

## Title: Fossil Focus - Cambrian arthropods

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# Fossil Focus: Cambrian arthropods

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by [David A. Legg](#)<sup>\*1</sup>

## Introduction:

The arthropods make up a major and highly successful group of animals that includes insects and their kin (hexapods); arachnids and their kin (chelicerates); millipedes and centipedes (myriapods); crabs, lobsters, shrimp and their relatives (crustaceans); and the extinct trilobites. In fact, arthropods are the most diverse, abundant and ubiquitous animal [phylum](#). Members of the group outnumber those of all other phyla on Earth, both in terms of species, with more than 1,200,000 currently described (and a potential 10,000,000 remaining to be described), and in terms of abundance. For example, if you gathered all the world's Arctic krill in one place, it has been estimated that they would weigh 500 million tonnes! Arthropods are found in all oceans and on all continents — from the depths of the Mariana Trench to the slopes of Mount Everest — and have colonized nearly every [ecosystem](#) including hot hydrothermal vents and subterranean caves nearly 2,000 metres below sea level. They play a key role in many ecosystems as pollinators, decomposers, parasites, food sources and disease vectors. They are also ubiquitous in the fossil record, forming a dominant component of most early ecosystems.

Despite their riotous diversity, all living arthropods possess (and the group is defined by) a number of shared features (Fig. 1), the most obvious of which is the tough [exoskeleton](#) made mainly of the polymer [chitin](#). This outer layer may have evolved primarily for muscles to attach to, and — by providing protection from the harsh external environment — may have been important in helping arthropods to colonize new environments. However, a rigid exoskeleton impedes both growth and movement, so mechanisms have evolved to get around these problems. For example, arthropods develop in stages, between which they moult: the older exoskeleton is shed (ecdysed), and replaced with a larger one. The exoskeleton is divided into distinct hardened plates (sclerites) made of chitin. These plates are separated by a soft material called arthrodial membrane. This arrangement is known as arthrodization, and allows for increased flexibility and movement of the main body axis, while still protecting the body. The segmentation of the appendages is called arthropodization (from the Greek *arthros* meaning jointed, and *podus*, legs); this what gives the group its name. Arthropods' segments and appendages are divided into specialized groups, or tagmata. The grouping of segments into tagmata is known as tagmosis. The arrangement of segments and appendages present in the animal is one of the main ways of differentiating between groups of arthropods (Fig. 1).

Like most animal phyla, the arthropods are thought to have originated during the [Cambrian period](#) (542 million years ago to 485 million years ago). They are an important group in the 'Cambrian explosion' — a period when the first representatives of most animal phyla appeared [relatively suddenly](#) in the fossil record. We know about many of these early arthropods because they are common constituents of many Cambrian *Konservat-Lagerstätten* (sites of exceptional fossil preservation) such as the Burgess Shale in Canada, and the Chinese Chengjiang Lagerstätte. During the Cambrian a wide variety of body plans evolved — some considered so aberrant and hard to classify that they were called “weird wonders” by evolutionary biologist Stephen J. Gould (1941–2002) in his 1989 book “*Wonderful Life: The Burgess Shale and the Nature of History*”. In this regard, the arthropods are no exception.

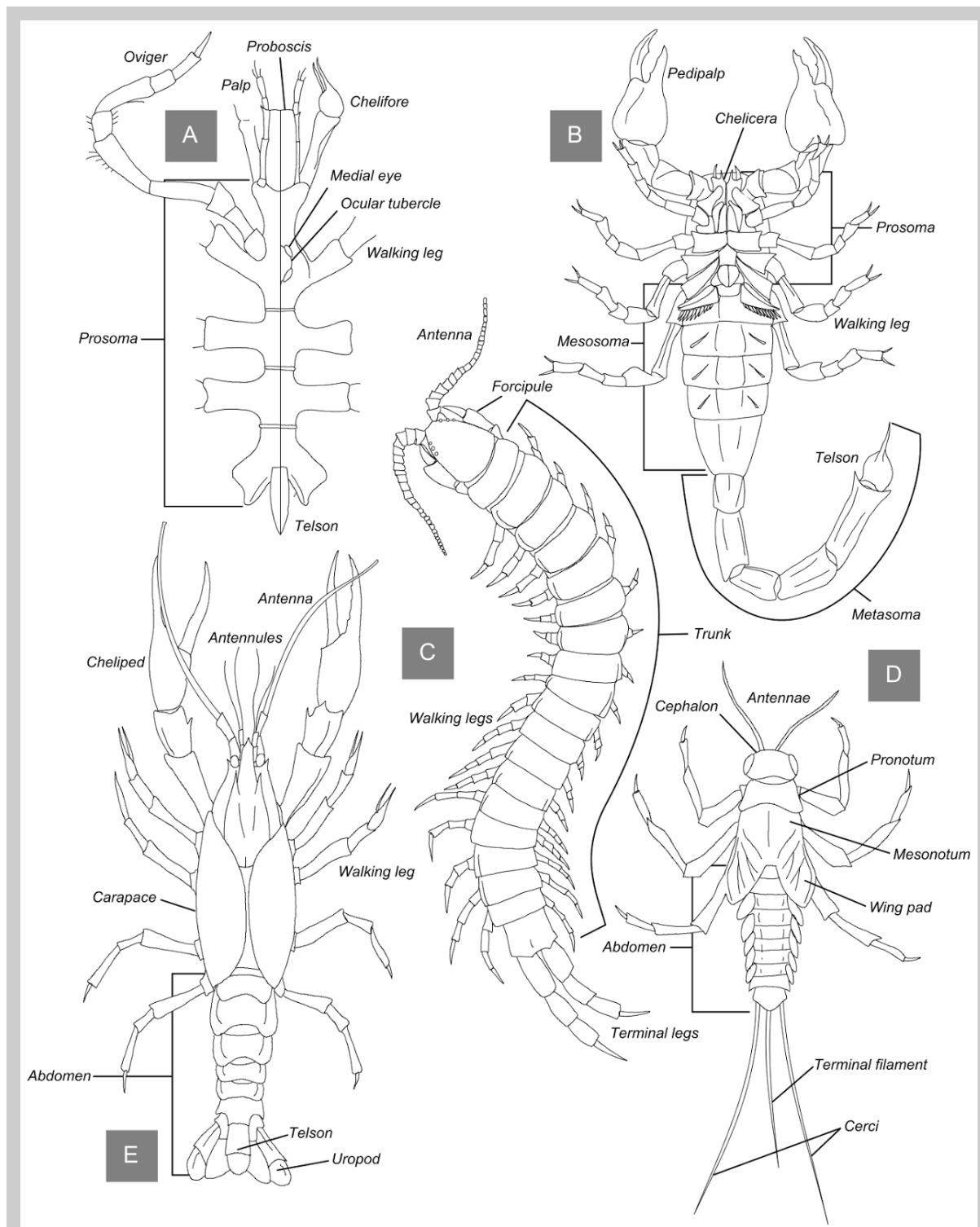


Figure 1 — Examples of the ‘big five’ groups of modern arthropods, including A, a partial reconstruction of the pycnogonid (sea spider) *Nymphon gracilis*; B, the scorpion (chelicerate) *Pandinus imperator*; C, the giant centipede *Scolopendra giganteus*; D, a nymph of the mayfly *Baetis* sp.; and E, the common lobster *Homarus gammarus*.

When originally described, many Cambrian species were considered highly unusually representatives — but already true members — of groups that are still alive. Many are now recognized as belonging to lineages that went on to evolve into the forms alive today. This article provides a brief description of selected Cambrian arthropod groups, and a discussion of their potential relationships. A summary of recent opinion regarding the relationships of modern and Cambrian arthropods is given in Figure 2.

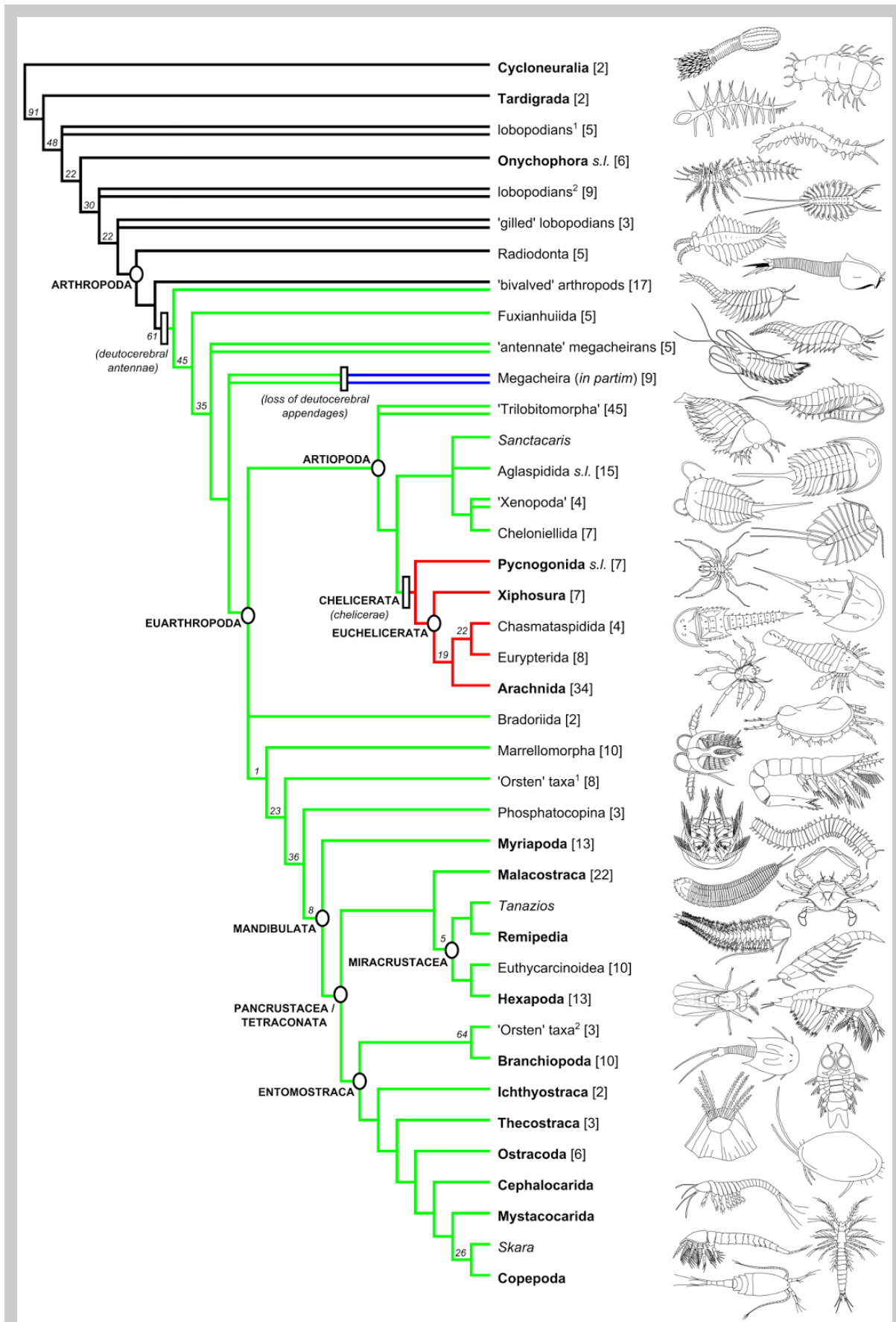


Figure 2 — A summary of relationships of major arthropod groups ([source](#)).

## Bivalved arthropods:

Bivalved arthropods (Fig. 3A, B) — those with two shells, or valves, covering the majority of their bodies — are common in many Cambrian *Konservat-Lagerstätten*. They represent an important component of some of the earliest animal communities in the water column, and display a number of different anatomies (Fig. 3A, B). There are disagreements about how Cambrian bivalved arthropods were related to modern arthropods, with some authors considering them to be primitive crustaceans. Others argue that any similarity to crustaceans is superficial and that the groups share few, if any, unequivocal features. Instead, some researchers suggest that various Cambrian bivalved arthropods belong to the lineage that led to all living arthropods (Euarthropoda; Fig. 2). For example, a number of studies have highlighted similarities between Cambrian bivalved arthropods, particularly *Isoxys* (Fig. 3B) and anomalocaridids — giant predators with a close relationships to the arthropods, but not true members of the group. This has highlighted the importance of bivalved arthropods species in understanding the early evolution of arthropods and the origin of Euarthropoda. It is also possible that both hypotheses are true, and that some species belong to one group, whilst others belong to another.. Furthermore, some researchers have discovered unusual limbs at the front of the body in Cambrian bivalved arthropods from the Burgess Shale. These limbs are similar to those seen in a group called the megacheirans, or ‘great-appendage arthropods’ — which we will introduce shortly — so it has been suggested that there could be a close relationship between some bivalved species and this group.

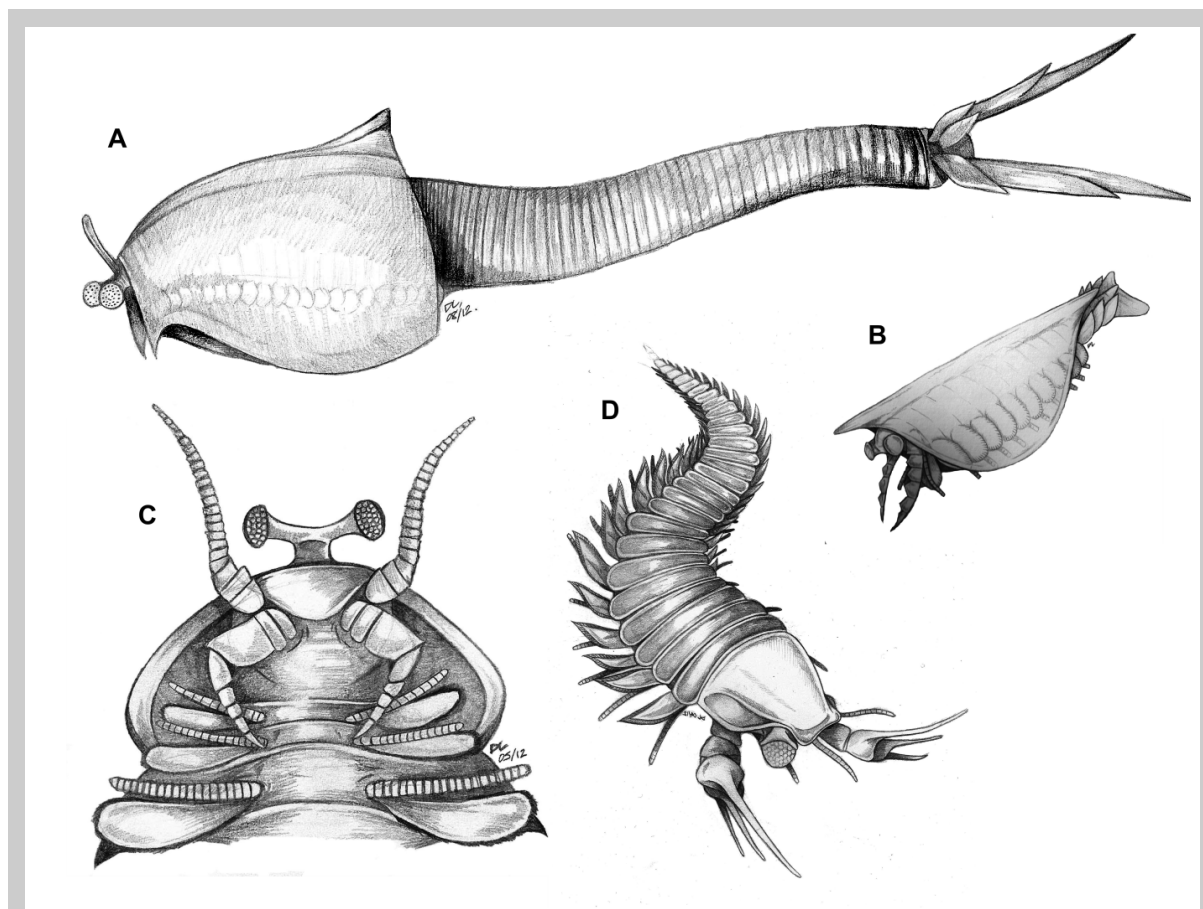


Figure 3 — The diversity of Cambrian arthropods. A, The bivalved arthropod *Nereocaris exilis* ([source](#)). B, The bivalved arthropod *Isoxys acutangulus* ([source](#)). C, The head region of *Fuxianhuia protensa*. D, The great-appendage arthropod *Kootenichela deppi* ([source](#)).

## **Fuxianhuiids:**

Fuxianhuiids are generally regarded as the most primitive arthropods, and have figured prominently in discussion of arthropod origins. Members of this group have multisegmented appendages, similar to those of modern [velvet worms](#); an elongate body; and a head capsule formed by the fusion of an eye-bearing plate with a protective head shield (Fig. 3C). Seven unequivocal species of fuxianhuiid have been described, all from lower and middle Cambrian *Konservat-Lagerstätte* of southwest China.

## **Great-appendage arthropods:**

Great-appendage arthropods — which are defined by multisegmented hunting appendages attached to their heads (Fig. 3D) — have been prominent in recent discussions of arthropod relationships. However, when they were first discovered, their importance was not instantly recognized. Neither was the close relationship between various great-appendage-bearing groups. Palaeontologist Charles Doolittle Walcott (1850–1927), the discoverer of the Burgess Shale and the original describer of many Cambrian arthropods, thought that his new Burgess Shale species *Leanchoilia superlata* and *Yohoia tenuis* were closely related to separate branches of living crustaceans called the branchiopods (which include fairy shrimp, clam shrimp and the genus *Triops*). These crustacean affinities, or close relationships, were generally accepted by later workers. In the 1930s, Percy Raymond recognized the uniqueness of the appendage at the front of *Leanchoilia* and coined the term great appendage, which was also applied to *Yohoia* in the 1970s. Other workers compare the frontal appendages of *Leanchoilia* to the chelicerae (think of a spider's fangs!) of [chelicerates](#), suggesting that great appendages might be precursors of chelicerae. Both structures end in a pincer, are used for hunting or prey capture and have a distinct 'elbow' joint.

Further great-appendage arthropods were discovered from the Chengjiang biota, including *Jianfengia*. In 1997, Jan Bergström, a renowned expert on Cambrian arthropods, classified the great-appendage arthropods as a new group: Megacheira. Since then, megacheirans have generally been considered precursors either to chelicerates, or to a group containing all living arthropods.

## ***Sanctacaris uncata*:**

*Sanctacaris uncata* (Fig. 4) is a species of Cambrian arthropod that was originally considered an ancestor of chelicerates. Marine chelicerates include the [horseshoe crab](#); like the horseshoe crab and other chelicerates, *Sanctacaris* has a head with at least six pairs of appendages and a heart-shaped lobe at the back, division of the body into a head ([prosoma](#)) and trunk ([opisthosoma](#)), and an anus on the last body segment. However, some people criticized the idea that *Sanctacaris* was related to chelicerates, because it did not have chelicerae. Instead, the head appendages (Fig. 4) were reinterpreted as a great-appendage-like 'limb basket'. Recent studies have reaffirmed chelicerate affinities, making this one of the earliest members of the lineage that led to spiders, scorpions and their relatives.

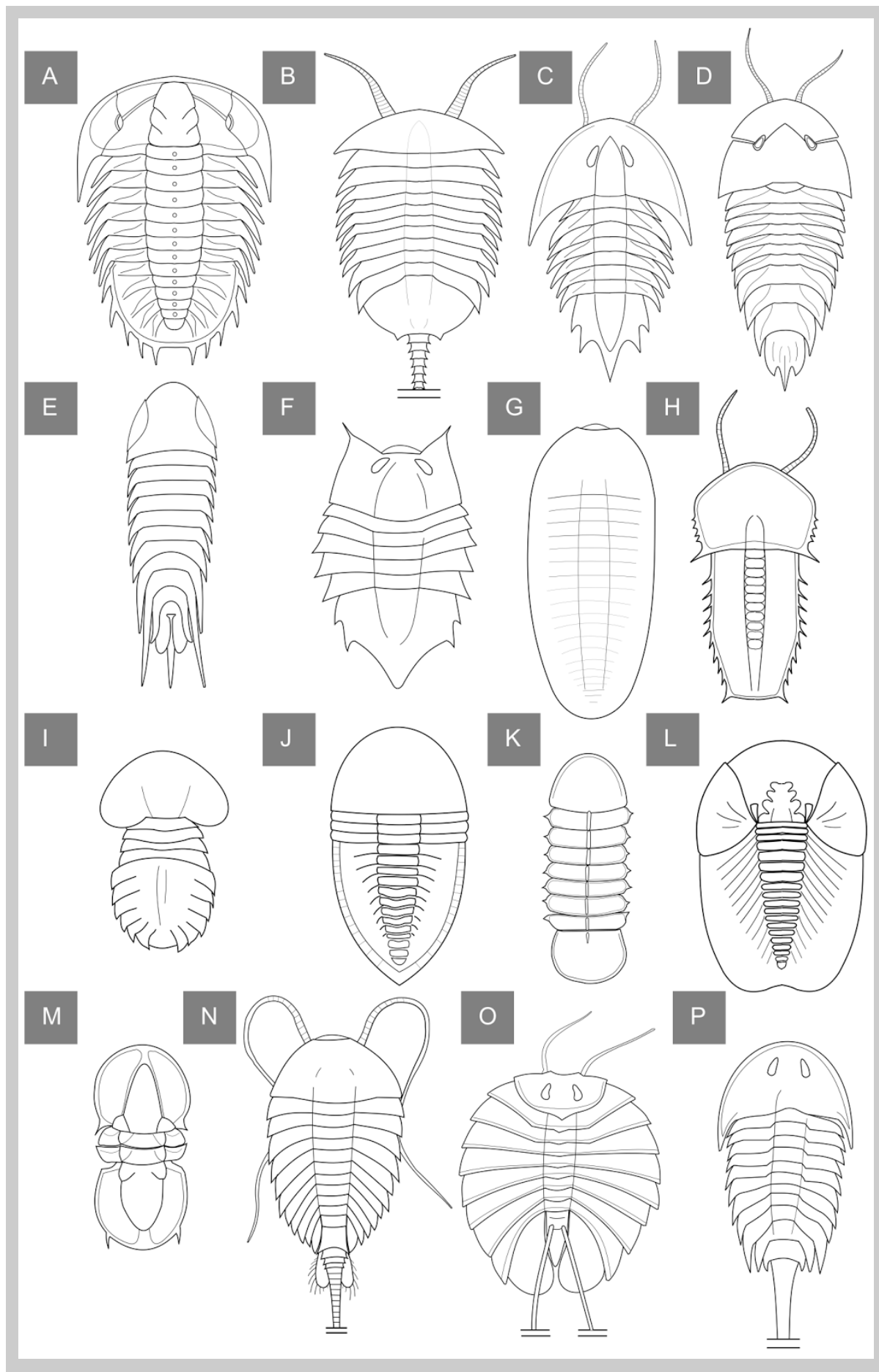


Figure 4 — The ‘claws’ of *Sanctacaris uncata*, from the Burgess Shale, Canada (courtesy of [Royal Ontario Museum](#), holotype ROM 43502).

## Trilobites and trilobitomorphs:

Trilobites make up one of the most recognizable fossil groups (Fig. 5A), and have an extensive fossil record. More than 5,000 [genera](#) have been described, encompassing some 19,606 species. They first appeared in the fossil record about 521 million years ago. Trilobite diversity reached its peak in the late Cambrian, before declining in the [Ordovician period](#) (488 million to 444 million years ago). The group died out in the [mass extinction](#) at the end of the Permian period, around 251 million years ago. Despite trilobites’ ubiquity in the fossil record, the anatomy of their soft parts is known from just 19 species. The commonly recovered calcium-carbonate-reinforced exoskeleton of trilobites is divided into three tagmata, each with three lobes (hence the name trilobite). The tagmata are: head at the front; pygidium at the back; and thorax in between. There is a similar tagmatisis in a number of species that are similar to the trilobites, but are a little too different to fit in the group proper. These, along with the trilobites, are termed trilobitomorphs.

Figure 5 (overleaf) — Examples of trilobites, trilobitomorphs and vicissicaudates. A, The trilobite *Olenoides serratus*. B, The retifaciid *Retifacies abnormalis*. C, The petalopleuran (sinoburiid) *Sinoburius lunaris*. D, The petalopleuran (xandarellid) *Xanderella spectaculum*. E, The potential petalopleuran *Acanthomeridion serratum*. F, The concilitergan (helmetiid) *Helmetia expansa*. G, The concilitergan *Saperion glumaceum*. H, The nektaspid (naraoid) *Naraoia spinosa*. I, The nektaspid (liwiid) *Soomaspis splendida*. J, The nektaspid (emucaridid) *Kangacaris zhangi*. K, The mollisonid *Mollisonia symmetrica*. L, *Phytophilaspis pergamena*. M, The agnostid *Agnostus pisiformis*. N, The vicissicaudate (xenopod) *Emeraldella brocki*. O, The vicissicaudate (cheloniellid) *Cheloniellon calmani*. P, The aglaspidid *Aglaspis spinifer*.





Despite numerous efforts, relationships among these trilobitomorphs are unclear. However, when the relationships of some groups are analysed (a [phylogenetic analysis](#)), they return consistent results. These [clades](#) are introduced below.

The retifaciids (Retifaciida) are characterized by the possession of a short, broad head shield, a large, oval pygidium and an elongate multisegmented structure (called a [telson](#)) at the end (Fig. 5B).

The petalopleurans (Petalopleura) all have well-defined lobes on either side of the central lobe, with distinct overlap between adjoining segments (Fig. 5C–E).

Concilitergans (Conciliterga) are probably more closely related to trilobites than other trilobitomorphs, based on recent studies, although there are few obvious features to support this. A suite of characters that does support the suggestions that this is a true ([monophyletic](#)) grouping includes: teardrop-shaped growths from the second branch of their limbs; a notch cutting into the very front margin of the animal; and a separate plate on the upper side towards the front (Fig. 5F, G).

Of the non-trilobite trilobitomorphs, the nektaspids (Nektaspida) are the longest-ranging and most geographically widespread. Other groups are restricted to the Cambrian, but the nektaspids range from the lower Cambrian of Poland to a species called *Naraoia bertiensis* from the Upper [Silurian period](#) (423 million to 419 million years ago) of Canada. Nektaspids have three distinct shapes (Fig. 5H–J). The naraoiids have a very simple tagmosis (Fig. 5H), with just a hinge between plates on the front and back half of the animal. Unlike trilobites, they do not have a thorax made of segments capable of moving. Other nektaspids do have this flexible thorax, albeit with a reduced number of segments, and are represented by the liwiids (Fig. 5I), and the emucaridids (Fig. 5J). Emucaridids are most easily recognized through their elongate pygidium, which accounts for more than half the length of the body behind the head. By contrast, liwiids typically have a pygidium and [cephalon](#) roughly equal in size.

Other taxa of interest, such as the mollisonids (Fig. 5K), clearly belong within Trilobitomorpha, but their exact relationships remain uncertain. *Phytophilaspis pergamena* (Fig. 5L), from the lower Cambrian Sinsk Biota of Siberia, was originally considered a concilitergan, based on the fact that its thorax and pygidium were fused together. However, this feature is also observed in some nektaspids. Other researchers have highlighted the presence of eye slits and a head that overlaps the thorax, which may be indicative of another group called the xandarellids (Fig. 5D), although *P. pergamena* also has a plate on the underside called a hypostome, which is similar to that of trilobites.

### ***Agnostus pisiformis*:**

The agnostids — an arthropod order found from the early Cambrian period to the late Ordovician, which peaked in diversity during the middle Cambrian — have long been considered a highly unusual group of trilobites. However, the discovery of very well preserved *Agnostus pisiformis* specimens (Fig. 5M) from the late Cambrian 'Orsten' Lagerstätte led to a re-evaluation of agnostid affinities. They are now commonly regarded as the ancestors of crustaceans, based on their appendages. Cambrian arthropods are rarely simple, however, and some researchers have challenged this opinion, regarding agnostids as specialised trilobites.

## Vicissicaudates:

Perhaps one of the most recent groupings to be recognized, the vicissicaudates make up a clade of [Palaeozoic](#) arthropods united by the shared presence of a differentiated set of segments at the back that lack appendages (a bit like a scorpion's tail; Fig. 5N–P). This group may be closely related to the trilobitomorphs. Trilobitomorphs and vicissicaudates share limb features which suggest that they may be closely related. The grouping of the two has been called the Artiopoda.

Vicissicaudates themselves have been split into three groups. The Xenopoda include three species: *Emeraldella brocki* (Fig. 5N), *E. brutoni*, and *Sidneyia inexpectans*. These species have a set of flaps projecting from their back ends. This is similar to an arrangement seen in the species *Malaria spinifera*, which may also belong to this group.

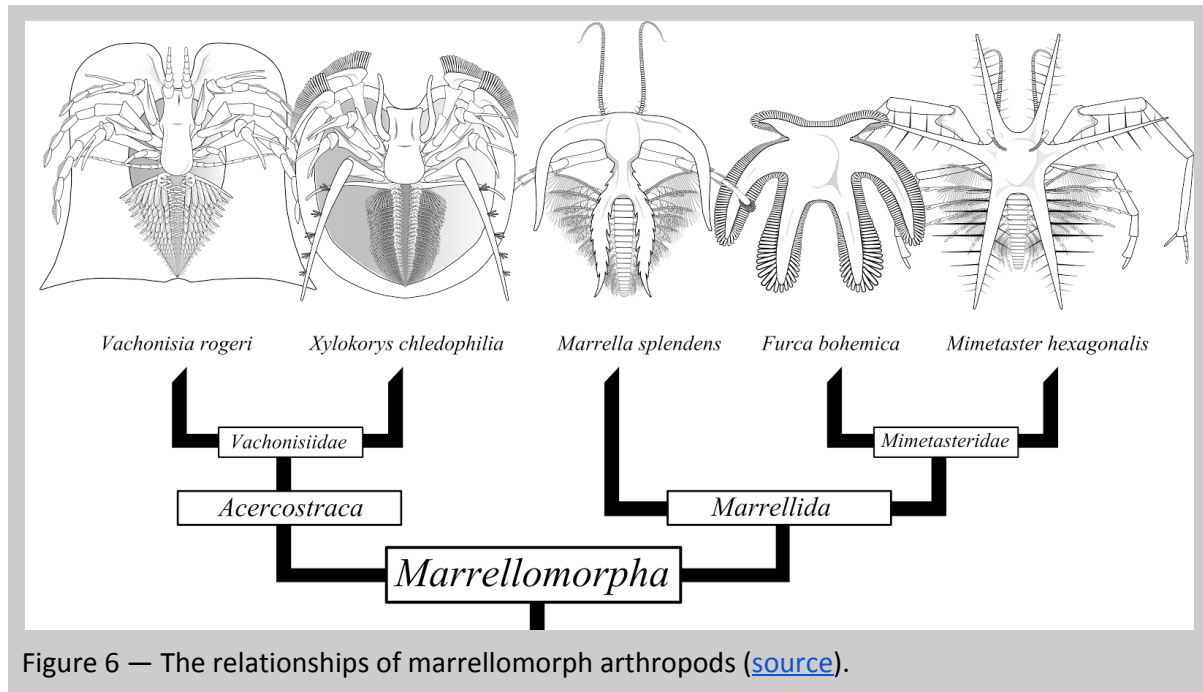
Like xenopods, the cheloniellids (the second line of Vicissicaudates) have modified limbs at the back of the animal — instead of these flap-like, these are more like appendages, attaching to the upper surface of the body (structures called furcae; Fig. 5O). Unusually, they also have an unfused or reduced head shield.

For a long time the last of the three vicissicaudate lineages, the aglaspidids (Fig. 5P), was treated as a 'bucket taxon' for species that would not really fit elsewhere. Systematic study of these species has helped to 'clear out the wastebasket', and as a result, shared features that define the aglaspidids are starting to emerge. The group is loosely identified by a raised rim around the outside of the head, and spines at the side of the head. The majority of the group, and those considered 'true aglaspidids' (*Aglaspidida sensu stricto*), also have a mineralized exoskeleton, and a few more shared features of the head and body. This group was originally considered to be closely allied to horseshoe crabs, but such affinities were rejected after additional preparation of *Aglaspis spinifer* was unable to reveal chelicerae. Despite this, some workers continued to recover close affinities between aglaspidids and chelicerates.

## Marrellomorphs:

The marrellomorphs make up a small group of Palaeozoic arthropods, renowned for their bizarre anatomy (Fig. 6). Although they are generally regarded as being closely related, some workers have suggested otherwise. The marrellomorphs can be broadly divided into two groups: the Marrellida and the Acercostraca (Fig. 6). The marrellids have extensions travelling backwards from the head.. By contrast, the acercostracans have the entire body and all appendages tucked under a single large plate. There are few characters shared by these two groups, although the possession of more than 25 trunk appendages, which reduce in size towards the back of the animal, has been considered a possible means of identifying members of the group.

Like those of many other Palaeozoic arthropods, the affinities of marrellomorphs have remained unclear, but nowadays these species are generally considered distant relatives of mandibulate arthropods (the group that includes crustaceans, insects, millipedes and centipedes, but not chelicerates).



## Conclusion:

Although many Cambrian arthropods were originally considered aberrant members of modern arthropod groups, their exact affinities have been challenged many times. Thanks to recent studies, however, a general consensus regarding their relationships is starting to emerge, and they can even help to reveal the potential relationships of many modern groups. Some Cambrian arthropods represent lineages that evolved before the origin of modern arthropod groups, whereas others may represent very early members of the groups with which we are familiar. Ongoing study using modern analytical methods will continue to help us to understand the true importance and affinities of the first arthropods.

## Further reading:

Edgecombe, G. D. & Legg, D. A. 2013. The arthropod fossil record. In *Arthropod Biology and Evolution: Molecules, Development, Morphology* (eds Minelli, A., Boxshall, G. & Fusco, G). pp. 393–415. Springer. ISBN: 978–3–642–36159–3

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Legg, D. A., Sutton, M. D. & Edgecombe, G. D. 2013. Arthropod fossil data increase congruence of morphological and molecular phylogenies. *Nature Communications* 4, 4285. doi:[10.1038/ncomms3485](https://doi.org/10.1038/ncomms3485)

<sup>1</sup>Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK