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Fossil Focus: Marrellomorph arthropods

by [David Legg](#)*¹

Introduction:

The [Palaeozoic era](#) was a time of incredible biological [diversification](#), which saw the origins and establishment of most modern animal [body plans](#) and [phyla](#), particularly during the [Cambrian explosion](#), an event which lasted for about 20 million years during the early Cambrian Period (starting about 542 million years ago), and the subsequent [Great Ordovician biodiversification event](#). During this time, there was a lot of 'evolutionary experimentation', with many ancient communities dominated by alien-looking creatures unlike any of their modern counterparts. One such peculiar group is the marrellomorph [arthropods](#), roughly 11 species known exclusively from the lower [Cambrian](#) (starting about 542 million years ago) to the lower [Devonian period](#) (ending about 393 million years ago).

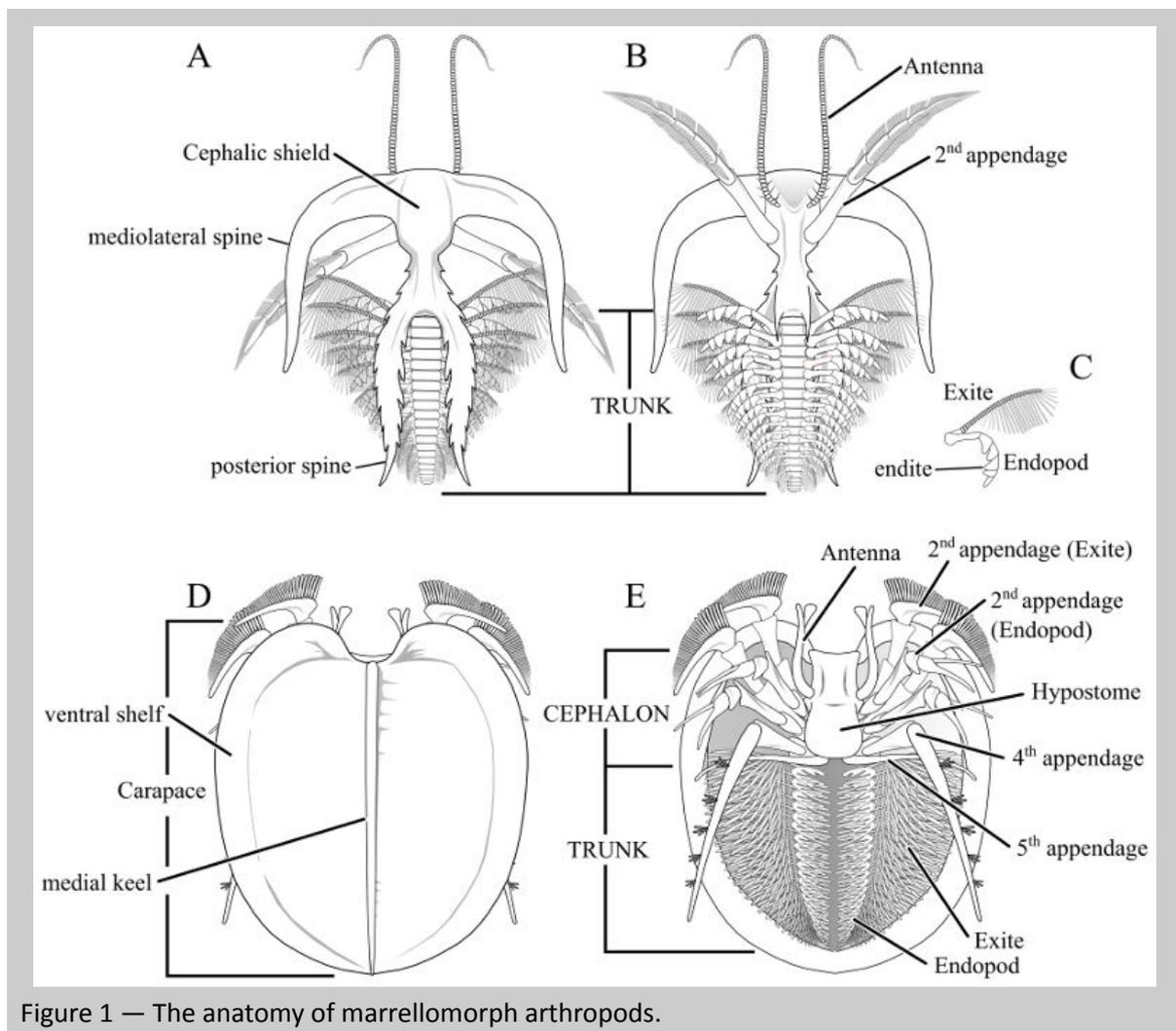


Figure 1 — The anatomy of marrellomorph arthropods.

Morphology:

The marrellomorphs can be broadly divided into two groups, distinguished primarily by the shape of their cephalic shields — the tough outer covering of their heads — and associated structures.

Members of the first group, the marrellids — typified by *Marrella splendens* (Fig. 1A,B), the most abundant arthropod in the 505-million-year-old middle Cambrian Burgess Shale — all have a short head, bearing two pairs of appendages and covered by a cephalic shield with extensive spines that are sometimes as long as the entire trunk. These spines may be fringed with secondary spines (Fig. 2). The function of these is unclear, but they may have warded off predators.

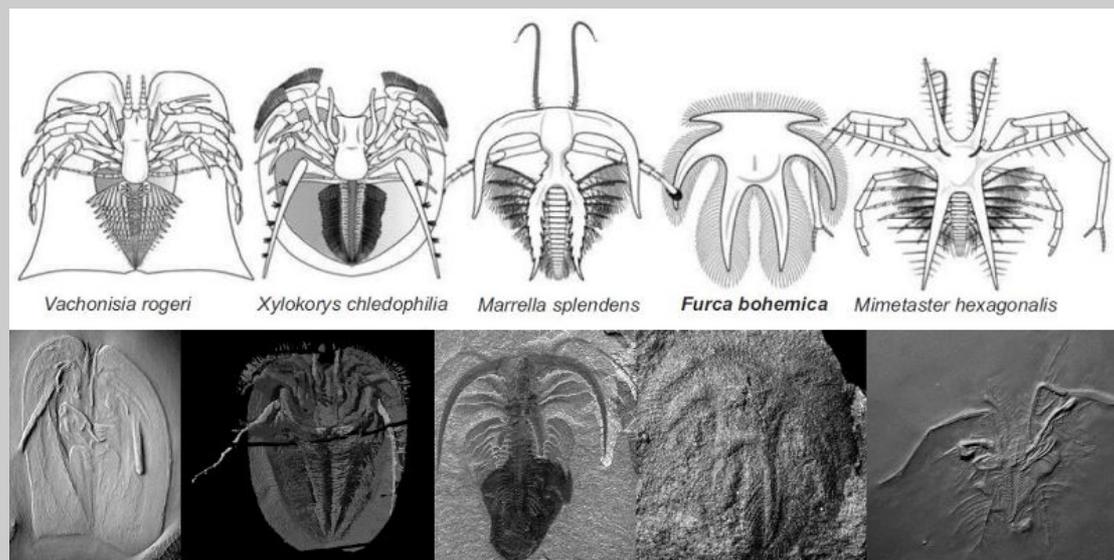


Figure 2 — All species recognised as marrellomorphs circa 2013. Source: [Rak et al. \(2013\)](#).

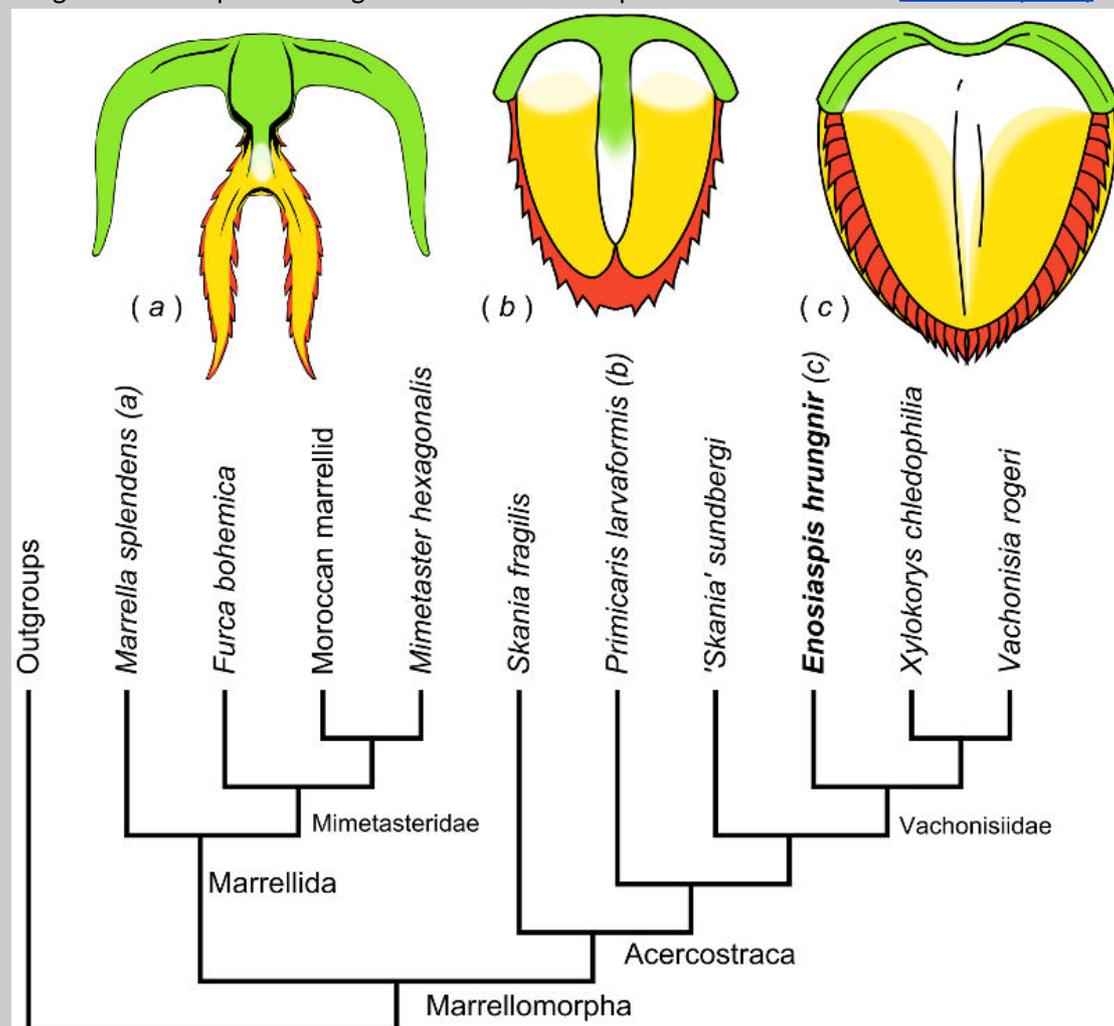


Figure 3 — The phylogeny of marrellomorph arthropods and the evolution of the acerrostracan head shield. Source: [Legg \(2016\)](#).

Members of the second group, the acercostracans, possess a large [cephalic shield](#), which extends to the sides and back into a heart-shaped [carapace](#) that covers the entire body (Fig. 1). Although this is very different from the cephalic shield of marrellids, a recent study suggested that the acercostracan carapace may have formed from the fusion of marrellid-like spines during the evolution of the group (Fig. 3).

These two seemingly disparate groups have similarities in other aspects of their anatomy. Both groups possess: a long, thin body bearing numerous limb pairs (typically more than 25), which get smaller towards the back of the animal; appendages bearing a multi-segmented outer branch, the [exite](#), which is covered in fine bristles that may have been used for respiration; and an inner limb branch made of roughly seven segments, each tipped with a rounded inner projection (Fig. 1). Both groups have long, thin exites on their heads. In *Marrella*, these are single-branched ‘swimming paddles’ (Fig. 1); in the acercostracans, represented here by *Xylokorys* (Fig. 1), they are tipped with a bristly brush.

Composition and distribution

Until 2013, just five species of marrellomorph were recognized (Fig. 2). There were three marrellids — *Marrella splendens* from the middle Cambrian Burgess Shale Formation of British Columbia, Canada (505 million years old), *Furca bohémica* from the Middle [Ordovician](#) Letná Formation of the Czech Republic (455 million years old) and *Mimetaster hexagonalis* from the lower Devonian Hunsrück Slate of Germany (407 million years old) — and two acercostracans, *Vachonisia rogeri* from the Hunsrück Slate and *Xylokorys chledophilia* from the middle Silurian of Herefordshire, UK (roughly 430 million years old).

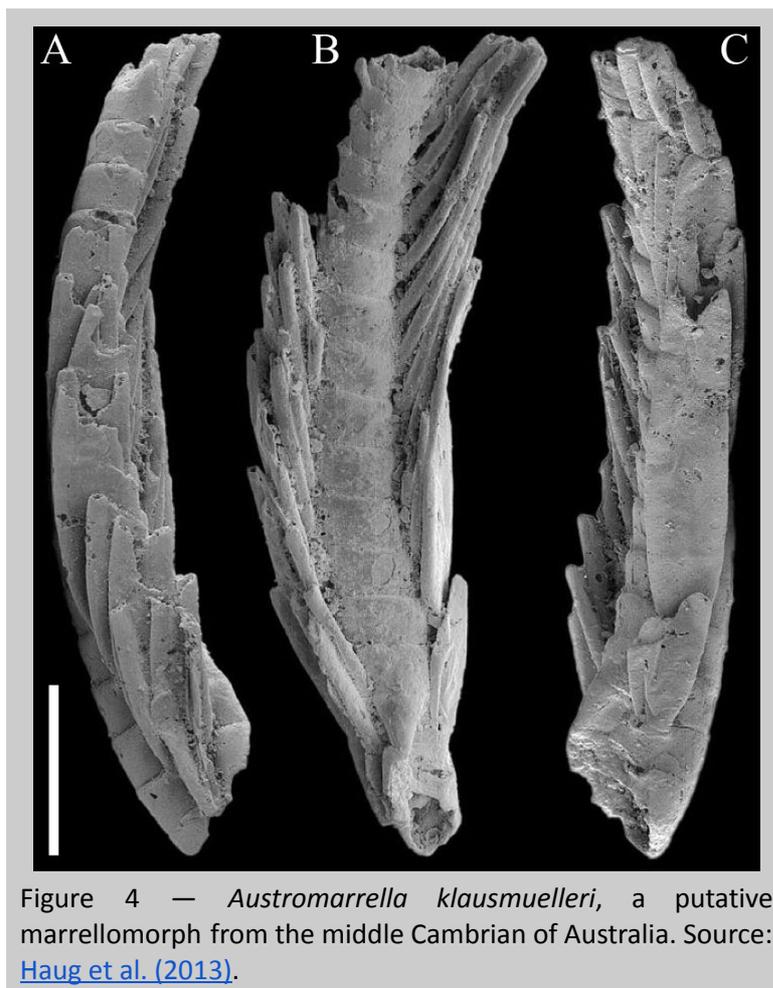


Figure 4 — *Austromarrella klausmuelleri*, a putative marrellomorph from the middle Cambrian of Australia. Source: [Haug et al. \(2013\)](#).

In the past three years, three new species have been described: *Enosiaspis hrungnir*, an acercostracan from the lower Ordovician of Morocco (480 million years old; Fig. 3); *Dyrnwynia conollyi*, thought to be a marrellid from the Middle Ordovician of Wales (460 million years old); and *Austromarrella klausmuelleri*, a potential marrellomorph from the middle Cambrian of Australia (roughly 505 million years old; Fig. 4). The skaniids, three species of enigmatic lower and middle Cambrian arthropods from China and British Columbia, were in 2015 found to belong to the acercostracans, because they have, amongst other features, a heart-shaped carapace which covers the entire body (Fig. 5).

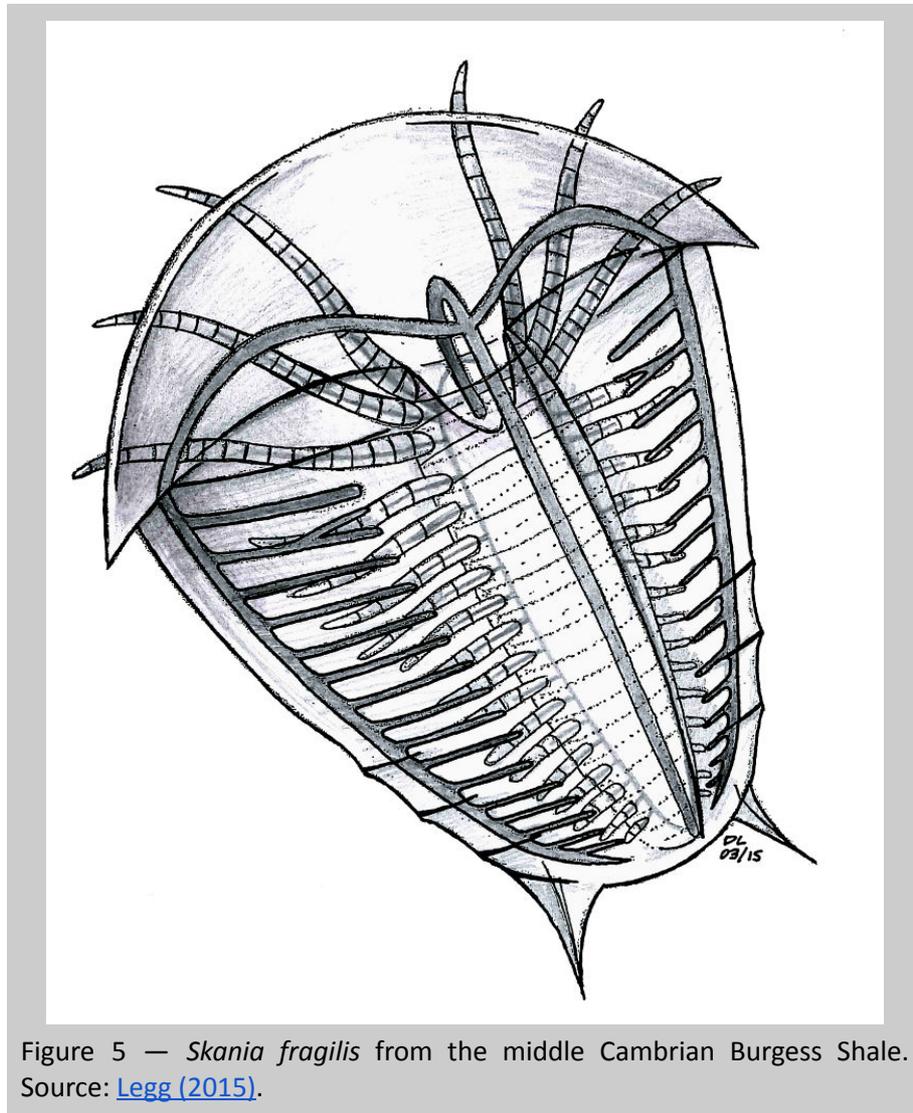


Figure 5 — *Skania fragilis* from the middle Cambrian Burgess Shale. Source: [Legg \(2015\)](#).

Although not formally described yet, there are also records of marrellids from the lower Ordovician of both Morocco and Argentina, and isolated remains comparable to *Marrella* from the lower Cambrian of China. This indicates that although marrellomorphs are relatively rare in the fossil record, there may be many more still waiting to be discovered.

Phylogeny:

Although most people agree that the acerrostracans and marrellids are closely related to each other, it has been quite challenging to work out how they are related to other arthropods. This is because their body plan is undoubtedly very different from that of their relatives, and offers few clues about their ancestry.

Like many fossil arthropods discovered in the early twentieth century (*Marrella* was first described in 1911 by US palaeontologist [Charles Doolittle Walcott](#)), the marrellomorphs were typically compared to [crustaceans](#) or [trilobites](#), with some researchers even mistaking the distinctive head of *Furca* for a trilobite mouthpart. The majority of later studies, however, have considered them to be much more primitive. This was bolstered by the advent of studies in the early 1990s that used [computational methods](#) to determine evolutionary relationships, although the results have been far from

consistent. Some studies have concluded that marrellomorphs are the ancestors of all arthropods that have biramous (two-branched) limbs, a relationship which seems increasingly unlikely given our current knowledge of relationships between living arthropods. Others have concluded that they are the most primitive members of the line that leads to either chelicerates (horseshoe crabs and arachnids) or mandibulates (insects, centipedes, millipedes and crustaceans). For now, it seems that features such as the anatomy of the trunk limbs and the presence of a carapace (at least in acerrostracans) are most consistent with the latter interpretation.

Mode of life:

Very little is known about how marrellomorphs lived. With their bizarre anatomy and lack of living relatives, we have few, if any, appropriate species to compare them with, although a number of hypotheses have been proposed on the basis of their anatomy and the environments in which they lived.

Many early studies considered the marrellomorphs to live in the water column, based in part on comparisons with the [zooplanktonic](#) larvae of crustaceans. Others have argued that the heads of marrellomorphs were too bulky and rigid for the creatures to actively swim.

The marrellid *Mimetaster hexagonalis* (Fig. 2) is often found covered by tentaculoids, a presumably [suspension-feeding](#) organism of uncertain affinities, known from the Ordovician period (starting 485 million years ago) to the [Jurassic](#) period (ending 146 million years ago). These organisms may have acted as a form of camouflage for the marrellid, although this is almost impossible to test. It does, however, lend support to the idea that marrellomorphs were not active swimmers, because it is incredibly unlikely that a bulky covering of such organisms could accumulate on an animal living in the open ocean.

Summary:

Although our knowledge of marrellomorph arthropods has substantially increased in the past few years, thanks to improvements in methods for analysing their evolutionary relationships and the discovery of new Palaeozoic fossil sites, they still remain enigmatic. Their aberrant anatomy makes determining both their relationships and their potential modes of life extremely difficult. With new discoveries and the proliferation of new analytical techniques, however, we are likely to find out much more about this enigmatic group in the next few years.

Suggestions for further reading:

Haug, J.T., Castellani, C., Haug, C., Waloszek, D. & Maas, A. 2013. A *Marrella*-like arthropod from the Cambrian of Australia: A new link between “Orsten”-type and Burgess Shale assemblages. *Acta Palaeontologica Polonica* 58, 629-639. doi:[10.4202/app.2011.0120](https://doi.org/10.4202/app.2011.0120)

Legg, D.A. 2015. The morphology and affinities of *Skania fragilis* (Arthropoda) from the middle Cambrian Burgess Shale. *Bulletin of Geosciences* 90, 509-518.

Legg, D.A. 2016. An acercostracan marrellomorph (Euarthropoda) from the Lower Ordovician of Morocco. *The Science of Nature* 103:21. doi:[10.1007/s00114-016-1352-5](https://doi.org/10.1007/s00114-016-1352-5)

Rak, Š., Ortega-Hernández, J. & Legg, D.A. 2013. A revision of the Late Ordovician marrellomorph arthropod *Furca bohémica* from Czech Republic. *Acta Palaeontologica Polonica* 58, 615-628. doi:[10.4202/app.2011.0038](https://doi.org/10.4202/app.2011.0038)

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