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# Fossil Focus: Pycnogonida

by Jason A. Dunlop[*1]

## Introduction:

Pycnogonida, or sea spiders, are not true spiders at all. They are in fact a group of — probably rather primitive — marine arthropods, characterized by a small, slender body and in many cases by correspondingly long legs (Fig. 1). So unusual is their morphology that many of their internal-organ systems have been displaced into the legs. Because of their strange appearance, older studies occasionally referred to them as 'nobody crabs' (literally crabs without a body) — although it is important to stress that they are not crustaceans, any more than they are spiders. Pycnogonids are thought either to have evolved right at the very base of the arthropod tree — and thus not to be closely related to any particular group of arthropods — or to be related to arachnids, eurypterids (sea scorpions) and horseshoe crabs.

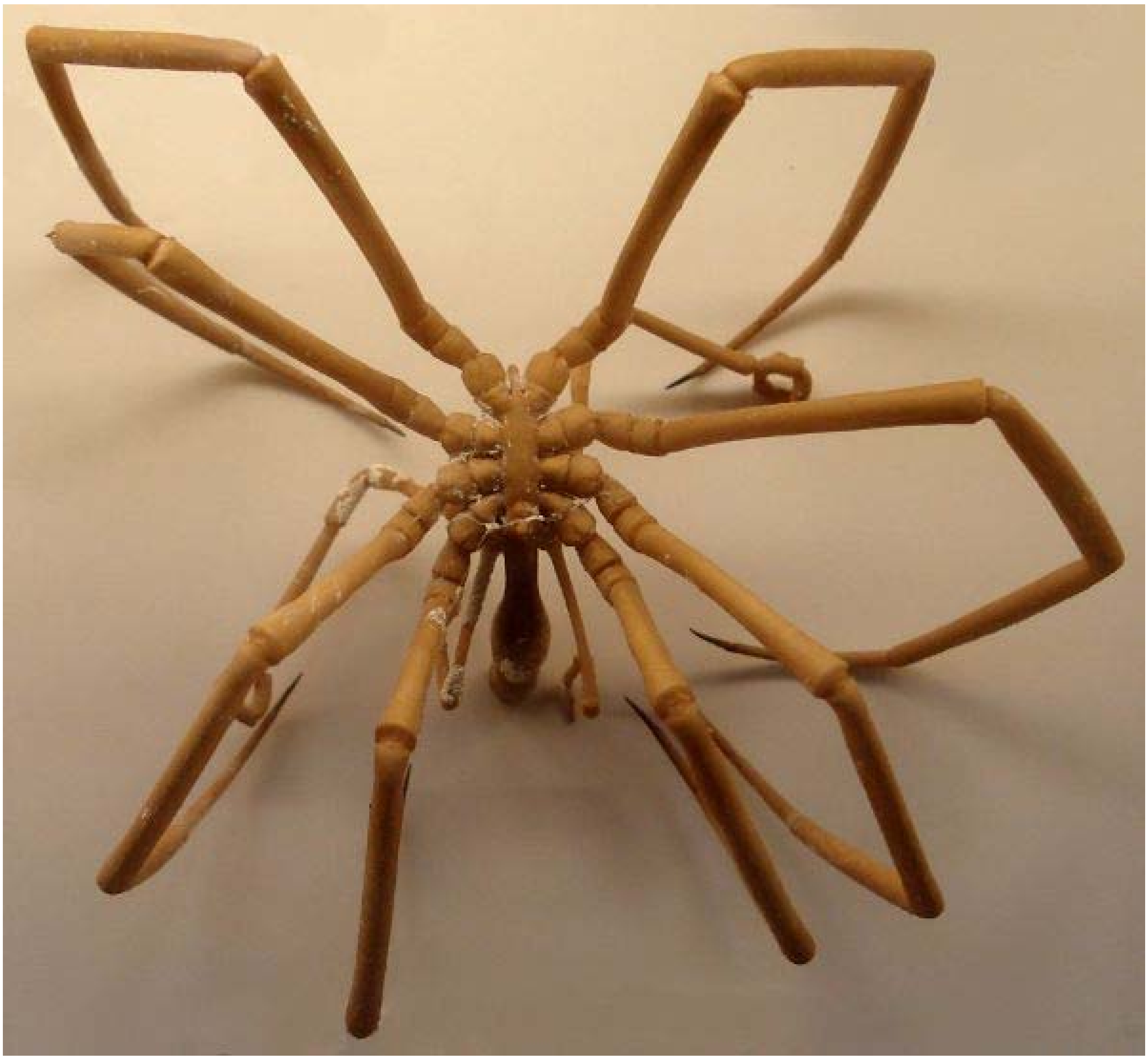

FIGURE 1 – A MODERN PYCNOGONID, COLESSENDEIS WILSONI, FROM ANTARCTICA. A MEMBER OF THE FAMILY COLOSSENDEIDAE..

## Morphology:

Sea spiders range from species about a centimetre in length, found in a range of environments, to huge cold-water varieties whose leg spans approach half a metre. They do not show an arachnid-like division of the body into two clear halves. The first four segments are fused together and form a 'head' region, usually referred to as the cephalon (the bottom of Fig. 1). This cephalon bears the eyes — four in total, seated together on a small tubercle — as well as a 'proboscis', which, among the chelicerates, is unique to the sea spiders. This tube-like projection bears the mouth opening, and fluid from the animal's prey is sucked up through it (see Lifestyle). Sea spiders can only feed on liquids, and the muscular proboscis contains a filter system to keep out particles of food.

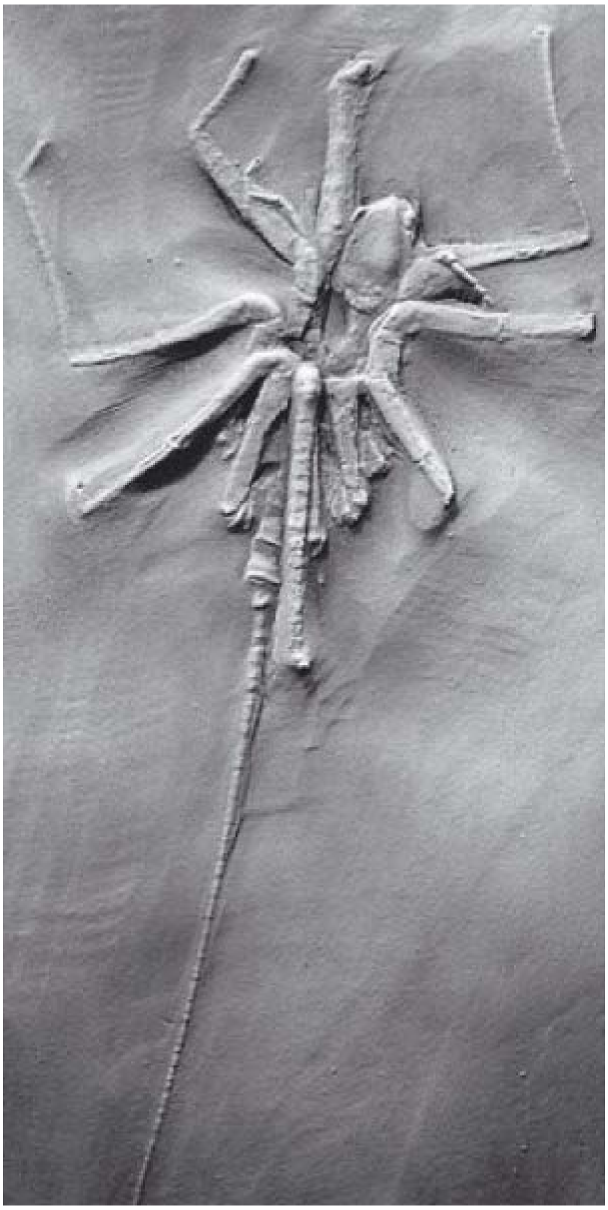

FIGURE 2 – FLAGELLOPANTOPUS BLOCKI, A SEA SPIDER FROM THE LOWER DEVONIAN HUNSRUCK SLATE, GERMANY. NOTE THE FLAGELLIFORM TAIL.

The cephalon also bears four pairs of appendages. The first are the 'chelifores', which are usually claw- or pincer-like. Most people who work on sea-spiders think that these are equivalent to the chelicerae of arachnids and their relatives. The chelifores are usually composed of three segments, but a few modern species may have four, and some fossils may have had up to five. In some species, the chelifores are reduced to stubby little structures, and in others they are missing completely (see also below). The chelifores are followed by the palps, similar to the arachnid pedipalps, and then another unique feature of sea spiders: the ovigers. These seem to represent an 'extra' pair of legs when comparing sea spiders with true spiders, and their function (as the name implies) is to carry the eggs. Curiously, it is the male that does the work here. Specimens can be found with a bundle of eggs wrapped around each oviger.

The final pair of limbs on the cephalon are the first pair of walking legs. These typically have nine segments, and although the individual parts may be named using arachnid terms (femur, patella, tarsus, etc.) it is not immediately clear that they correspond exactly to the same parts in arachnids. The legs are short and stubby in some species, but are long and slender in most, such that the whole body can appear to be made up of a tangle of spidery limbs. Legs are sometimes quite spiny, and usually end in claws. It should also be noted that in some species the chelicifores, palps and even ovigers can be absent. Thus, in the common species

*Pycnogonum litorale*, for example, the cephalon has only a single pair of legs.

The cephalon is followed by a series of three short trunk segments. Each bears another leg, to give a total of four pairs of walking legs. There are, however, a few species that have 10 or even 12 walking legs in total. How these arose, and whether they are of evolutionary significance, remains a mystery. Sea spiders lack certain organ systems: they have a simple heart, but do not have any gills and presumably take up oxygen directly over the cuticle. Projections from the gut (so-called diverticulae) and parts of the reproductive organs are pushed into the legs, and unlike in other arthropods, the genital openings are at the base of the legs.

Behind the legs there is a small tail piece. It is sometimes called the abdomen, but it is not really equivalent to the arachnid opisthosoma. The piece has no real function, and simply contains the anal opening. However, some of the fossils have three to five ring-like segments here instead. This is probably the primitive condition. Two fossils from the Devonian Period of Germany even have tails. In one example, the tail is a pointed spine, with the anus opening halfway along. In the other example, the tail is long and whip-like with many short segments (Fig. 2), quite similar in appearance to the flagellum of whip scorpions and an arachnid group called the palpigrades (microwhip scorpions).

## Phylogeny:

Early attempts were made to link pycnogonids to crustaceans on the basis of similarities in their larvae, but this idea has now been largely abandoned. In general, the unusual appearance of the sea spiders — and the fact that many of their body systems may have become reduced or lost — has made it very difficult to determine their closest living relatives. Realistically, there are now only two serious ideas about their origins. Some biologists argue that sea spiders are effectively the most primitive of the living arthropods. As noted above, pycnogonids have their genital openings at the base of the legs, whereas all other arthropods (insects, myriapods, arachnids and crustaceans) have genital opening(s) directly on the body. The question is whether this is a shared, advanced (=derived in evolutionary terms) character of all non-pycnogonid arthropods (the name Cormogonida has been proposed to

FIGURE 3 - A LARVAL PYCNOGONID FROM THE CAMBRIAN OF ORSTEN, SWEDEN.

encompass this group), or whether the genital openings shifted to the legs in sea spiders because there was no more space left on the evolving narrow body.

The other possibility, which has more widespread support, is that the pycnogonids should be grouped with arachnids and horseshoe crabs within the broad group Chelicerata. In this model, the pincer-like chelifores of sea spiders are assumed to be the same thing as the chelicerae of arachnids. This suggestion has generated much debate in recent years, and everything from nerve branches to developmental genes has been studied in minute detail to see whether these two sets of claw-shaped mouthparts really are built from the same set of limbs. This does now seem to be the case, and chelifores/chelicerae can be used as evidence that sea spiders are related to arachnids. Sea spiders are probably an early branch of the Chelicerata. All the other chelicerates — the so-called Euchelicerata — have an advanced pattern of development, in which the larva hatching from the egg is very similar to the adult. By contrast, the hatching protonymphon of a sea spider has chelicerae

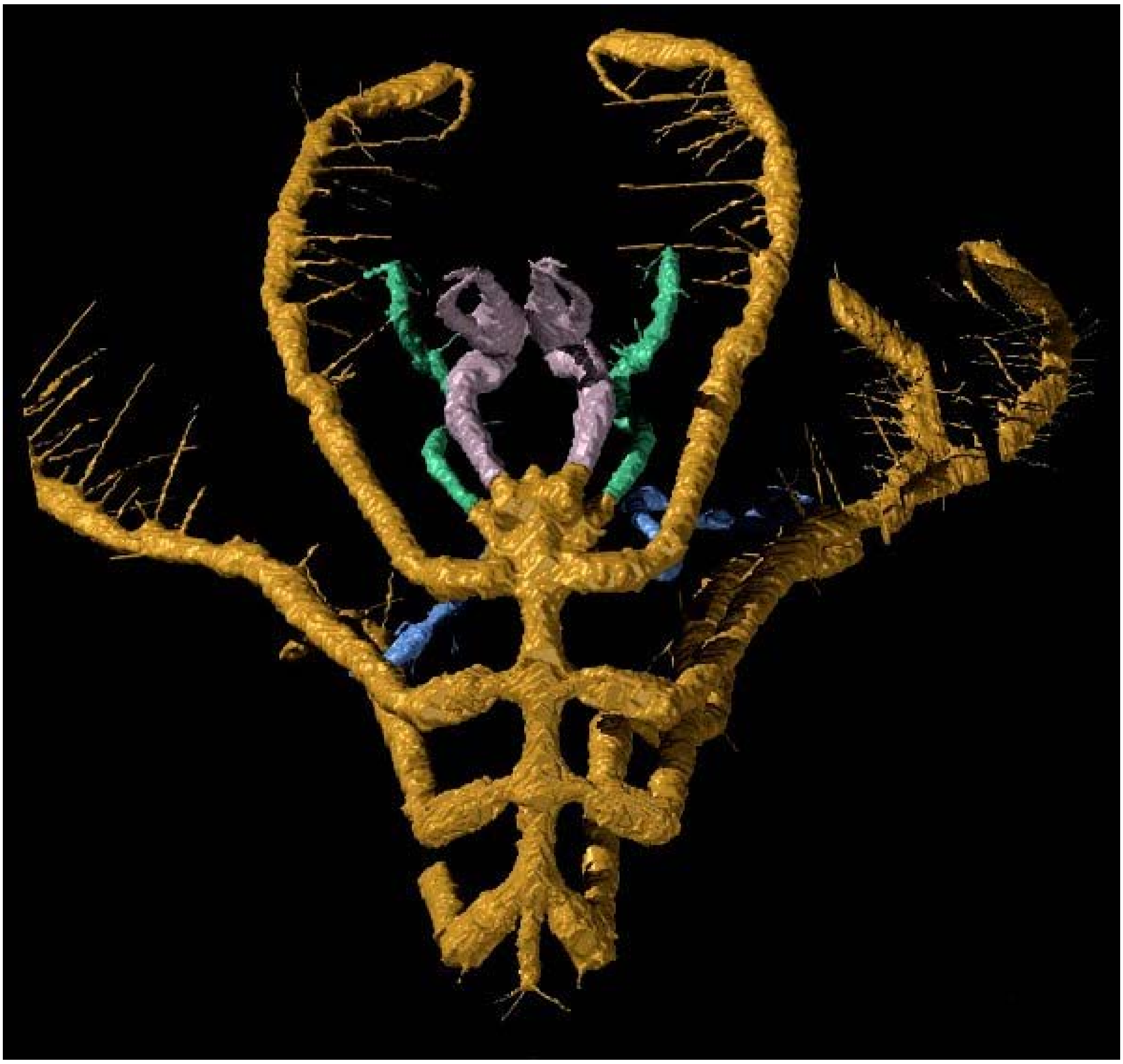

FIGURE 4 - A DIGITAL RECONSTRUCTION OF A SILURIAN PYCNOGONID FROM HEREFORDSHIRE, UK. COUTESY OF SIVETER ET AL. (SEE SUPPLEMENTARY READING)

(Fig. 3), but only two pairs of legs!

Relationships within the sea spiders are currently under debate. Nine or ten families of living species are currently recognized. It used to be thought that families that have lost the chelicerae, palps and/or ovigers must be more advanced, but as with much of sea-spider biology, there are no clear answers here and fossils must be considered. A simple scheme was proposed in which the those Devonian fossils having a tail and a longer segmented body behind the legs were assumed to be primitive, and there was assumed to be a subsequent trend towards losing the tail and then losing segments until only a single tiny tail end remained behind the legs. Some studies (particularly in the German literature) referred to sea spiders as Pantopoda. Pycnogonida and Pantopoda originally meant the same thing, but it was later suggested that Pantopoda could be used for a more advanced group within Pycnogonida; specifically, for one fossil and all living species, which had lost all these extra body segments and the tail. Modern techniques of study suggest a more complex picture: the fossils are not always 'primitive', and do not all emerge right at the base of the sea-spider evolutionary tree.

## Lifestyle:

Living sea spiders are entirely marine, and there is no suggestion that any of their fossils inhabited fresh water. The modern examples can be found from the shore region down to the deep sea. In general, they tend to be rather ponderous, slow-moving creatures, which crawl among seaweed or across the sea floor, although some are capable of bursts of swimming activity. In keeping with their relative lack of movement, pycnogonids typically prey on sessile (non-moving) organisms such as sponges, sea anemones or bryozoans. The proboscis is simply stuck into the victim and the fluid contents are sucked up — a feeding strategy resembling that of a parasite. Other species make more of an effort and attack active prey such as worms, grabbing them with the help of the chelifores.

## Fossil Record:

Sea spiders have a rather sparse fossil record. The oldest suggested member of the group comes from the late Cambrian 'Orsten' of Sweden, and is preserved as a minute, three-dimensional, phosphatized larva, which resembles the larvae of modern pycnogonids (Fig. 3). The next-oldest fossil comes from the Silurian of England. Again preserved three-dimensionally, they are embedded in nodules of rock and could be revealed only using tomography: a process that involves grinding away the rocks containing the fossils, photographing each successive layer and then building these slices together into a single 3D computer reconstruction (Fig. 4). This Silurian sea spider closely resembles certain modern species.

The majority of the Palaeozoic fossils come from the early-Devonian Hunsrück Slate of Germany. Four species have been recorded so far, and (as noted above) they exhibit a range of body plans not seen in living species. Some have a series of body segments behind the legs, as well as either a pointed tail or, in one case, a whip-like structure (Fig. 2). At least one of the Hünsruck fossils was thought to have only a single, unsegmented tail end, and was traditionally interpreted as the most 'modern' Palaeozoic species.

Beyond the Palaeozoic, some long-legged arthropod fossils from the famous Jurassic locality of Solnhofen in Germany were thought at one stage to be pycnogonids. Later work showed that they are in fact the larvae of rock-lobster crustaceans. More-convincing

Mesozoic sea spiders have been described from the Jurassic of La Voulte-sur-Rhône in southwestern France. Some details are lacking, but they were tentatively assigned to the living families Colossendeidae, Ammotheidae and Endeidae. There are no sea-spider fossils known from the Cenozoic Era.

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## Suggestions for further reading:

Arango, C. P. & Wheeler, W. C. 2007 Phylogeny of the sea spiders (Arthropoda, Pycnogonida) based on direct optimization of six loci and morphology. ***Cladistics*** **23,** 255–293 (doi:10.1111/j.1096-0031.2007.00143.x).

Brenneis, G., Ungerer, P. & Scholtz, G. 2008 The chelifores of sea spiders (Arthropoda, Pycnogonida) are the appendages of the deutocerebral segment. ***Evolution & Development*** **10,** 717–724 (doi:10.1111/j.1525-142X.2008.00285.x).

Charbonnier, S., Vannier, J. & Riou, B. 2007 New sea spiders from the Jurassic La Voulte-sur-Rhône Lagerstätte. ***Proceedings of the Royal Society B*** **274,** 2555–2561 (doi:10.1098/rspb.2007.0848).

Dunlop, J. A. & Arango, C. P. 2005 Pycnogonid affinities: a review. ***Journal of Zoological Systematics and Evolutionary Research*** **43,** 8–21 (doi:10.1111/j.1439-0469.2004.00284.x).

Masta, S. E., McCall, A. & Longhorn, S. L. 2010 Rare genomic changes and mitochondrial sequences provide independent support for congruent relationships among the sea spiders (Arthropoda, Pycnogonida). ***Molecular Phylogenetics and Evolution*** **57,** 59–70 (doi:10.1016/j.ympev.2010.06.020).

Poschmann, M. & Dunlop, J. A. 2006 A new sea spider (Arthropoda: Pycnogonida) with a flagelliform telson from the Lower Devonian Hunsrück Slate, Germany. ***Palaeontology*** **49,** 983–989 (doi:10.1111/j.1475-4983.2006.00583.x)

Siveter, D. J., Sutton, M. D., Briggs, D. E. G. & Siveter, D. J. 2004 A Silurian sea spider. ***Nature*** **431,** 978–980 (doi:10.1038/nature02928).

Waloszek, D. & Dunlop, J. A. 2002 A larval sea spider (Arthropoda: Pycnogonida) from the Upper Cambrian 'Orsten' of Sweden and the phylogenetic position of pycnogonids. ***Palaeontology*** **45,** 421–446 (doi:10.1111/1475-4983.00244).

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