Fish Like Me

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Placoderms are the iconic prehistoric fish from the Devonian. Recent 3D scans have revealed their astonishing anatomical similarities with us humans.

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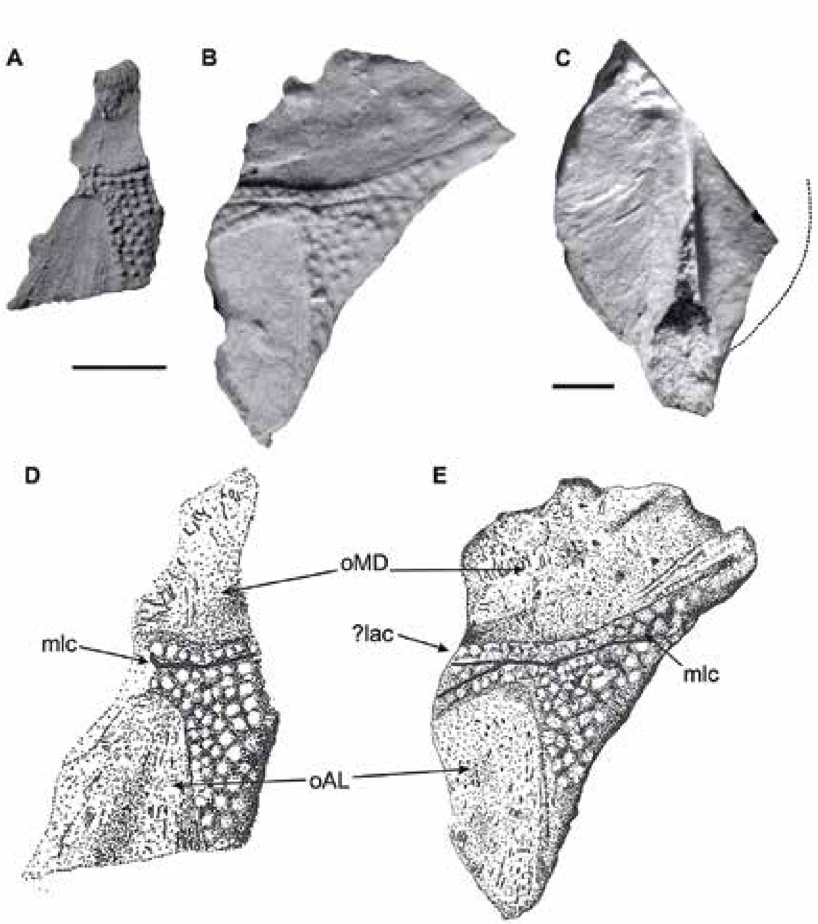
The Devonian – the geological era spanning the period of between 420 and 360 million years ago – is frequently dubbed the Age of Fish. Apart from the aquatic vertebrates as we know them today (bony and cartilaginous fishes), the planet's seas and oceans were also home to two other classes: Acanthodii and placoderms. Both are now extinct, but their fossils have been studied extensively.

Placoderms first appeared in the Early Silurian as small demersal fishes in shallow, brackish waters. They were a highly diverse group – hardly a surprise, given that they existed for around 70 million years. They were present all over the globe and inhabited almost all marine ecological niches; they ranged from active predators several meters in length, to creatures between one and two meters long feeding on invertebrates, to bottom feeders just a centimeter or so long. Their evolution shows clear signs of an increasing drive to inhabit marine environments, and in late Devonian, large predators reached the top of the marine food pyramid. Placoderms also made a secondary move back to more brackish environments, and representatives of Ptyctodontida even found their way into freshwater rivers.

Placoderms' heads and thoraxes were covered by articulated armored plates. These plates, which served as the animals' exoskeleton, are the most commonly fossilized remains. In ostracoderms (armoured jawless fish from the Paleozoic, predating placoderms), such armor had protected the animals and served as store of mineral salts, but its role changed significantly during the course of evolution. Apart from the armor, the bodies of placoderms were sometimes covered with scales of all shapes, sizes and ornamentations. However, apart from a few species in the Antiarcha and Rhenanida orders, the majority of placoderms were naked.

For a long time, evolutionary biologists were not especially interested in placoderms. The fish were widely regarded as a primitive evolutionary dead-end whose morphology made little or no contribution to current vertebrate structure and anatomy. It was only the influence of placoderms on the ecosystems of Devonian oceans which remained undisputed – until the publication of paleontological discoveries in China. They originate from the Yunnan province during the late Silurian, when different kinds of aquatic vertebrates were emerging.

The advent of jawed fishes was one of the most important turning points in vertebrate evolution. Armed with newly fangled jaws, fish rapidly became alpha predators in their food chain. Placoderms dominated almost all aquatic environment in the Devonian and created the first vertebrate superpredator *Dunkleosteus*, which could reach up to ten meters in length. However, fossil remains of placoderms originating from the preceding Silurian are incredibly rare. The Yunnan fossils date back to that period; the earliest articulated bony fish, known as the *Guiyu oneiros*, and the *Entelognathus primordialis* plac-



Silicone casts of elements of placoderm skeletons from Lower Devonian placoderm sandstones found in the Holy Cross Mountains (A, B, C) with sketched interpretations (D and E).

oderm are regarded as key in solving evolutionary puzzles. Both fossils are an anatomical mosaic linking extinct placoderms and bony fish living today. In cladistical terms, the latter group also includes humans. The *Entelognathus* jaw, or more specifically the structure and composition of the bones, is a mystery for evolutionary biologists.

Jaw-dropping

So which came first: the complex structure of the first jaws comprising several bones – as in *Entelognathus* and bony fishes – or simple single-bone jaws as in the majority of placoderms? If the first jaws were indeed complex, then the earliest known complete placoderms were more advanced than all later placoderms. Phylogenetic analyses place the *Entelognathus* as a sister group to all higher gnathostomata (jawed vertebrates), to certain placoderms and all higher gnathostomata, or a direct sister group to bony fishes.

The recent discovery of the *Qilinyu* placoderm in China, made by the team led by Min Zhu, has shed some light on the problem. In contrast to the *Entelognathus*, the *Qilinyu's* lower jaw was a single bone while the upper comprised two bones, as is the case in other placoderms. The paper describes them as maxilla and premaxilla, reflecting the similarity to bony fishes; in humans the maxilla and premaxilla are fused with the cranium and there is a single mandible. In *Qilinyu* we see the next stage of the evolution of jaws in placoderms, with the external bony layer starting to strengthen the jaw (Meckel cartilage). The tendency is most advanced in the *Entelognathus*. The simplicity of placoderm jaws is regarded as a primitive trait for vertebrate because they didn't have an external bony covering. *Qilinyu* offers a good explanation why other placoderms lost their complex jaw structure and how jaws evolved in bony fishes. This improves the homology between elements of jaws of placoderms and bony fishes. The *Qilinyu* cheek also reveals the lacrimal bone, found in the *Entelognathus* and early bony fishes but absent in all other placoderms. *Qilinyu* also provides the first hard evidence that early placoderms had paired ventral fins – the precursor to hind limbs in quadrupeds. Recent research reveals that they were also the first vertebrates with external genitals. Some much later placoderms were also the first to give live birth.

Mountain discoveries

The extensive literature on placoderms includes several important publications on fossils discovered in Poland. While Upper Devonian placoderms have been described on numerous occasions (e.g. Szrek 2008), those from the Lower Devonian have a rather more complicated history.

The first placoderm fossils were discovered in the Holy Cross Mountains by Georg Gürich, German geologist from Wrocław who made a huge contribution to geology research in Poland. In 1896, he introduced the term "placoderm sandstone." He described some of the formations of the Lower Devonian found in the Holy Cross Mountains, rich in vertebrate fossils, with his search focusing on placoderms. Writing about Devonian formations in the mountain range (based on research near Bieliny and Łagów), he described placoderm sandstones in the lower layers, in which preserved fauna comprised "only remains of placoderms, less frequently ganoids representing families including *Drepanaspidae*, *Coccosteidae*, *Asterolepidae*, *Hybodontidae* (...) and *Machaeracanthus polonicus*". Gürich made no illustrations of the specimens he described, and since his papers were all lost during the two world wars, it is now impossible to offer any meaningful discussion on his comments. For some reason, representatives of jawless and cartilaginous fishes and acanthodians were all described as a single group even though they could be classified more precisely using existing taxonomy. This was likely done for simplicity's sake.

Telling imprints

Placoderm sandstone is an informal name for quartz-bearing sandstone comprising vertebrate fossils. However, only empty spaces where those remains were once contained remain until the present day, reflecting the morphology immediately after the organism was buried in sediment. How do we go about studying these voids? Until recently, researchers filled the gaps with a silicone mass, which, once set, provided an accurate representation of the original fossil. The main limitation of this method is that some of the imprints can only be accessed by breaking up the rock and thus reducing the number of casts which can be made. Tomography is a far more effective, non-invasive method gaining widespread use. As well as making it possible to examine all imprints, it also means their spatial arrangement can be studied, which helps establish how the remains were accumulated. Another major advantage is that it allows teams studying the same site from different locations to rapidly exchange information. In Poland this was tested last year, when a 3D scanner was used to scan traces of fish feeding, with imprints of their snouts, covered in soft tissue. The 3D scans circulated between Warsaw, Kraków, and Uppsala within a few seconds, significantly facilitating analysis and discussion.

It is in part thanks to the use of a 3D scanner that research on the fauna of the placoderm sandstones of the Holy Cross Mountains has gained significant momentum of late, 50 years after their discovery. After a series of studies and excavations, a number of issues have been understood concerning basic questions of their genesis and taxonomic composition. The Lower Devonian placoderm sandstones represent an accumulation of fossils of storm genesis. They cannot, therefore, be used to identify precise age. It has also become clear that placoderms as such represent only a 20% share of the boney material of the sandstones. Taxonomic composition research has also yielded interesting results. It turns out that the Holy Cross Mountain assemblage of Lower Devonian (Emsian) placoderms is very reminiscent of the deposits in Podole in Ukraine (the Lower Devonian – Lokhovian), with the former most likely being descendants of the latter.

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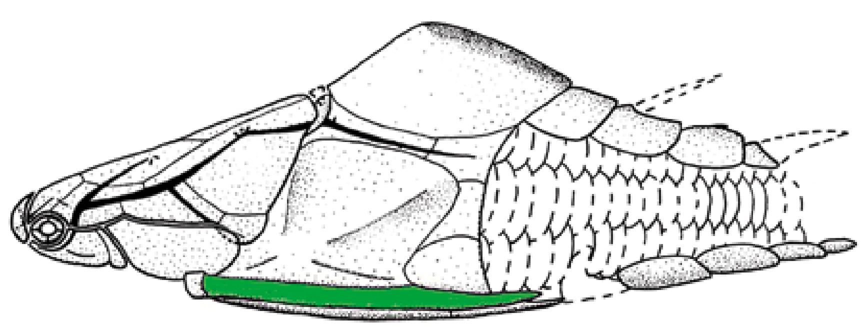
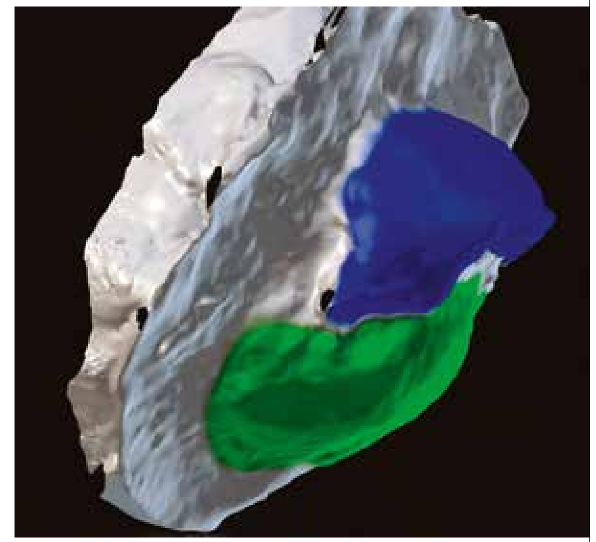
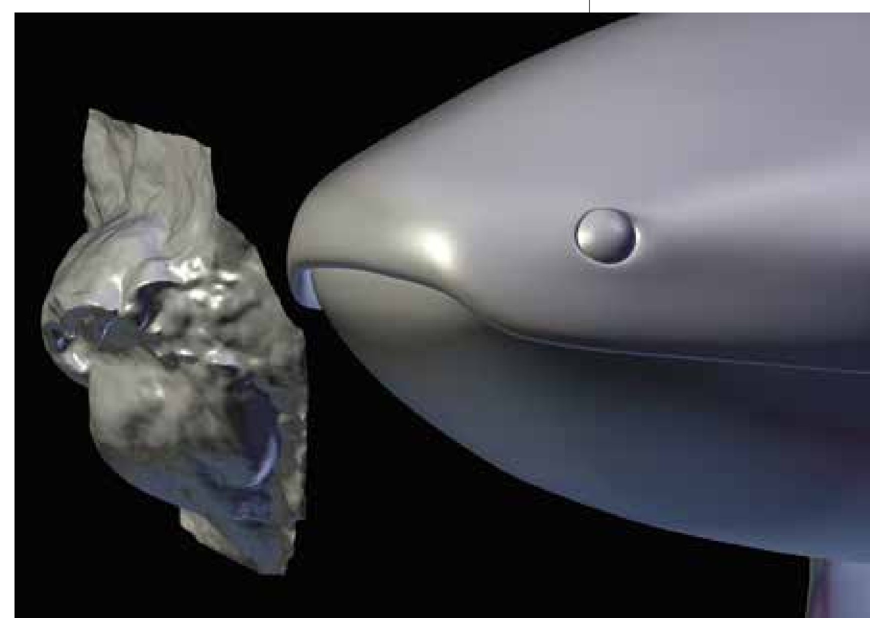


Artist's impression of Kujdanowiaspis – a placoderm whose remains were found in Lower Devonian deposits in the Podole region and in Holy Cross Mountains.



3D scan of a snout imprint of the *Osculichnus tarnowskae* lungfish found in Lower Devonian deposits in the Świętokrzyskie Mountains; lower jaw marked in green, upper jaw in blue



Fossil imprint made by *Osculichnus tarnowskae* (lungfish), with a reconstructed visualization of the likely culprit.

Further reading:

Long J. (2016). The first jaws. *Science* 354 (6310): 280–281.

Szrek P., Dupret V. (2017). Placoderms from the Early Devonian "placoderm sandstone" of the Holy Cross Mountains, Poland with biostratigraphical and palaeobiogeographical implications. *Acta Palaeontologica Polonica*. doi.org/10.4202/app.00395.2017

Zhu M., Ahlberg P. E., Pan Z., Zhu Y., Qiao T., Zhao W., Jia L., Lu J. (2016). A Silurian maxillate placoderm illuminates jaw evolution. *Science* 354 (6310): 334–336.