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Fossil Focus: Xiphosura

by Jason A. Dunlop [*1]

Introduction:

The Xiphosura are commonly known as horseshoe crabs because the front part of their bodies is horseshoe-shaped. They have sometimes been called king crabs, although this name is also used for a group of large true crabs. Despite their various common names, xiphosurans are not crustaceans. Older studies assumed that they were some sort of crab, mostly because they have gills and live in the sea, but careful anatomical studies towards the end of the nineteenth century showed that they are actually more closely related to arachnids. The name Xiphosura means 'sword tail' and refers to another obvious feature of these animals: a long, pointed tail spine. Horseshoe crabs — especially earlier fossil ones — also look quite a lot like trilobites. This has led to the suggestion that arachnids actually evolved from trilobites, but in modern studies this idea has fallen out of favour.

Morphology:

Living horseshoe crabs can be more than half a metre long when fully grown. The body is divided into a prosoma at the front and an opisthosoma, or abdomen, at the back (Fig. 1). The prosoma is covered from above by the prosomal dorsal shield, or carapace: this is the large, horseshoe-shaped plate that gives the group its common name. Towards the middle of the dorsal shield there is a raised area called the cardiac lobe. This bears two tiny eyes, sometimes called ocelli. Towards the sides of the dorsal shield run a pair of distinct 'ophthalmic' ridges. These carry the lateral, or side, eyes, which have many individual lenses like those of insects or crustaceans. In some fossil horseshoe crabs the ophthalmic ridges merge into long, backwards-pointing (ophthalmic) spines. The two 'corners' at the back of the dorsal shield are called the genal angles. In modern species each comes to a blunt point, but in some fossils they are stretched out into longer, backwards-pointing (genal) spines.

Turn a horseshoe crab over and its prosoma is rather like a soup bowl containing a series of legs. They feed by churning up sediment underneath themselves, and using their legs to grab any prey animals caught in the 'bowl' and to pass them into a food groove behind the mouth. This groove is formed by the first leg segments, called the coxae, which sit next to each other and bear rows of inward-facing teeth. These special 'chewing' coxae are called gnathobases and can be moved from side to side to break up food into small pieces, which are then passed forwards towards the mouth.

Xiphosurans have a similar pattern of limbs to the arachnids. The first two limbs, the chelicerae (Fig. 2), are small, three-segmented and claw-like. The second to sixth pairs of limbs are all considered walking legs, and in the living species they usually end in small pincers — although certain limbs in some modern species are not fully claw-shaped. The limbs have six segments, called, starting closest to the body, the coxa, trochanter, femur, patella, tibia and tarsus. The sixth limb of modern species is unusual for two reasons. First, it has a small, flap-like projection coming from the coxa, called the flabellum. This may be a remnant of when these animals' ancestors had two-branched (so-called biramous) limbs. Second, the limb has a series of blades towards the end: these spread out rather like a snow-shoe when the leg is placed on the ground. This sixth limb is often called the pusher and is thought to help push the animal forwards when it is walking on soft sediment.

FIGURE 1 - A VIEW OF THE TOP AND UNDERSIDE OF AN EXTANT HORSESHOE CRAB.

Modern horseshoe crabs also have a pair of tiny structures immediately behind the legs. These are called the chilaria and are thought to be highly reduced legs. They may help the feeding process by pushing a current of water along the food groove. Interestingly, some of the early fossil horseshoe crabs have fully developed legs in this position; thus they have seven pairs of 'prosomal' limbs, unlike the six seen in modern Xiphosura and arachnids. This 'extra' pair of limbs has led to some debate about where the prosoma/opisthosma boundary actually lies in horseshoe crabs.

It seems that the opisthosoma of the earliest xiphosurans consisted of 11 segments; these are easiest to see in fossils with clearly defined segment boundaries. You can still see segmentation in the larvae of the modern species, which are called trilobite larvae because they look like tiny trilobites. In the earliest horseshoe crabs, the last three segments of the opisthosoma seem to form a small tail end in front of the tail spine, whereas the other opisthosomal segments could move relative to one another (see Phylogeny, below) such that the animals could probably roll up a bit like a trilobite or a woodlouse. Later in the horsehoe crabs' evolution the three tail segments became less distinct and the whole top surface of the opisthosoma fused into a single plate. This plate has been called the thoracetron or tergum.

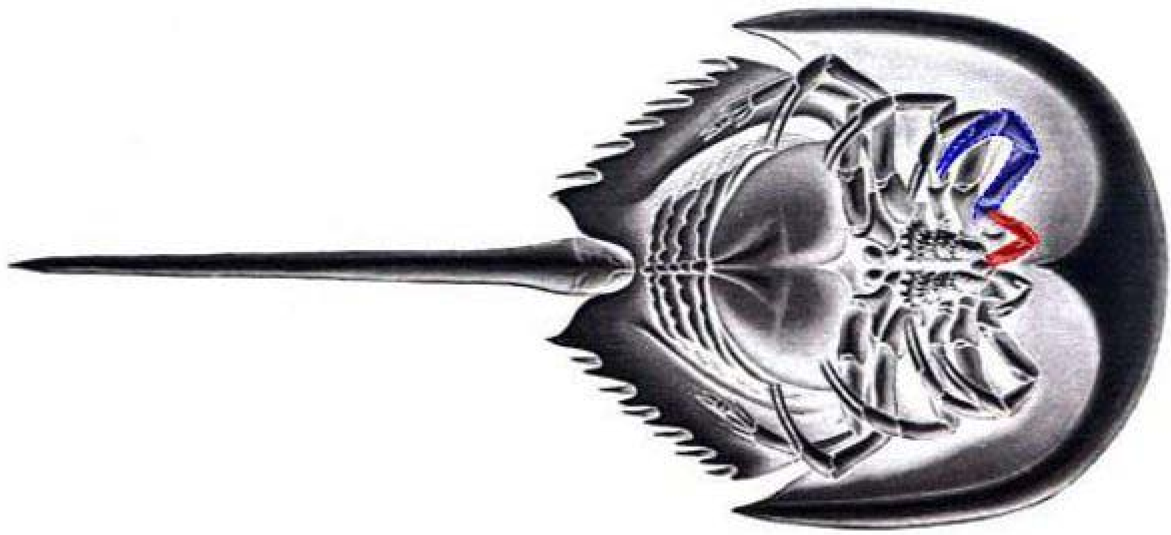

FIGURE 2 — THE CHELICERAE (COLOURED IN RED) AND FIRST WALKING LIMB (BLUE) OF A XIPHOSURAN.

In adults of modern species, segmentation is visible only as small indents in the exoskeleton of the thoracetron where internal muscles attach. The middle part of the thoraceron forms a central band, or axis — another feature that is quite trilobite-like and is easier to see in some of the fossils. The edges of the opisthosoma are often spiny. These can take the form of fixed spines, which do not move, or movable spines that sit in little sockets. The opisthosoma ends in the telson or tail spine. This tends to be short and wide in the fossils, and longer and thinner in the living species. If the animal gets turned over, it can use its tail spine to help to right itself.

Finally, on the underside of the opisthosoma there are a series of flap-like limbs. The first of these is called the genital operculum, and bears a pair of openings for the reproductive organs. The next five flaps bear pairs of gills. These are called book gills because they each consist of a stack of thin, flat sheets — like the pages of a book — which together provide a large surface area for the uptake of oxygen and the release of carbon dioxide. Juvenile horseshoe crabs can turn on their backs and swim by flapping these appendages.

Phylogeny:

The evolutionary relationships of horseshoe crabs are still debated. Traditionally, they were placed in class Merostomata, together with the extinct eurypterids (sea scorpions). Eurypterids may actually be closer to arachnids, so it is not clear whether merostomes really form a natural group. As noted above, horseshoe crabs were at one stage thought to be somehow intermediate between trilobites and arachnids (Fig. 3). However, trilobites have antennae, unlike arachnids or horseshoe crabs, so it may be better to place the trilobites on the evolutionary branch leading up towards myriapods, insects and crustaceans. Nevertheless, horseshoe crabs help us to imagine what arachnid ancestors may have been like. For example, these ancestors probably had gills and multifaceted eyes — although it should be stressed that modern Xiphosura are not ideal models for the origins of all the arachnids' anatomical features. In some respects they are more advanced than arachnids; for example, many arachnids still have segmented opisthosomae.

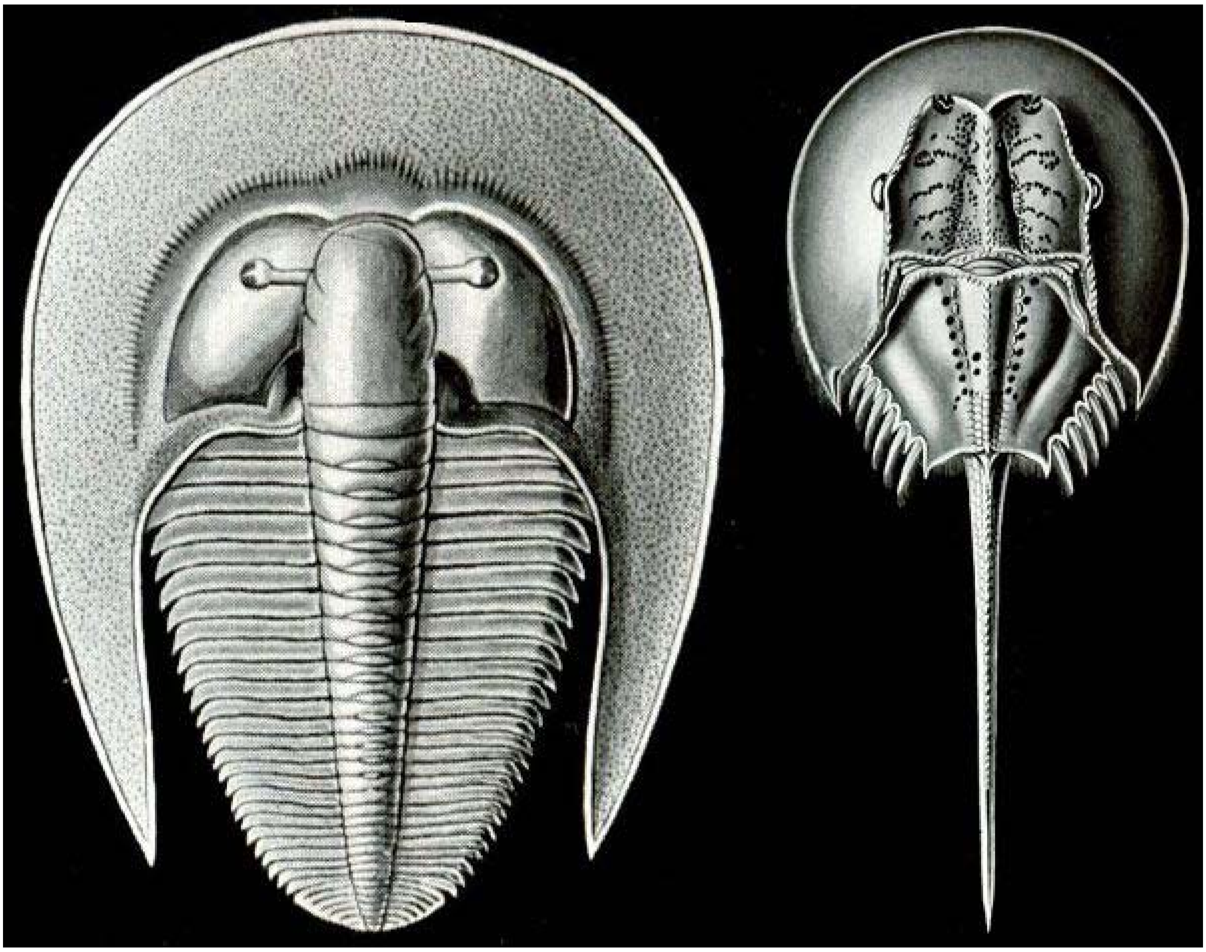

FIGURE 3 — A TRILOBITE (LEFT) AND HORSESHOE CRAB (RIGHT), WHICH ON THE BASIS OF THEIR SIMILAR APPEARANCE WERE TRADITIONALLY CONSIDERED RELATED. THIS IS LESS WIDELY SUPPORTED BY MODERN WORK.

Horseshoe crabs used to be split into two main orders: the primitive Synziphosurina and the more derived Xiphosurida. In fact, the synziphurines are probably not a natural group, but consist of a number of early branches from the evolutionary tree, all of which were able to roll themselves up to some degree, thanks to their movable opisthosomal segments. In one of these branches, the opisthosomal segments fused together to form the plate-like thoracetron that defines the Xiphosurida. The xiphosurids can be further divided into two main groups. The bellinurina include many of the classic horseshoe crabs found in the Coal Measures of the Carboniferous (360 – 259 Ma), such as ***Bellinurus*** and ***Euproops***. Its members are characterized by clear segmentation of the opisthosoma (which is fused in living horseshoe crabs). The limulina have a more modern appearance, with less evidence of external segmentation. They originated in the Carboniferous, and they came to dominate the group during the Mesozoic era (251 million to 65 million years ago).

There are four living species of horseshoe crab. ***Limulus polyphemus*** is found along the Atlantic coast of North America; ***Tachypleus tridentatus*** around southern Japan; and ***Trachypleus gigas*** and ***Carcinoscorpius rotundicauda*** more widely around south-east Asia and its islands. The living species are placed in the family Limulidae, together with the most modern-looking of the fossil Limulina: animals such as ***Mesolimulus***, which was found in Germany, in rock dating from the Jurassic period (200 million to 146 million years ago).

Lifestyle:

Modern horseshoe crabs are (mostly) marine animals and are usually found fairly close to the shore. The young can live in the area between the high-water levels of low and high tide, but they tend to move into deeper water as they get older. They generally feed on small animals living in the sediment — creatures such as worms or molluscs — or whatever they can scavenge from the sea floor. As noted above, they dig food out of the mud using rapid movements of the limbs, and then pass it into the gnathobases to be chewed. Modern species are capable of burying themselves in the sediment and it is easy to imagine the fossil species doing this too. Some palaeontologists think that trilobites might have lived in a similar way, given their anatomical resemblance to xiphosurans.

One of the most remarkable aspects of modern horseshoe-crab behaviour is their mating. Massed groups of males and females clamber onto beaches at high tide to spawn. Males have a pair of legs modified as claspers and use these to hold on tight to a female, who must then carry him around on her back. The female digs a nest close to the high-water mark, into which she lays her eggs. These are then fertilized by the male, and hatch during a subsequent high tide. Given that horseshoe crabs are a very ancient group, it is possible that this behaviour dates to a time before there was much life on land. Laying eggs on a beach would be a safe option for the offspring in a world with few land-based predators. Now, however, birds often attack horseshoe crabs as they struggle onto land to lay eggs, sometimes deliberately turning them over to expose the softer gills (Fig. 4).

FIGURE 4 — AN EXTANT HORSESHOE CRAB, LIMULUS POLYPHEMUS, OVERTURNED SHOWING THE SOFTER GILLS.

One modern species, ***C. rotundicauda***, uses the banks of estuaries or even freshwater rivers for egg laying. Interestingly, it seems that at least the Carboniferous horseshoe crabs also lived in fresh, or perhaps brackish, water. Thus it is possible that these animals have been able to adapt to different environments during their long evolutionary history.

Fossil Record:

Although there are only four horseshoe-crab species now living, almost 100 fossil species have been described. As a group they go all the way back to the late Ordovician period, 488 million to 444 million years ago, and are often treated as classic examples of 'living fossils': effectively unchanged for tens or hundreds of millions of years. The modern family, containing the living species, does indeed go back to at least the Triassic period, 251 million to 200 million years ago. There have been reports of Cambrian horseshoe crabs, 542 million to 488 million years old, but these are unconvincing and are mostly based on older schemes in which extinct arthropods called the aglaspids were thought to be primitive horseshoe crabs.

Until last year, the oldest unquestionable xiphosuran came from the Silurian period, 444 million to 416 million years ago, and there seemed to be a fairly straightforward progression in their evolution through the Devonian (416 million to 359 million years ago) and Carboniferous periods as the animals became more and more like the modern Limulina group. All this was turned on its head by the discovery of horseshoe crabs from the Ordovician of Canada, which not only comprise the oldest record of the group, but also seem to have a fused thoracetron covering the opisthosoma. Thus they belong to the 'advanced' Limulina group. This suggests that Limulina split off from the synziphosurines at a very early stage in their evolution, and reinforces the 'living fossil' theory.

FIGURE 5 — AN FOSSIL OF THE GENUS MESOLIMULUS FROM THE SOLNHOFEN LIMESTONE (© RAIMOND SPEKKING / CC-BY-SA-3.0 (VIA WIKIMEDIA COMMONS))

Most Synziphosurines have been found from the Silurian and Devonian periods, and just make it through into the Carboniferous, when the bellinurid group begins to dominate. Many species have been described from the Coal Measures, although a lot of them subsequently turned out not to be separate species — their diagnostic characters had been based on nothing more than slight differences in the way the fossils had been preserved. Nevertheless, it is fair to say that the Coal Measures horseshoe crabs were more diverse in terms of the number of species and families than the living fauna. Earlier fossil horseshoe crabs are comparatively small (a few centimetres long), but the Carboniferous contains the first fossils that approach the size of living species.

The bellinurids did not survive beyond the Carboniferous, and the modern-looking limulid group arose in the Permian period (299 million to 251 million years ago) and on into the Mesozoic era. Some Mesozoic species, such as the Jurassic ***Mesolimulus*** (Fig. 5), are really very similar to living horseshoe crabs. A few species have even been placed in the modern genus ***Limulus***, but this has not been checked in any recent studies. Other Mesozoic fossils were more extravagant and unusual-looking, with wide wing-like extensions of the carapace. There is only one fossil xiphosuran from the Cenozoic era (65 million years ago to the present day); this has been assigned to the living genus ***Tachypleus***.

Horseshoe crabs are not only known as body fossils. There is also a fairly extensive record of trace fossils interpreted as having been made by xiphosurans. These include feeding traces — fossilized scratch marks in the sediment consistent with what we know about how modern species feed — and walking traces consisting of trackways with distinct imprints from the legs. Perhaps the most famous of these are examples of a trackway called ***Kouphichnium*** from the Jurassic of Solnhofen in Germany. It includes an unusual 'crow-foot' mark and was at one stage thought to have been made by an early bird. In fact, the crow-foot was made by the splayed-out pusher leg of ***Mesolimulus***. This was confirmed by some remarkable 'death marches' from the same locality, in which the animal ended up in a toxic pool and struggled round in a half circle before it died, fossilized at the end of its trackway.

Suggestions for further reading:

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