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Fossil Focus: Chelicerata

by Jason A. Dunlop*1

Introduction:

Chelicerata is one of the main divisions of the arthropods, and essentially consists of arachnids and their closest relatives. The name was coined in 1901 by the Berlin-based zoologist Richard Heymons (Fig. 1). It means the 'claw-bearers', in reference to the claw- or fang-shaped mouthparts that characterize the group. In addition to the arachnids, Chelicerata also includes the horseshoe crabs (Xiphosura), the extinct sea scorpions (Eurypterida) and little-known chasmatapaids (Chasmataspidida), and the sea spiders (Pycnogonida).

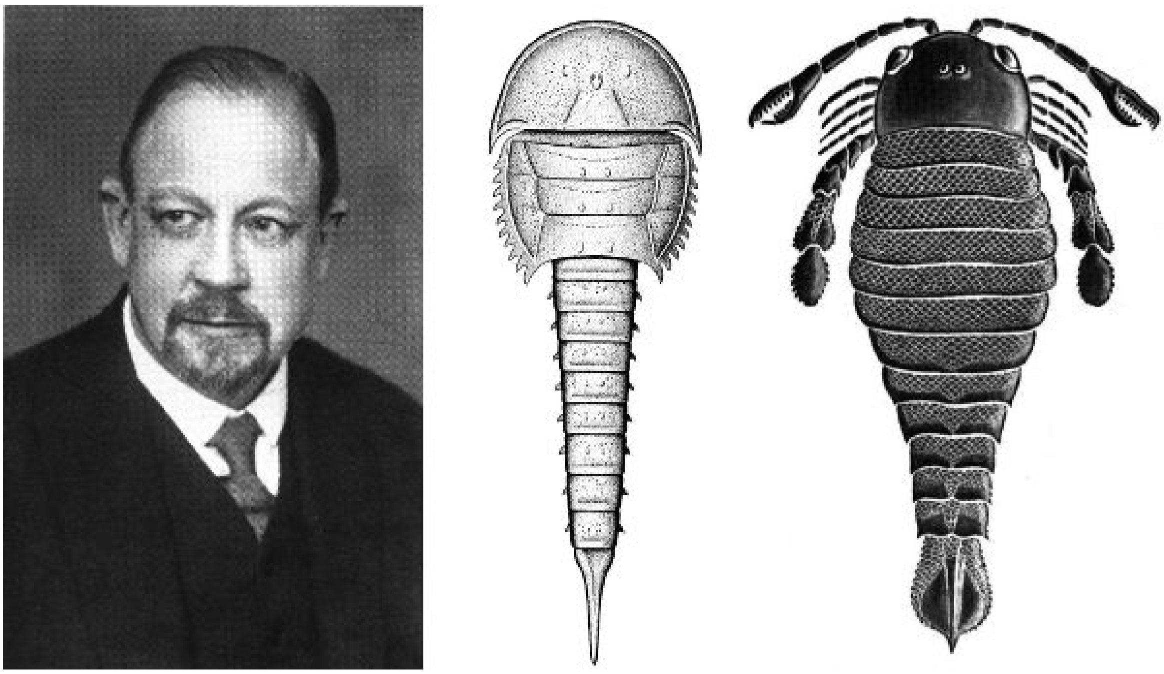

FIGURE 1 - LEFT: RICHARD HEYMONS, WHO COINED THE TERM CHELICERATA. MIDDLE: AN EXAMPLE OF THE EXTINCT GROUP CHASMATASPIDIDA. RIGHT: AN EXAMPLE OF THE EURYPTERIDA.

The inclusion of sea spiders within this group is controversial, as we shall see below, and arachnids, horseshoe crabs, eurypterids and chasmataspids are sometimes grouped together as the Euchelicerata. The name Merostomata (used for horseshoe crabs and sea scorpions) is also common in older publications, although most experts now feel that this is not a natural group, and that eurypterids are probably more closely related to arachnids. Currently, there are over 100,000 living species of chelicerates, the most diverse groups being mites and spiders. More than 2,000 fossil species, some of which go back to the late Cambrian period, have been recorded so far.

Morphology:

As noted above, chelicerates are defined by their jaws. Whereas most modern arthropods have chewing mouthparts called mandibles, the jaws of chelicerates — the chelicerae, which give the group its name — are usually shaped like claws or pincers and are mostly used for grasping and tearing up prey (Fig. 2). In spiders, these chelicerae have been further modified into fangs, which function more like a folding pocket knife. In sea spiders, the chelicerae are sometimes called 'chelifores'. Chelicerates lack antennae, and recent work has shown that the appendage pair that makes up the antennae of other arthropods is actually the same set of limbs that form the chelicerate mouthparts. Thus, insects feel with the first pair of limbs on their heads; chelicerates bite with them.

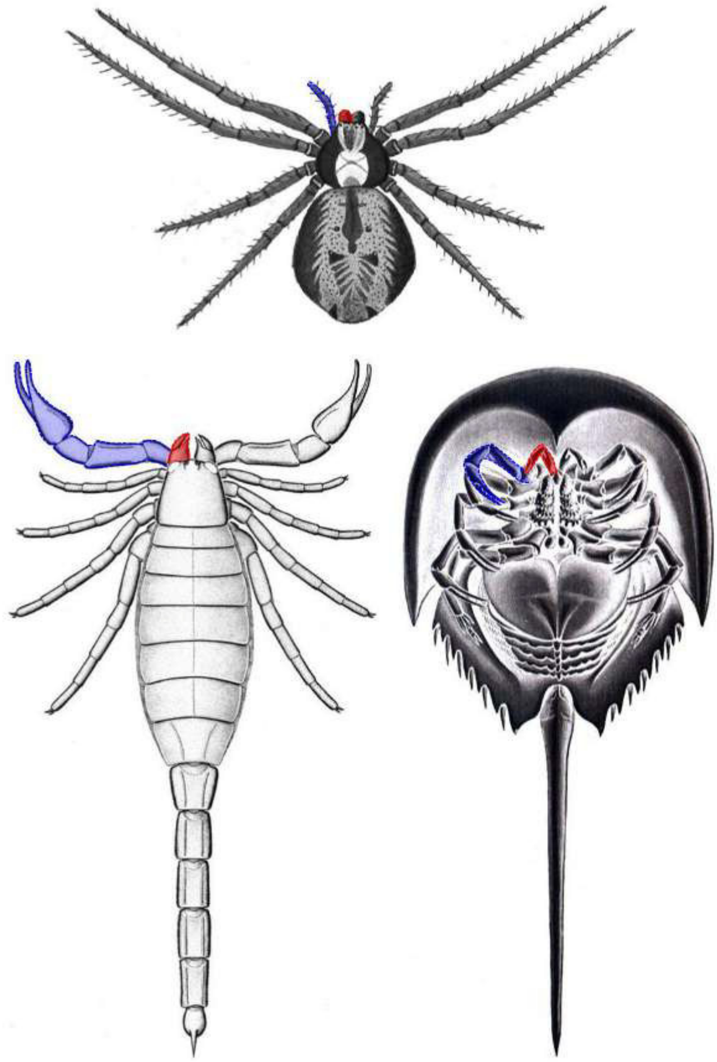

FIGURE 2 - THE CHELICERAE ON DIFFERENT GROUPS OF CHELICERATES (COLOURED IN RED). TOP IS SPIDER, BOTTOM LEFT IS A FOSSIL SCORPION SPECIES, AND BOTTOM RIGHT IS A HORSESHOE CRAB. A SECOND HEAD APPENDAGE, THE PEDIPALP, IS COLOURED IN BLUE FOR EACH.

Classic textbook accounts of the chelicerates usually refer to the presence of six pairs of limbs: chelicerae, pedipalps and four pairs of walking legs. This body plan doesn't quite work for sea spiders, which — oddly — have an 'extra' pair of appendages. The sea spiders (Fig. 3) also cause problems for another textbook character: the division of the body into two separate halves, a prosoma (or cephalothorax) and opisthosoma (or abdomen). While this simple division of the body into two halves works for (most) arachnids, it does not really define Chelicerata as a whole. Further discussion of body plans can be found in the section on arachnids.

Phylogeny:

By the early 19th century, arachnids — as we understand them today — were widely recognized as a natural group (Fig. 4). The position of the horseshoe crabs was more controversial. As their name implies, they were initially assumed to be crustaceans, largely because they lived in water. Some early workers pointed out their arachnid-like features, but it was a classic paper entitled '*Limulus* an arachnid', written in 1881 by the London zoologist E. Ray Lankester, which convincingly showed where horseshoe crabs' true affinities lay. Ill-tempered debate followed, but eventually Lankester's ideas became accepted and Heymons offered the name Chelicerata for the group. Sea spiders (despite their name) are not really spiders at all, and only resemble them superficially. They were later accepted as probably belonging to Chelicerata too.

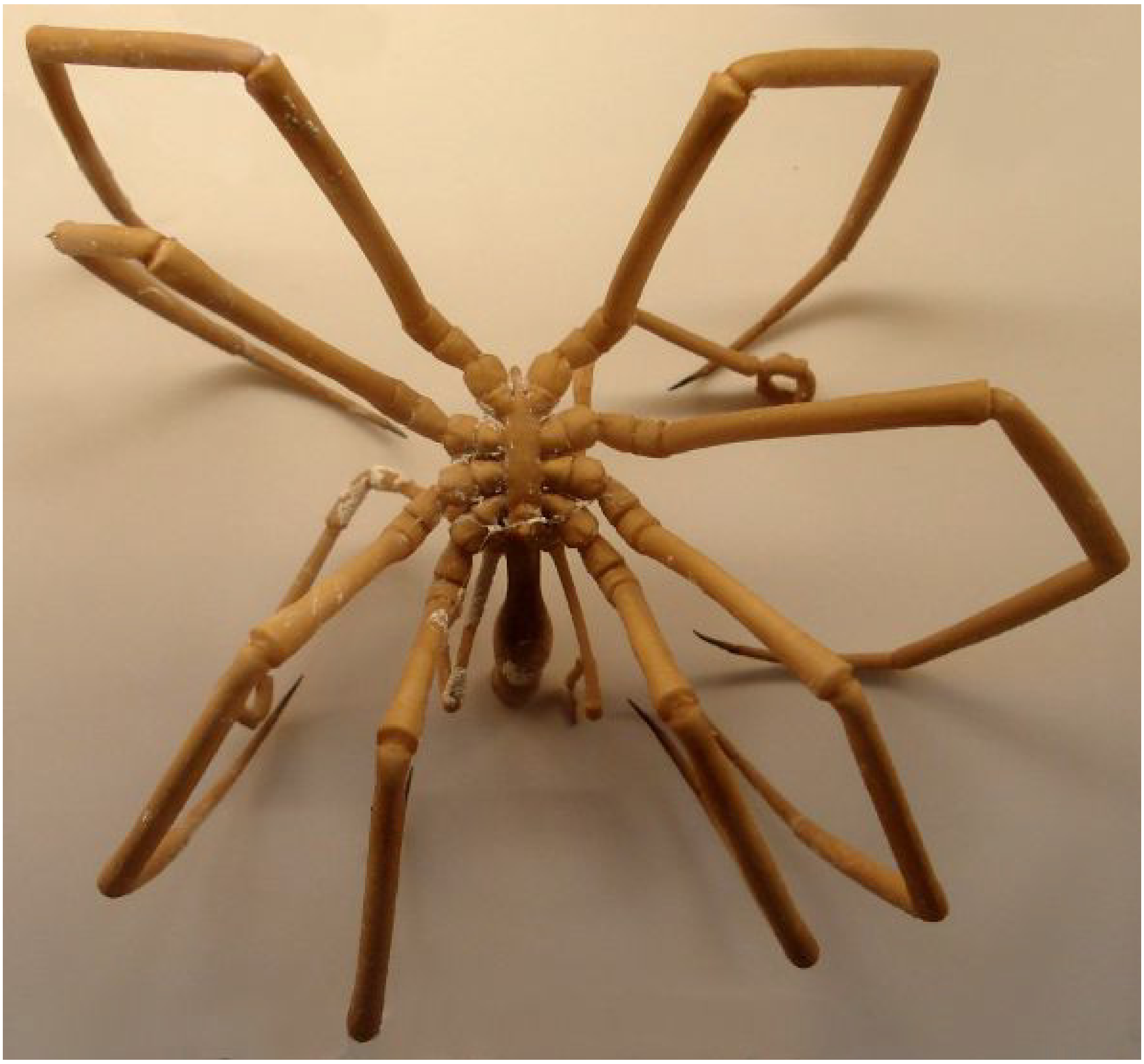

FIGURE 3 - A MODERN MEMBER OF THE SEA SPIDERS (PYCNOGONIDA).

The position of chelicerates, relative to other arthropods, in the overall tree of life has proved controversial. Essentially, three main hypotheses have been proposed. One idea that was once particularly favoured by palaeontologists grouped together trilobites, crustaceans and chelicerates, calling them 'Schizoramia'. This name effectively means

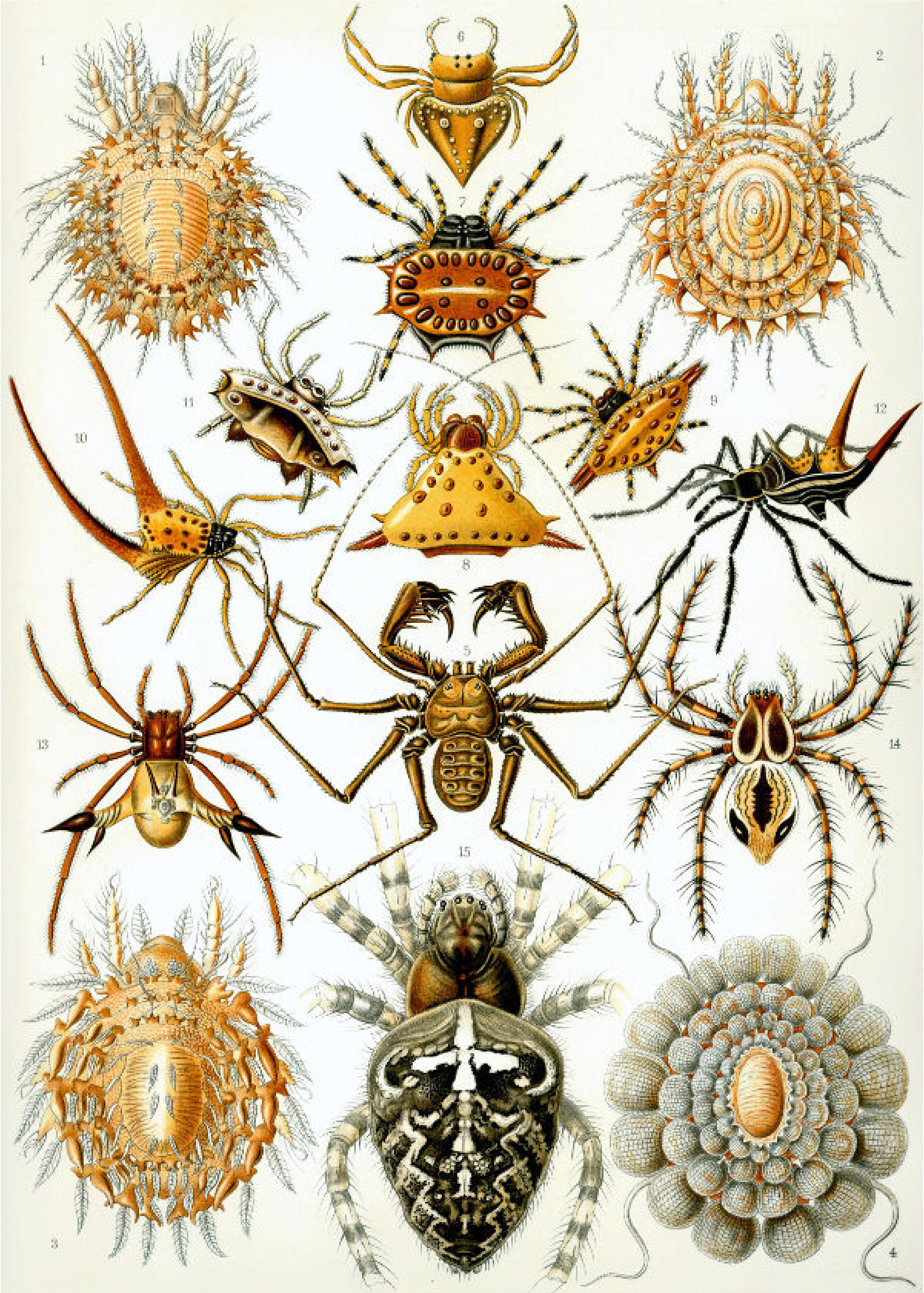

FIGURE 4 - EXAMPLES OF THE ARACHNIDS, FROM ERNST HAECKEL'S FAMOUS BOOK KUNSTFORMEN DER NATUR.

'divided leg', and refers to the branched limbs of crustaceans and trilobites. This feature doesn't really work for arachnids, but the last leg of horseshoe crabs does show remnants of this division. Some modern molecular studies have offered an alternative idea, in which chelicerates are most closely related to millipedes and centipedes (Myriapoda). This combined group has been called 'Myriochelata' or, because the idea is so strange, 'Paradoxopoda'. It remains controversial since it is mostly supported by molecular data, and few convincing anatomical features unique to chelicerates and myriapods have been uncovered. Perhaps the best-supported view sees chelicerates as primitive arthropods with a fairly simple 'head' region and pincer-shaped jaws followed by numerous legs used for walking. The more 'advanced' arthropods (including trilobites) evolved antennae instead of claws; then, in crustaceans, myriapods and insects, the head region became more complex and structures like the mandibles and maxillae — all of which are highly modified head limbs — appeared.

Tied to this debate are questions about the origins of the chelicerates. For many years it was assumed that they were related to — or even evolved from — trilobites, since the body shape of a horseshoe crab is superficially quite similar to that of a trilobite (Fig 5). The fact that trilobites have antennae rather spoils this party; the troublesome sea spiders are also unwelcome gatecrashers, because they do not resemble trilobites at all. In recent years, an alternative hypothesis has been gaining ground. There is a group of enigmatic Cambrian fossils that is often loosely referred

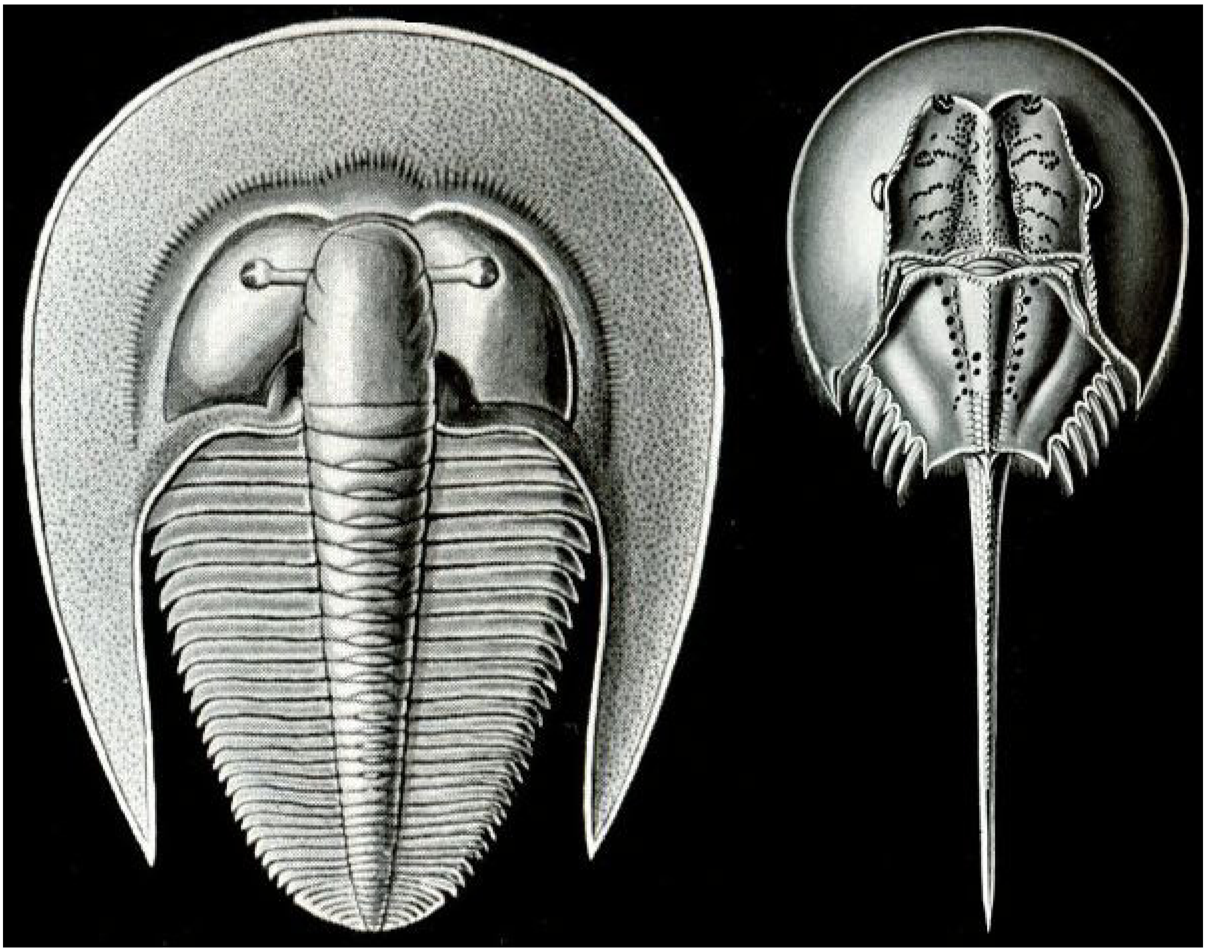

FIGURE 5 - A TRILOBITE (LEFT) AND HORSESHOE CRAB (RIGHT) WHICH ON THE BASIS OF THEIR SIMILAR APPEARANCE WERE TRADITIONALLY CONSIDERED RELATED. THIS IS LESS WIDELY SUPPORTED BY MODERN WORK.

to as the 'great appendage' arthropods. These creatures do not have antennae, but they do have a large pair of sometimes spiny limbs at the front of the body, which look as though they were adapted for grasping prey. Conceivably, these 'great appendages' evolved into the more robust, claw-like chelicerae; in this scenario, some of the 'great appendage' arthropods may turn out to be the ancestors of arachnids and related forms.

Lifestyle:

Given that arachnids make up the vast majority of the modern Chelicerata species, most chelicerates can be classified today as terrestrial. As a group, they are found in all almost all habitats, even deserts, mountaintops and arctic environments. They have been on land since at least the Silurian period, although a few spiders and certain groups of mites have subsequently returned

FIGURE 6 - LEANCHOILIA, AN EXAMPLE OF THE CAMBRIAN 'GREAT APPENDAGE' ARTHROPODS. IMAGE COURTESY OF DIEGO GARCIA-BELLIDO.

to the water. Horseshoe crabs and sea spiders are found only in marine settings today, although some fossil horseshoe crabs may have lived in freshwater or perhaps brackish river-estuary environments during the Carboniferous period. Eurypterids were a diverse aquatic group in their heyday and there seems to have been a trend for them to move from marine to more freshwater environments (again in the Carboniferous) during their geological history.

Most chelicerates are predators, and most catch live prey which is then chewed or dismembered using the chelicerae. The aquatic horseshoe crabs and eurypterids have rows of teeth on the inner sides of their leg coxae (the segment where the leg joins the body), and these 'gnathobases' chew up the food before it is passed to the mouth. This style of feeding is only practical in water; arachnids tend instead to regurgitate enzymes onto their food and begin the digestion process in front of the mouth, sometimes in a special 'preoral cavity'. Harvestmen (Opiliones, Fig. 6) are one of the few arachnid groups that can eat solid food; they are capable of eating both plant and animal material. Numerous groups of mites have given up on being predators, and as a group they show the greatest diversity of habitats and feeding strategies: they include blood-sucking parasites and feeders on plant sap or decaying material. Sea spiders uniquely have a proboscis and either prey on sedentary animals, sucking up their body fluids, or — in some cases — actively hunt moving prey.

FIGURE 6 - AN EXAMPLE OF THE HARVESTMEN (OPILIONES). PICTURE COURTESY OF GONZALO GIRIBET, NOT FOR COMMERCIAL USE.

Fossil record:

The fossil record of Chelicerata goes back to the late Cambrian. The oldest records are a larval sea spider from the 'Orsten' Lagerstätte of Sweden and some resting impressions, probably left by one or more chasmataspids, from Texas. Horseshoe crabs and eurypterids are first known from the Ordovician period, and arachnids are definitely present from the Silurian onwards; an older record of a mite remains controversial. Fossils of chelicerates are generally quite rare and tend to occur in particular 'windows' of time, usually associated with unusual conditions of exceptional preservation. Examples include the Devonian period Rhynie chert depost, the Carboniferous Coal Measures or the numerous sources of amber found from the late Mesozoic through to the Cenozoic eras.

Suggestions for further reading:

Chen, J., Waloszek, D. & Maas, A. 2004 A new 'great-appendage' arthropod from the Lower Cambrian of China and homology of the chelicerate chelicerae and raptorial antero-ventral appendages. Lethaia 37, 3–20 (doi:10.1080/00241160410004764).

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Lankester, E. R. 1881 Limulus an arachnid. Quarterly Journal of Microscopical Science 21, 504–548. (http://jcs.biologists.org/cgi/reprint/s2-21/83/504).

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