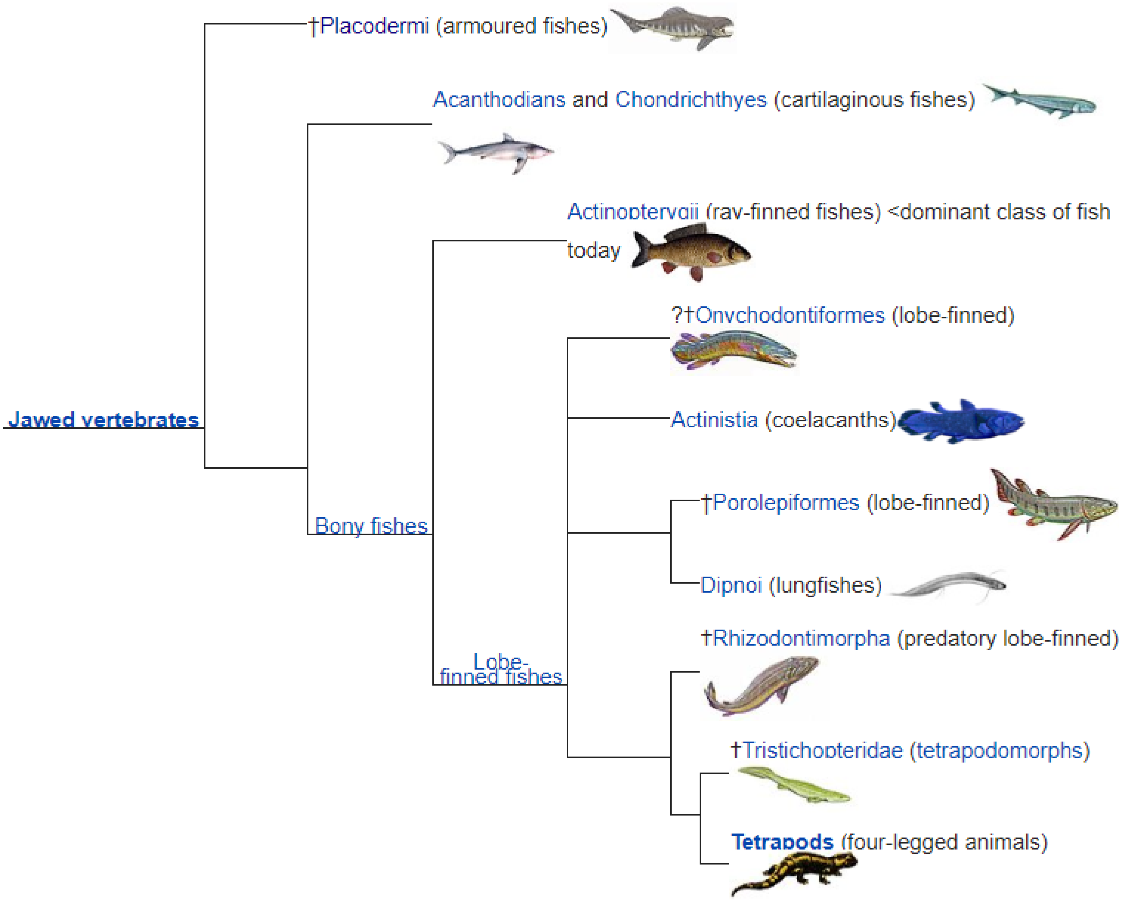
Notwithstanding the intimidating adaptations of some of the Placoderms, they went extinct at the end of the Devonian possibly when sea levels dropped because of land ice formation during global cooling. This or other calamities, such as meteorite impact or large scale volcanic eruption, is thought to have caused a reduction in oxygen and triggered a mass extinction, the “Hangenberg Event”.

How do you like Fish Fingers?

Mass extinctions are times of Biological opportunity: ecosystems collapse exposing gaps soon filled by survivors, which in turn adapt. What can we do to avoid our fate? Nothing, our part is that of the mystical "Wanderer" of European legend, passing through vast spaces of time, a half blind spectator unable to deflect evolution's ruthless application of rules we cannot change that will in time have hidden writing for our species too. This knowledge is the true burden of being Human.

The cladogram below shows the relationships between the fishy groups, notice that we need to leave the Placoderms and follow the adventures of the Bony Fish, the Osteichthyes to trace the origins of the tetrapods.

Credit: wikipedia.org/wiki/Evolution_of_fish



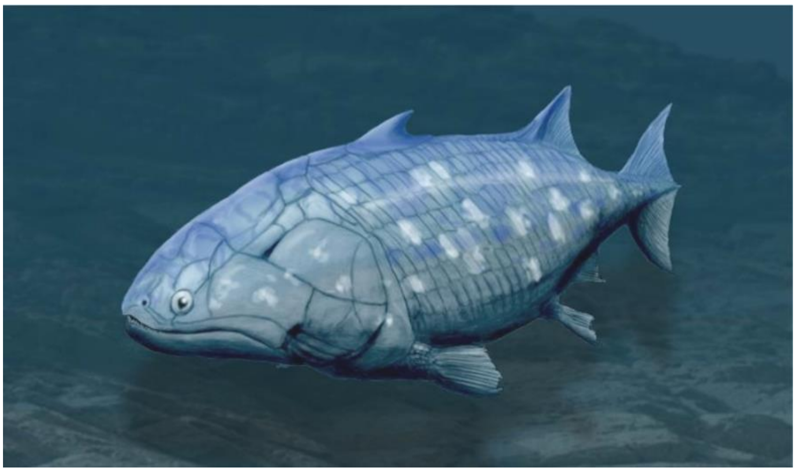
† indicates extinct group

The cartilaginous fish are today represented by sharks and rays

From this Cladogram, you could say that we and other tetrapods are just a type of fish! This is a serious biological classification problem. It shows the difficulty of bringing together traditional classification where groupings are based on similar visible attributes (for example, mammalian skin, reptilian scales) and Cladistics, a classification which is based on inheritance through genetic relationships. With cladistics, the placement of sub groups depends very much on your starting point. Starting with gnathostomes (jawed vertebrates) as in the cladogram above, the Tetrapods are a group within the clade Bony Fish. However if you move the starting point back into the Cambrian or further to the Precambrian, even Bony Fish become a small insignificant group within the vast number of genetically related groups of animals to have arisen over such a huge space of time.

To find where the bony fish originate, we need to move back 419Ma ago to the late Silurian. Recent fossil finds by Zhu and others in Yunnan, China have identified an ancestor from the marine rocks of the Kuanti formation; this was dated using Conodont fossils (see Bioblog 23). This fossil, despite its age, is remarkably complete and important to us not only as an early bony fish, but also as an animal with the hidden potential to make Tetrapod life possible: limbs.

Credit: Arthur Weasley, Wikimedia Commons



This is *Guiyu oneiros* which translated means Ghost Dream.

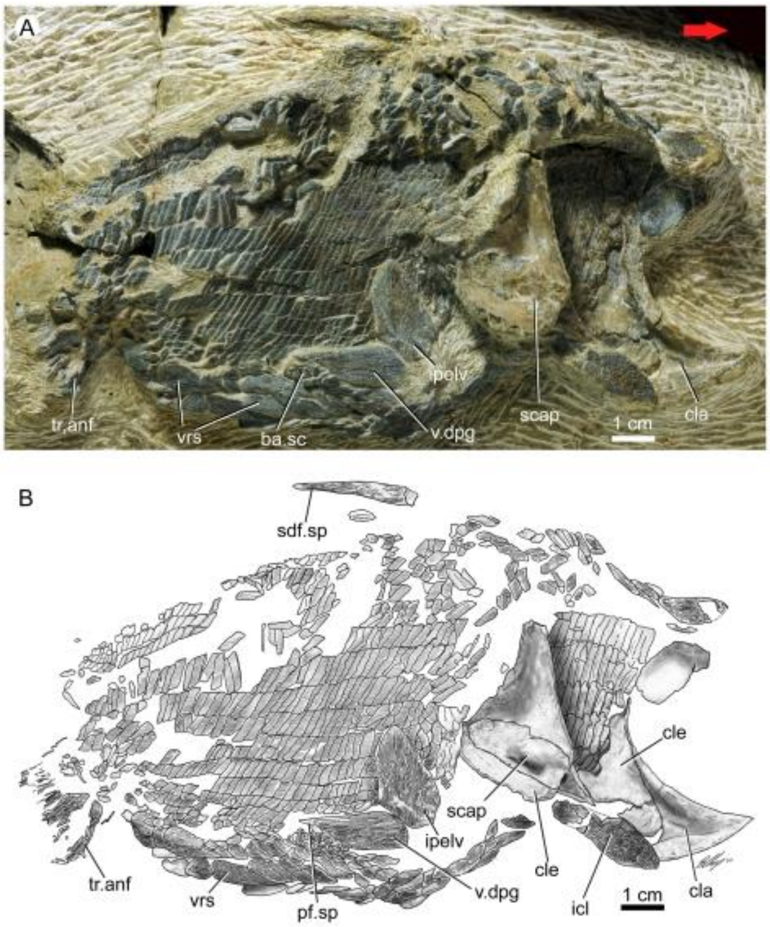
And an evolutionary biologist's dream it certainly is. The fossil was found as an articulated skeleton missing only its caudal (tail) fin. Have a look at the artist's reconstruction and then compare this to the next image of the modern Coelacanth,

Credit:Sybarite48, Wikimedia Commons

This is a picture of *Latimeria chalumnae*. The parts of the animals to compare are the fins. Notice how in both animals, pectoral and pelvic fins emerge from the body on a "stalk". These are "Lobe Fin Fish" and important because they are direct ancestors to the Tetrapods. You can't see the significance in these views and we have to look at the skeleton to see the incredible truth.

Here is a picture of part of the original Chinese fossil, lying on its left side with the dorsal side uppermost, remember that the fossil of this remarkable animal is 419Ma old, given the time interval, a good looking pensioner! Below the fossil picture is an interpretive drawing.

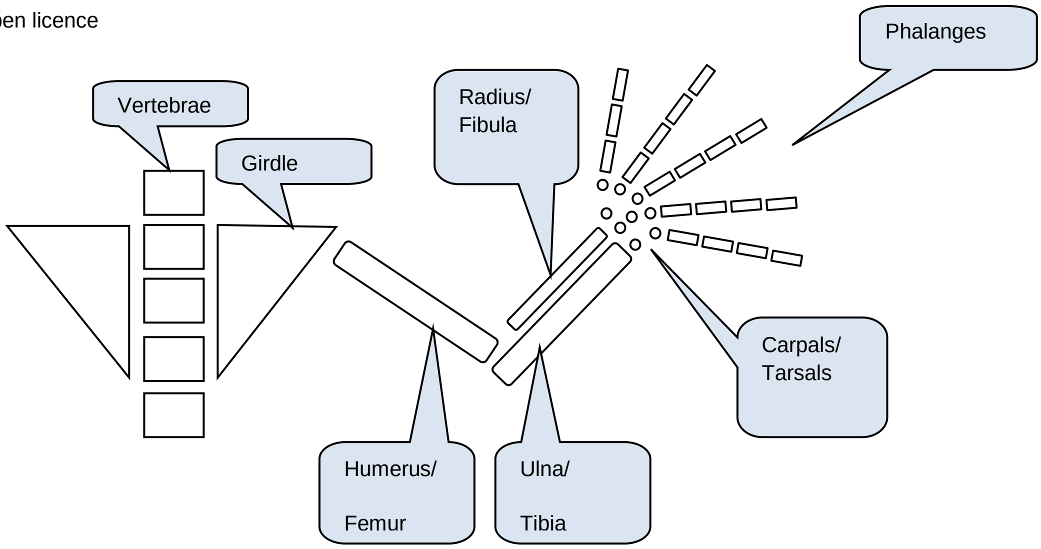
Credit: *Guiyu oneiros* Zhu et al., 2009, Published in PLosOne (2012), an Open Access Journal



A. New articulated specimen of *Guiyu oneiros* (V17914, lateral view) from the Kuanti Formation (Late Ludlow, Silurian), Qujing, Yunnan, showing a right dermal pelvic girdle in near-natural position. Red arrow points to the anterior end of the fish. **B.** Interpretative drawing. **Abbreviations**: **ba.sc**, basal scales of pelvic fin; **cla**, clavicle; **cle**, cleithrum; **icl**, interclavicle; **ipelv**, interpelvic plate; **pelv.sp**, pelvic fin spine; **scap**, scapulocoracoid; **sdf.sp**, second dorsal fin spine; **tr.anf**, lepidotrichia of anal fin; **v.dpg**, ventral lamina of dermal pelvic girdle; **vrs**, ventral ridge scale.

What excites the Paleobiologists is the evidence of internal girdle structures, let's remind ourselves of the classical structure of the tetrapod limb:

Credit: Self, open licence

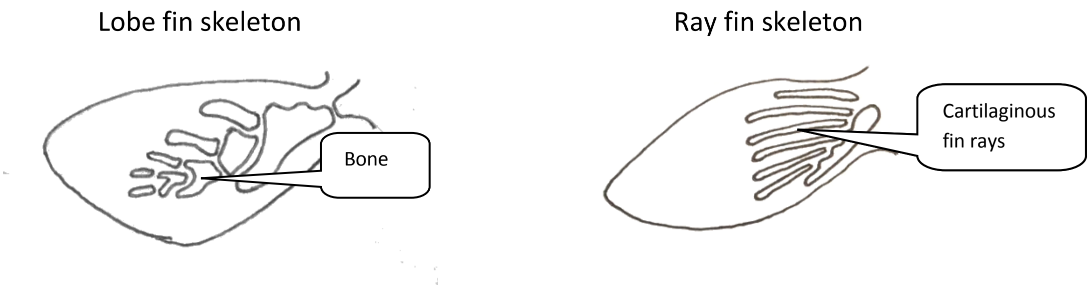


Modern tetrapods have pectoral and pelvic girdles consisting of several bones which form two bony rings attached to the vertebral column, followed by similar limb structure both in hind and fore limb of one bone followed by two and ending in 5 digits. The above diagrams is of just one limb and the labels show the name for the fore limb bone followed by the hind limb bone.

Here are some drawings of the internal structure of fins from Lobe Fin and Ray Fin fish, you can see that the lobe fin variety shows internal bone structure as in the classical tetrapod limb shown above, whereas the ray fin lacks bone, its structure reliant on cartilaginous rays:

Bony Fish Fins

Credit: Self, open licence



You can see the differences, in the Lobe fin there are obvious skeletal elements whereas the ray fin is supported by thin rays. We cannot see how the fish use these fins in locomotion without referring to modern examples of lobe and ray fin fish.

In both types of fish the major propulsion comes from the caudal tail, wagged from side to side by the musculature of the body, steering the fish is done by the fins. There is a difference though, in both living types of lobe fin fish, the fins enable the modern day animal to crawl along the bottom, in the case of the Lung Fish (see above Cladogram) this enables the animal to exit a drying out pond and crawl to new one or even bury itself in mud to survive a dry season.

When looking at the Coelacanth as a “Living Fossil”, that is an animal unchanged from earlier times, in this case over 400Ma, we need to be cautious and ask more searching questions. You see, the modern Coelacanth may look like the real deal and match those lobe fin ancestors found in the fossil record, BUT could modern Coelacanths have evolved recently to match the ancient fossil remains? After all, the environmental pressures could well be the same for both a modern and a genetically totally unrelated ancient animal; they would independently evolve to match both the environment **and** evolve **similar structures** to deal with it, but remaining evolutionary unrelated to each other. This situation is called Convergent Evolution. To guard against confusing similarity of structure in two organisms with true evolutionary relationship, we have to investigate how likely it is that the original genome (that is the original DNA coding) of the ancestor has remained intact and is now represented in the modern possible relative. Obviously we do not have access to ancient DNA, we have to look for genetic stability in the modern animal of this possible relationship. In the case of modern Coelacanths they do not show this. We could be looking at an impostor! However, there are the undoubted structural similarities such as the lobe fins; you don’t have to demolish the whole story, just use some caution based on scientific methodology.

The fossil record remains, and its similarity to definite pentadactyl skeleton structure of later animals is clear as we will see. However, does modern genetics help us to account for the development of the pentadactyl limb structure? How could such an assembly of bones arise through pure chance genetic changes? After all, the pentadactyl limb wouldn’t function with just one bone, it needs the complete structure and that would involve simultaneous change in a whole swathe of genes.

Here comes the answer!

All Bilaterians, that means all animals that have similar structures either side of their bodies (think of a worm or a human), have their bilateral shape organised by a similar set of genes called Homeobox genes or Hox for short. These appear to be a very ancient part of the genome of possibly all organisms, plant, animal and even single celled eukaryotes. Hox genes occur in 4 clusters, HoxA, HoxB, HoxC and HoxD. Limb development in vertebrates is controlled ("patterned" is the term used in the trade!) by HoxA and HoxD. It's genes within the HoxD cluster, Hoxd9 to Hoxd13 that are specifically involved in patterning the limb whether it is a developing fish fin or a Tetrapod limb. Expression of these genes is controlled by other sections of the DNA helix called non-coding regulatory units (CREs). The CREs do not code for protein synthesis, but instead act as enhancers of genes of the HoxD cluster. It appears that the DNA helix twists so that individual genes of the HoxD cluster register with its CRE. Several of these CREs have been identified and, rivetingly, expression of HoxD13 gene in **mice** is turned on by the CRE extracted from a **Coelacanth**. You see where this is going … if Coelacanths represent animals just before limbs were developed, then they already had the potential to turn on the genes for limb development in a Tetrapod, that is **no new genetic code was needed**, development of legs rather than fins is a matter of regulation of the existing code. Timing seems to be crucial since some of the genes HoxD cluster cause fin ray production while others have the reverse effect, reducing fin ray and instead causing cartilage growth body side of the fin. This cartilage is later suffused with calcium salts and becomes bone.

As you can imagine, this is a hot research topic and although the above represents contemporary thoughts, the landscape is rapidly evolving.

Well, enough of the fishy Devonian and onward to the damp Carboniferous! The Carboniferous was where Tetrapods first explored ecological niches on land, but like all geological periods, it didn't end well. How these early land cruisers dealt with the arid times at the end of the Carboniferous is also something for us to look at.

Until then,

Sphenodon.