

Head in the late
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Head Segmentation and Fossils The extensive discussion over how the head segments of existing arthropods are aligned was largely eliminated in the late 1990s when the expression domains of Hox genes was first applied to the study of Arthropod evolution. The traditional concept that chelicerates had lost a deuto cerebral segment and that the chelicerae was innervated by the tritocerebrum was disproved when the anterior expression domain of labial, the anteriormost gene of the arthropod Hox cluster, was found to align the chelicerae with the first antenna of mandibulates (Damen et al 1998). This alignment of the head was later confirmed by correspondence in the developing nervous systems of *Limulus* and crustaceans and is now widely supported by scientists. Another study that has been even more widely debated has been the segmental composition of the brains of the non arthropod Panarthropoda, the Onychophora and Tardigrada.

Researchers were looking into how many segments comprise the brain and their homologies with the tripartite brain of arthropods. The tardigrade brain is thought to be composed of a single segment, correlating to the arthropod protocerebrum alone, or to possibly include as many as two additional neuromeres (Meusemann et al 2010). According to nervous system development, the onychophoran brain is assigned just two segments, correlating to the arthropod protocerebrum and deutocerebrum.

Hox expression domains show that the third head segment of onychophorans, which contains the slime papilla, is segmentally equivalent to the tritocerebrum of arthropods, although the correlating ganglia do not originate from the central neuropils of the onychophoran brain (Edgecombe and Legg 2014). There is even greater debate surrounding the segmental

alignment of head structures in many fossil arthropods and those of existing taxa, an exhibition of the so-called arthropod head problem. Much of the debate involves the interpretations of structures in Cambrian fossils categorized as frontal appendages or great appendages. Whether predatory appendages in such taxa as anomalocaridids and megacheirans belong to the same head segment and with which neuromere of the brain they are associated is the heart of the problem (Edgecombe and Legg 2014).

More recent studies consider these appendages to either be or not be segmentally equivalent. In the case of megacheirans, the segmental affiliation of the great appendages ranges from them being proto cerebral, deuto cerebral or trito cerebral. The traditional basis for identifying the segmental association of modified appendages in fossil arthropods has been to use structural correspondence in appendage morphology, for example, the elbow joint and chelate tip of megacheiran great appendages suggest homology with chelicerate, and to integrate their relationships to other appendages, like using an apparent association of megacheiran great appendages and antennae in some taxa suggests the former are trito cerebral/postcheliceral if the antennae are deuto cerebral as in existing arthropods (Damen et al 1998).

Recently, a few studies have identified neural tissue in Cambrian fossils that allows putative neuromeres of the brain to be associated with appendages. The brain of *Fuxianhuia protensa* from the Chengjiang biota has identifiable neural tracts to the ocular lobes, antennae and postantennal appendages that associate these segmental structures with the proto-, deuto- and tritocerebrum, respectively (Chen et al 1995). This evidence has assisted the

interpretation of specialized postantennal appendages in *Fuxianhuia* that had alternatively been viewed as gut diverticulae. Segmental alignment with existing chelicerates was argued to favor deuto cerebral affinities for the short-great-appendages. Character Acquisition A number of new discoveries from early Palaeozoic Konservatory Lagerstätten, combined with the application of large-scale phylogenetic analyses, has had considerable impact on the understanding of the early stages of arthropod evolution. Specifically, characters that were thought to be suggestive of arthropod similarities have been shown to be acquired sequentially along the arthropod stem.

The lobopodians have traditionally been considered the stem-group representatives of the three existing pan-arthropod lineages and so they are very crucial for tracing the evolution of key characteristics in the arthropod stem lineage. *Diania cactiformis*, a lobopodian from the Chengjiang biota, was originally interpreted as possessing arthropodized appendages, a key characteristic of arthropods, prompting a proposal that sclerotization of the trunk appendages occurred before sclerotization of the body (Chen et al 1995). A phylogenetic analysis resolved *Diania* in the arthropod stem lineage amongst the dinocaridids, a clade of pan-arthropods that includes taxa with arthropodized cephalic appendages but lacking trunk appendages.

Subsequent analyses were unable to reproduce these results and instead resolved *Diania* more stemward in the lobopodian grade, and a study of new material of *Diania* cast doubt on the interpretation of the trunk appendages as arthropodized (Meusemann et al 2010). Existing arthropods possessed a diverse array of visual systems which differ in their number of visual

elements and their relative position. Numerous studies strongly support a common origin for rhabdomic compound eyes of arthropods based on the ultrastructure of existing exemplars, but details of their origins have been obscure. The eyes of the lobopodians *Hallucigenia fortis* and *Luolishania longicruris* have been interpreted as having a multicomponent structure formed of individual ocelli, prompting comparison with the lateral eyes of arthropods (Edgecombe and Legg 2014). Given the prior hypotheses of phylogenetic relation, this structure may represent the precursor of the compound eyes found in arthropods and dinocaridids, although conflicting evidence either agrees that some of these taxa with onychophorans rather than arthropods, like in the case of hallucigeniids, or interprets the eyes of Cambrian lobopodians as simple ocelli. The elucidation of the visual surface of anomalocaridids indicates that complex visual systems, in this case highly adapted to a macrophagous predatory lifestyle, evolved early in the arthropod stem, prior to the origin of arthropodized trunk appendages and sclerotization of the body (Waloszek et al 2005).

Another study of anomalocaridid taxa has contributed some features that encourage the case for arthropod relatedness. In particular, the lateral cephalic elements of *Hurdia* have been compared to the bivalved carapace of Cambrian bivalved arthropods, the last mentioned forming a paraphyletic grade of organization at the base of Arthropoda. Other assumed similarities between anomalocaridids and basal members of the bivalved arthropod grade include the possession of a weakly sclerotized trunk and a posterior tagma composed of multiple pairs of lateral flap-like processes (Waloszek et al 2005). Some studies have noted similarities in the structure of the frontal

appendages of anomalocaridids and the cosmopolitan Cambrian bivalved arthropod *Isoxys* and concluded that in both cases their frontal appendages originated from the protocerebral somite and were therefore homologous with the antennae of onychophorans (Pisani et al 2004). Others further noted that specialized predatory appendages or short-great appendages first appeared in basal bivalved arthropods and on that case then proposed non homology to the chelicerae of chelicerates. As noted above, the phylogenetic position of short-great-appendage arthropods and the segmental homology of their eponymous appendages have been points of discussion in recent studies. Neural arguments for a deuto cerebral affinity for the short-great-appendages are consistent with their structural similarities to chelicerae.

Analyses including a more diverse assembly of non arthropod taxa have tended to resolve megacheirans as the paraphyletic sister taxon of Euarthropoda, regardless of how the segmental affinities of the short-great-appendages were interpreted (Pisani et al 2004). Fossils and Divergence Dates Early attempts at molecular dating commonly found that arthropods had a long unfossilized history in the Neoproterozoic, and this has been maintained in some more recent studies. Improved relaxed clock methods and more precise integration of palaeontological constraints have for the most part weakened the argument for arthropod history extending as far back as the Cryogenian, but even modern molecular dates usually estimate the split of Arthropoda from its sister group and the fundamental splits within the arthropod crown group (Chelicerata-Mandibulata divergence) as being Ediacaran (Regier and Shultz 1997). Even this comparatively short phylogenetic fuse in the Ediacaran predates fossil evidence for arthropods.

Despite the attempts to accommodate Ediacaran fossils such as Spriggina, Parvancorina and Archaea Sinus into the arthropod stem- or crown groups, these organisms share no definitive characters with Arthropoda, and Panarthropoda as a whole is unrepresented in the fossil record until the first Rusophycus traces are found in the Fortunian (Edgecombe and Legg 2014). The Cambrian fossil record presents a strong case that lobopodians rather than Ediacarans represent a morphological grade in the stem groups of the three pan arthropod lineages.

If the palaeontological case for arthropod origins and diversification in the Cambrian rather than the Neoproterozoic is accurate, recovery of arthropod body fossils referable to such existing crustacean groups as Branchiopoda and Copepoda in palynological samples from the late early and late Cambrian signals an explosive radiation of crustaceans, and implicitly other arthropods, during the Cambrian (Regier and Shultz 1997). The identification of these fossils as members of existing crustacean total groups contributes to molecular and morphological clock estimates of rates of evolution amongst early arthropods several times faster than background levels regardless of how deeply in the Ediacaran the origin of Arthropoda is allowed to extend (Meusemann et al 2010). DiscussionThe study of arthropod evolution has progressively rapidly since the start of the 21st century. Most genomic techniques such as phylogenomics, data reconstruction, and RNA transcript mapping has played a large in this progression. Arthropoda is monophyletic, and with evolutionary mapping, it has been shown that Arthropoda splits into Pycnogonida + Euchelicerata and Myriapoda + Pancrustacea.

Researchers have also found a sister group relationship between Onychophora and Arthropoda that is supported by RNA transcripts and microRNAs. Although, molecular dating shows the first origins of Arthropoda to be in the Cambrian Period, there is some data that suggests it could have origins earlier than this time. These gaps are what makes it hard to answer some fundamental questions of arthropod evolution.

There are some terrestrial organisms whose stem groups have not been identified in arthropoda so this could be a point for further investigation. Some species of crustaceans have not yet come together on stable, well-supported groups. Fragments of crustacean fossils are found and used in analysis to determine groups, but the quality of the fossils also further complicates the process of determining their associations and positions.