Ecdysozoa

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--Protostomia
   |--SPIRALIA
   |
   `----ECDYSOZOA = paraphyletic Scalidophora?
      |==Palaeoscolecida
      |==Priapozoa
      |  |--Kinorhyncha
      |  `--+--Priapulida
      |     `-- Loricifera
      `--+--Nematoida
         |   |--Nematoda
         |    `--Nematomorpha
         `--Panarthropoda
            |--Tardigrada
            `--+--Onychophora
                `--+--Dinocaridida
                   `--ARTHROPODA
```

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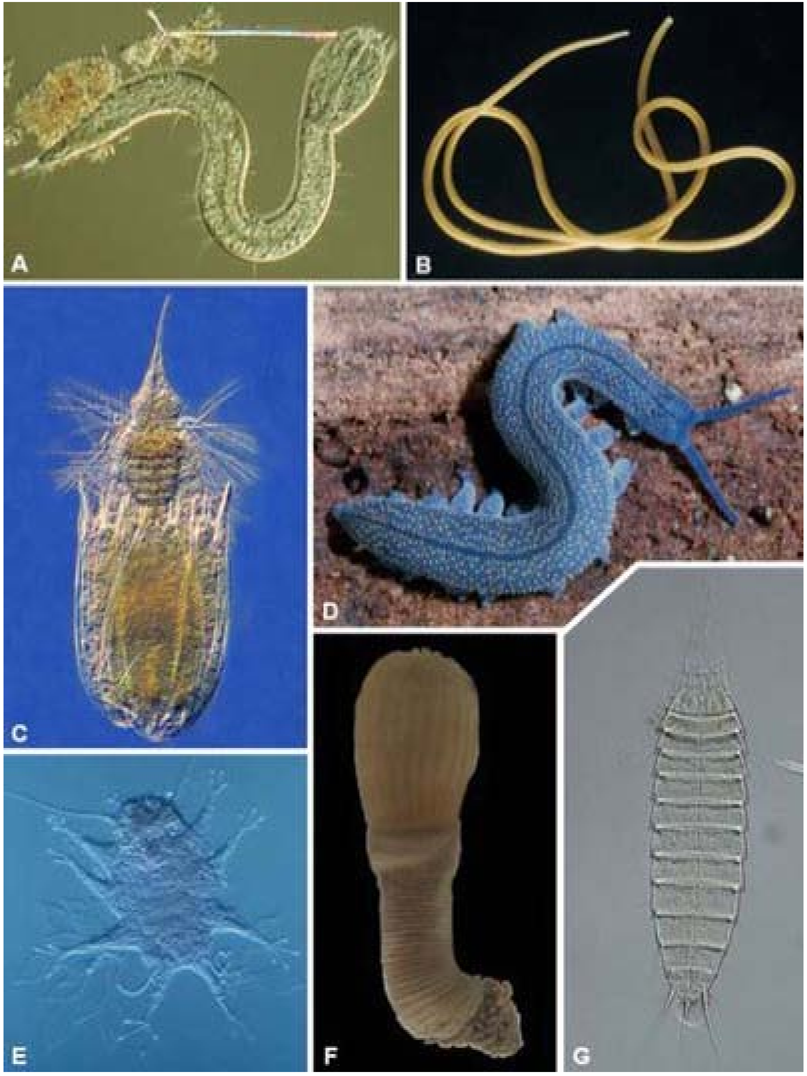

Examples of the phyla of molting animals grouped with arthropods in Ecdysozoa. **a** Nematoda (*Draconema* sp.); **b** Nematomorpha (*Spinochordodes tellinii*); **c** Loricifera (*Nanaloricus mysticus*); **d** Onychophora (*Peripatoides aurorbis*); **e** Tardigrada (*Tanarctus bubulubus*); **f** Priapulida (*Priapulus caudatus*); **g** Kinorhyncha (*Campyloderes macquariae*).

Collage and caption from Edgecombe 2009; images courtesy of Martin Sørensen (a, g), Andreas Schmidt-Rhaesa (b, f), Reinhardt Kristensen (c, e) and Gonzalo Giribet (d)

The Ecdysozoa, for our purposes, are treated as bugs > slugs -- a stem group leading to the Arthropoda. However, they are better known as the "molting clade" -- the animal phyla with a cuticle which is molted. Although there is still some suspicion that they might not be a clade, the validity of the Ecdysozoa is coming increasingly to be accepted among workers in this field. Phyla included are the Arthropoda, Tardigrada, Onychophora (which together make up the "Panarthropoda"), as well as the more primitive worm-like and "pseudocoelomate" groups like the Nematoda, Nematomorpha, Priapula, Kinorhyncha and Loricifera. However, the variability of definitions and uncertainty of the data in this region of phylospace make almost any assignment possible. ATW, revised MAK120415

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```
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   |
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      |==Priapozoa
      |  |--Kinorhyncha
      |  `--+--Priapulida
      |     `-- Loricifera
      `--+--Nematoida
         |   |--Nematoda
         |    `--Nematomorpha
         `--Panarthropoda
            |--Tardigrada
            `--+--Onychophora
                `--+--Dinocaridida
                   `--ARTHROPODA
```

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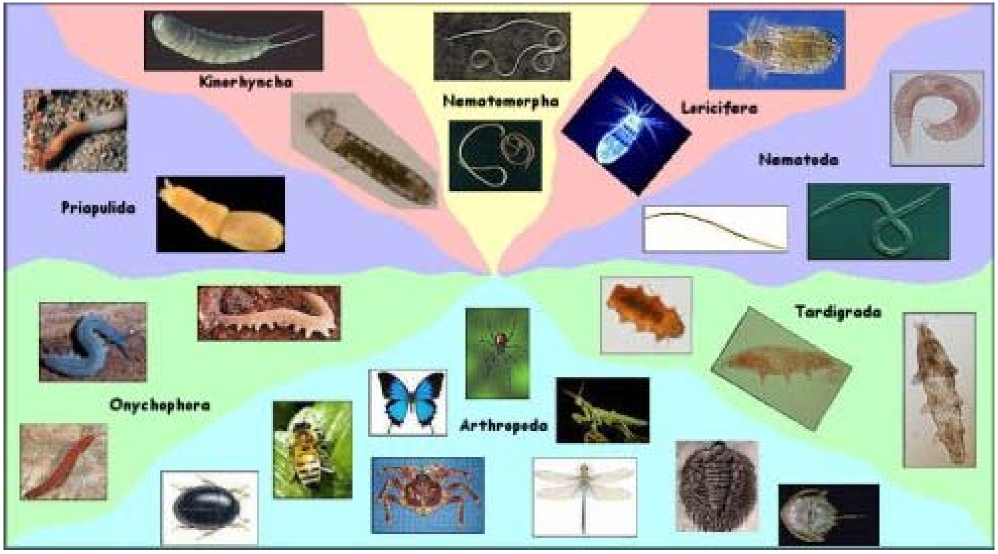
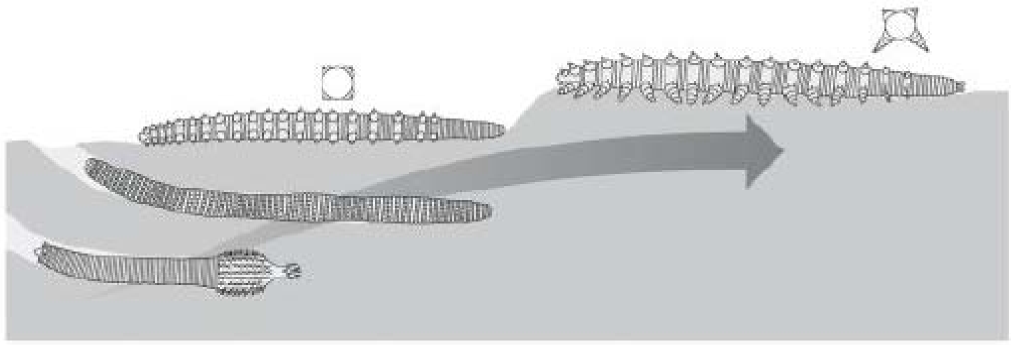


The diversity of Ecdysozoa, by The Dinosaur Fan, showing a random sleection from each of the eight major phyla (clockwise from lower left): Onychophora, Priapulida, Kinorhyncha, Nematomorpha, Loricifera, Nematoda, Tardigrada, and Arthropoda. Although today these phyla are very distinct, during the Cambrian period there were many intermediate and transitional forms linking them.

The Evolution of the Ecdysozoa

The Ecdysozoa or "moulting animals" include a number of phyla: Arthropoda, Onychophora, Tardigrada, Kinorhyncha, Priapulida, Loricifera, Nematoda and Nematomorpha that today are very distinct (see collage. above) and have in the past been classified among very different groups of animals. Whilst it is evident on both molecular and morphological grounds that they are related and form a single clade, exact relations between the various phyla remain unclear, reflecting the very rapid evolutionary radiation that occured with the Cambrian explosion.



Ecological and functional scenario of the early evolution of the ecdysozoa and the emergence of panarthropods from Dzik and Krumbiegel (1989) (via Harvey et al 2010)

The original Ecdysozoan was probably a largish worm-like organism with a centrally located mouth (Budd 2001). Presumably these would have been infaunal burrowing forms, but some later would have developed legs for greater mobility on the surface. The diagram at the right presents one possible ecological and functional scenario for the evolutionary emergence of ancestral panarthropods (lobopods) from worm-like palaeoscolecid or priapulid-like ancestors (. Other less specialised types would have remained as burrowing worms, while some took up a parasitic lifestyle and became the miniaturised nematoid group

And although the current (extant) ecdysozoan phyla are each very unique and different, this was not the case during the early Paleozoic, especially during the Cambrian, when there were so many transitional and intermediate forms - worms with protoarthropod armour, Dinocaridida that were neither onychophores nor arthropods but somewhere in between, and various forms such as *Markuelia* and *Mureropodia* that don't fit any extant phylum. To a Cambrian observer, the Ecdysozoa would have seemed like a single large and diverse, yet still coherent and clearly interrelated phylum, perhaps very much like the Mollusca today.

The ecological composition was also different; for example the palaeoscolecid worms filled many of the ecological roles now taken up by annelids. The anomalocarids filled the apex preditor nich that was since taken up first by large cephalopods and eurypterids, and then by large fish. Some ecolomorphs, such as the soft-bodied and the armoured walking worms, don't seem to have any modern equivalents at all.

At some point, perhaps the Ordovician biodiversification event, this extraordinary range of organisms was pruned, with only a few very distinct lineages surviving. A few holdovers survived to the Silurian and Devonian, but it seems that by the Carboniferous the bulk of taxa belonged to extant groups. Some of these groups, such as the arthropods and the nematodes, became incredibly succssful, others persisted as relics, represented today (and presumably during the Cenozoic and Mesozoic) by a few dozen or a few hundred species.

A similar thing seems to have happened with many taxa during this time, such as molluscs and arachnomorph and crustaceomorph arthropods. One of the reason why phylogeny is so difficult today is that we have so few intermediate types to work with; this is why neontological studies alone can be misleading. Even though fossils don't provide as much data as living species, they do help to show the great diversity of life in the past. MAK120421

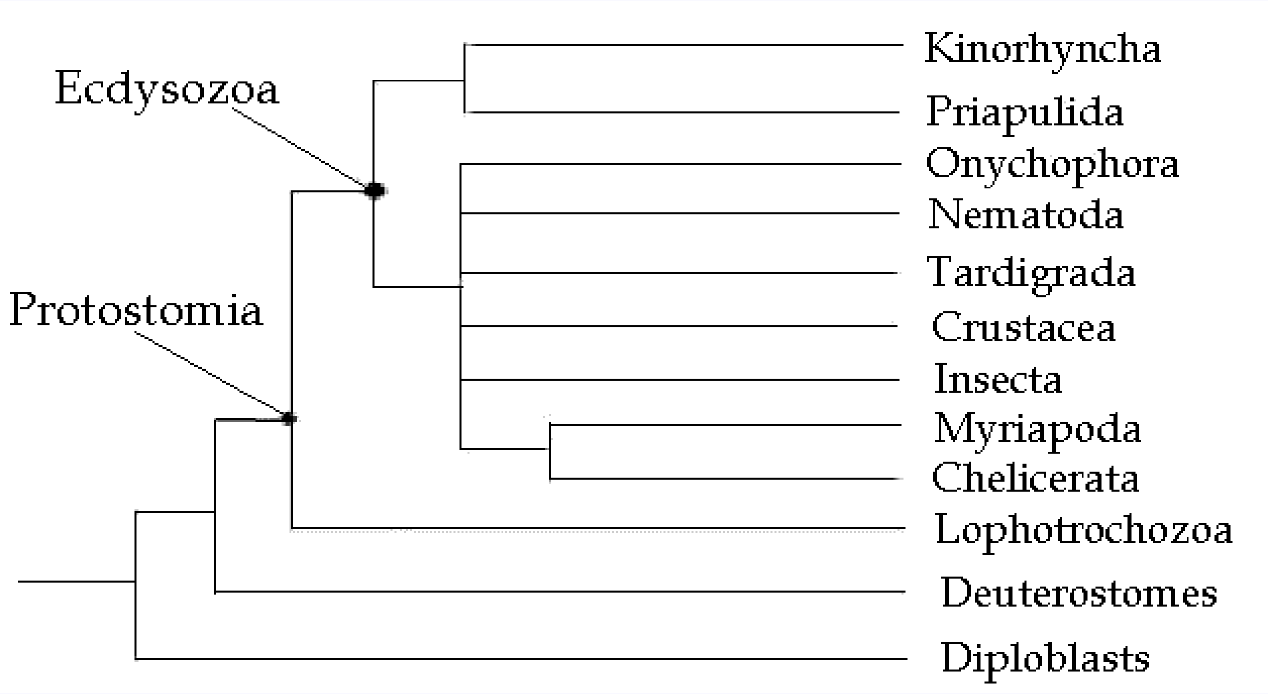
Changing phylogenies regarding the Ecdysozoa

The phyla that constitute the ecdysozoa have in the past been classified among very different groups of animals. The Kinorhyncha, Priapulida, Nematoda and Nematomorpha lack a true body cavity - they are pseudocoleomates rather than coelomates - and so were included with the rotifers and gastrotrichs. In other words, arthropods were considered more closely related to vertebrates and molluscs (all three being colemates) than to nematodes. The animal kingdom was largely organised according to a few basic parameters, such as radial and bilateral symmetry, and in the case of the latter, no body cavity (flatworms) versus false (psedocolemates / aschelminthes) versus true (colemate) body cavity (e.g. Margulis and Schwartz, 1982 for a recent version thereof). Similarily, the relation of the colemate phyla was determined by the most apparent similarities. So for example arthropods and onychophores were likewise considered together, along with the annelids, as all have a segmented or quasi-segmented body, and hence all were included under the superphylum Articulata (see e.g. the ideas of Snodgrass).

All this changed with the rise of molecular phylogeny. Though our knowledge of the Ecdysozoa is less than two decades old, this has proved to be a rich field of study, with many changing phylogenetic hypotheses that only now seem to converging on a more detailed consenus. A few of the changing interpretations are shown here on this page

The early interpretations

The Ecdysozoa are such an important concept in metazoan phylogeny that it is hard to imagine that they were only first discovered 15 years ago (at the time of writing). They were first described by Aguinaldo et. al. 1997 who divided the protostomes into the two clades, Ecdysozoa and Lophotrochozoa. He presented the following molecular-based phylogeny



Giribet & Ribera (1998), using 18S rDNA sequences also divide the protostome coelomates into two clades, the Ecdysozoa and the Spiralia. They used DNA sequencing as an alternative to morphology in determining Protostome phylogeny. From their abstract:

> "Here we report a cladistic approach to metazoan evolution including 133 18S rDNA sequences of 31 animal phyla. Despite the difficulties associated with analyzing large data sets, our data suggest that the Bilateria and Protostomia are monophyletic. The internal phylogeny of the protostomes is divided into two main clades. One clade includes the classical protostome worms (annelids, sipunculans, echiurans, pogonophorans, and vestimentiferans), mollusks, nemerteans, "lophophorates," platyhelminths, rotiferans, and acanthocephalans, although the internal resolution of the clade is very low. The second clade includes arthropods and other molting animals: tardigrades, onychophorans, nematodes, nematomorphans, kinorhynchs, and priapulans. The arthropods and related phyla lack a ciliated larvae, lack a multiciliate (locomotory) epithelium, and share many features, notably, a reduced coelomic cavity and the presence of a cuticle which molts."

Also this fits in with the modular nature of the Hox cluster of genes, which determine the overall ground plan of an animal. In *The Ancestry of the Hox Cluster* Guillaume Balavoine writes (from the abstract):

> "The 18S rDNA phylogeny of metazoans leads to the picture that the bulk of the bilaterian phyla is split into a double dichotomy giving three great superphyla, Deuterostomia, Ecdysozoa (including nematodes) and Lophotrochozoa (including brachiopods). The four-gene cluster in *C. elegans* must therefore be the remnant of a larger cluster. Comparison of the Hox [cluster of] genes sequences appears to confirm the position of some phyla in this three-branched tree of the Bilateria, notably brachiopods"

A different molecular phylogenetic study by Winnepennickyx *et al.* (1998) presents a cladogram that doesn't agree with Aguinaldo et al., although it, too, contains a clade made up of priapulids and arthropods. It also contains clade made by phoronids and brachiopods.

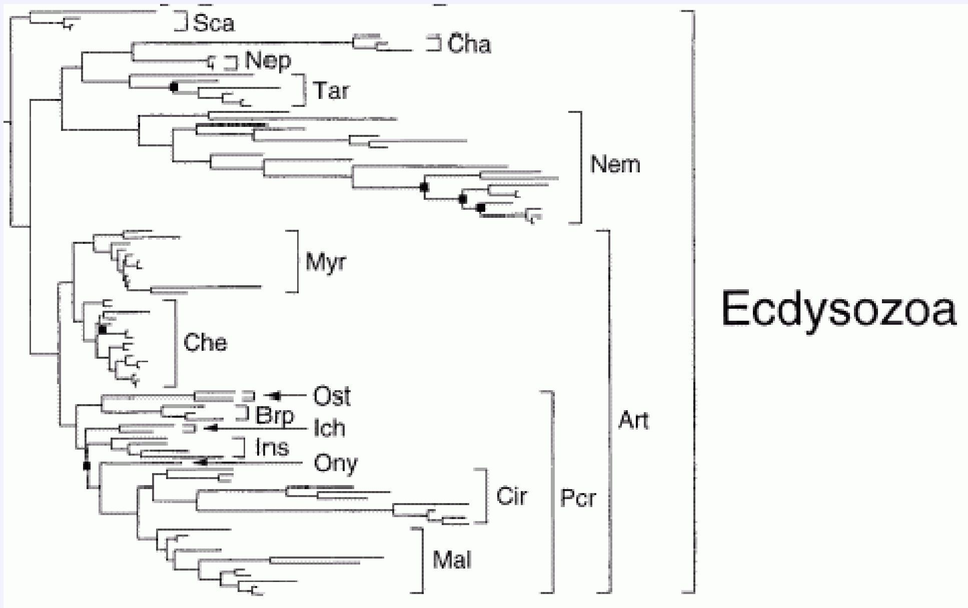
```
<==o Protostomia after Winnepennickyx et al., 1998
   |-- Mollusca
   |-- Annelida [+ Vestimentifera & Pogonophora sensu Rouse, 2001]
   |--+-- Phoronida
   |  `-- Brachiopoda
   |-- Entoprocta
   |-- Bryozoa [Ectoprocta]
   |-- Gastrotricha
   |-- Lobopoda [Onychophora sensu lato] (lobopods, velvet worms)
   |-- Nemata [Nematoda]
   `--+-- Priapulida
      `--+-- Crustaceomorpha
         `-- Hexapoda (insects)
```

In this context, the Ecdysozoa are more or less equivalent to Conway Morris, 1993earlier but now redundant Arthropodomorpha (dendrogram via Mikko's Phylogeny)

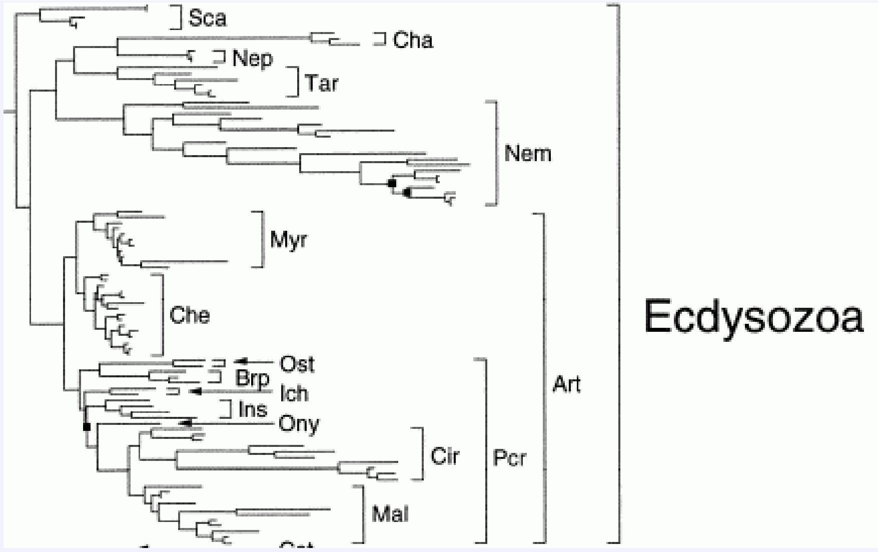
```
<==o ARTHROPODOMORPHA
        |-- Cephalorhyncha
        |--+--+-- †Protoconodonta
        |  |  `-- Chaetognatha
        |  `--+-- Nematomorpha
        |     `-- Nemata [Nematoda]
        `--+--o †Sprigginida
           |  |?- †Bomakellia
           |  `-- †Spriggina floundersi
           |?- Tardigrada
           `-- Arthropoda
```

Conway Morris' above morphology-based phylogeny follows the traditional (and in the opinion of the present writer very unlikely) hypothesis of *Spriggina* as some sort of proto-arthropod. But the rapid Cambrian explosion scenario makes it exceedingly unlikely that *Spriggina* or its fellows are related (even as stem taxa) to amy extant phyla; indeed, it is not certain that these organisms are even metazoa at all

Peterson & Eernisse (2001) arrive at several different trees through a combination of methods. They indicate that the Lophotrochozoa are paraphyletic and hence not a true clade. Interestingly, all but the morphology only approach showed the sponges (Porifera) to be paraphyletic (i.e. that sponges were the direct ancestors of other forms of animal life) rather than a side-branch



Parsimony analysis of 18s rDNA



Combined parsimony analysis of morphology and 18s rDNA

The above cladograms by Peterson & Eernisse (2001), show the relationship of the various Ecdysozoa subclades. (Molecular phylogeny). Here tardigrades and chaetognatha are grouped with nematodes

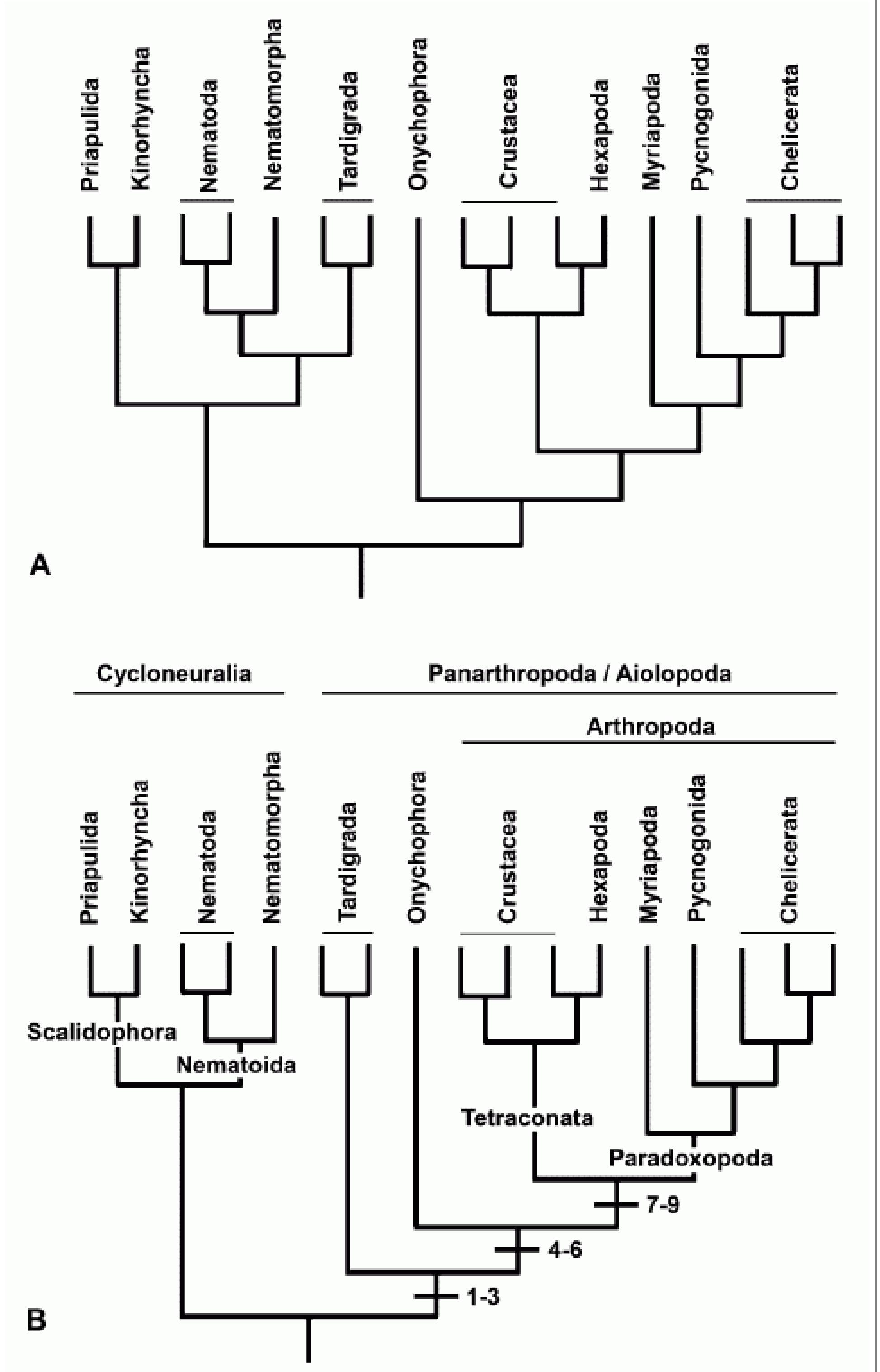
These studies demolished the Articulata, which was shown to be an invalid taxon, with very little morphological, and absolutely no molecular, support. It is clear that both annelids and arthropods acheived a segmented condition independently.

More recent interpretations

As both molecular sequencing and morphology-based cladistics became more refined, two groups emerged as possible subclades of the Ecdysozoa - the Cycloneuralia and the Panarthropoda - and almost as quickly dissappeared into a paraphyletic haze.

The *Cycloneuralia* are are a large group of sometimes microscopic or miniature mostly wormlike forms, such as the nematodes and kinorhyncha, or larger forms like priapulida. They are distinguished by a collar-shaped brain around the pharynx (also found by convergence in the Gastrotricha, which are lophotrochozoans) and eversible anterior end, or *introvert*, which terminates in the mouth and gives the alternative name of Introverta Telford et al 2008 p.1531). While often recovered as a monophyletic clade, they have also equally appeared as paraphyletic or as an unresolved polytomy (Telford et al 2008, Edgecombe et al 2011.

The *Panarthropoda* are a more tightly knit assemblage consisting of the three phyla: Arthropoda, Onychophora and Tardigrada. They share a segmented body plan, the presence of legs and



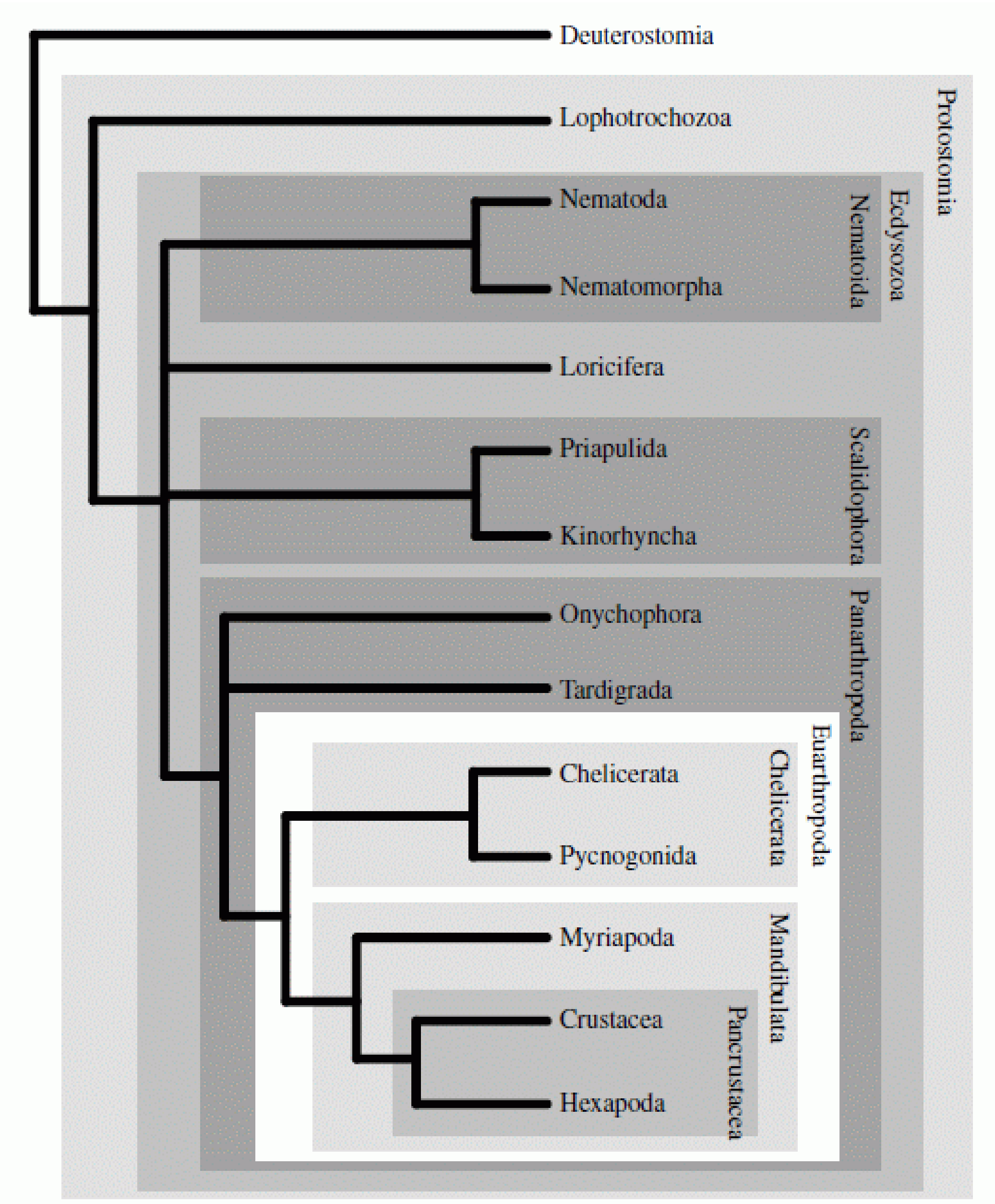
Cladogram according to Edgecombe 2009 fig2

claws, and a ventral nervous system. While the Onychophora and the Arthropoda are clearly related, as shown by both molecular and morphological evidence, the tardigrades' placement is less clear, as in both molecular and morphological details they share characteristics of both panarthropods and cycloneuralia, and can and have been included in either. Indeed, few organisms are more contreoversal than these enigmatic little animals, which have variously been linked with nematodes (Peterson & Eernisse 2001), onychophora (Cavalier-Smith 1998), and arthropods (Budd 2001).

The cladograms on the left present these two alternative hypotheses for ecdysozoan relationships based on molecular data from expressed sequence tags, after Dunn et al. 2008 (see also larger cladogram incorporating phylogeny B) showing the unstable position of the tardigrades. In one analysis (a), tardigrada are placed within a monophyletic Cycloneuralia, in another (b) in a monophyletic panarthropoda, as sister to Onychophora + Arthropoda. Here Cycloneuralia and Panarthropoda are the two sub-clades within the Ecdysozoa. It iis also in accord with cladistic morphological analysis (synapomorphies indicated) whereas the first involves a great deal of parallelism (diagram from Edgecombe 2009 fig.2)

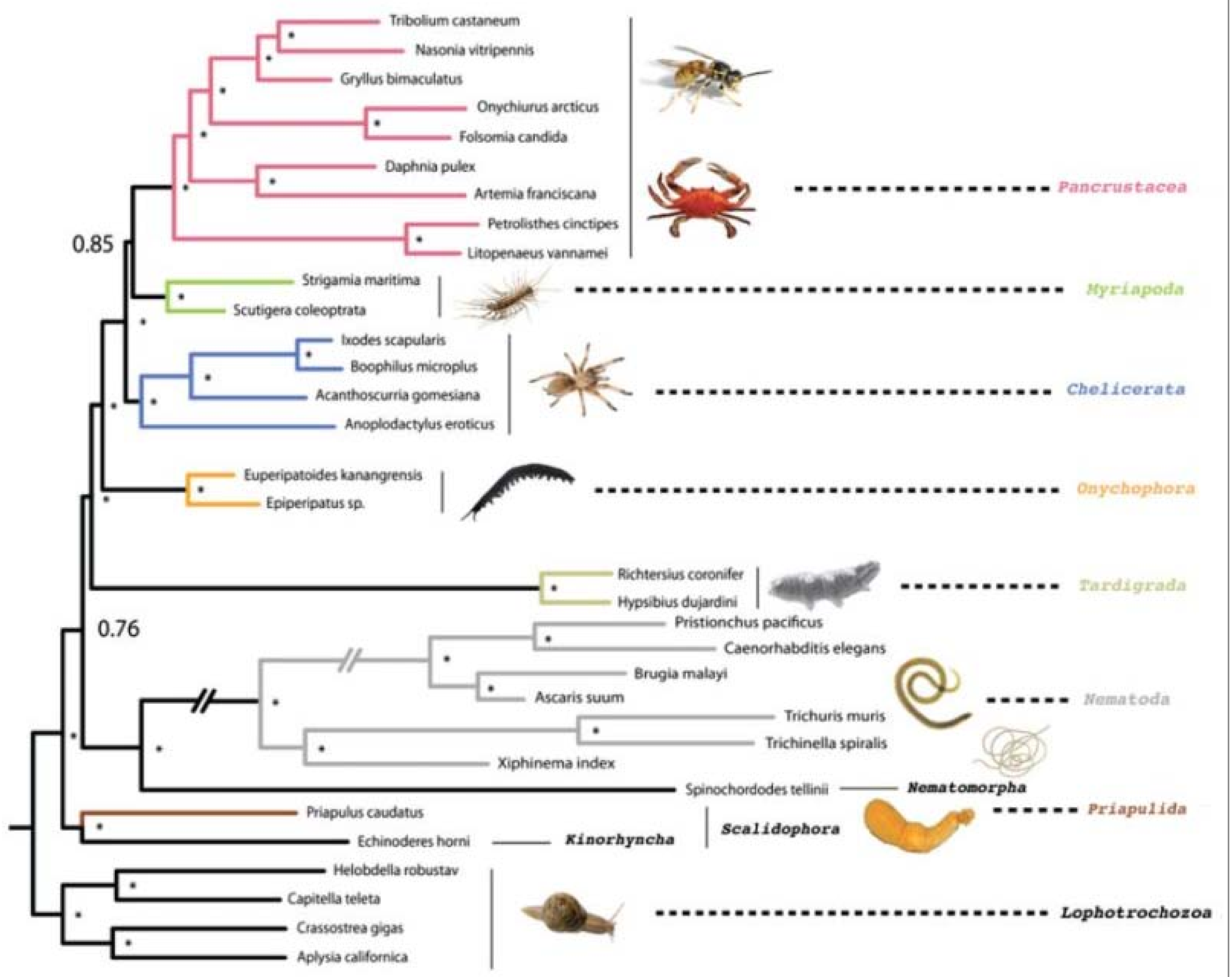
Telford et al 2008, reviews previous work and combines molecular and morphological information to give the following consensual phylogeny

Here the Mandibulata (including Myriapoda) and Panarthropoda (including Tardigrada) are shown as monophyletic groups because of convincing morphological evidence despite some molecular uncertainty.. The Cycloneuralia are now paraphyletic, although the Panarthropoda retain their monophyletic status, even if the relations of the three component phyla remain unresolved.

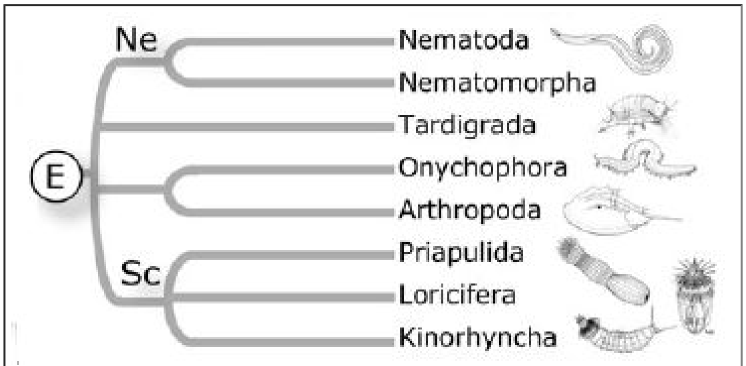


Ecdysozoan phylogeny according to Telford et al 2008

Rota-Stabelli et al 2010, in addressing arthropod phylogeny from a molecular perspective, sought to avoid conflicting phylogenetic results from molecular datasets by analysing two independent molecular datasets: a phylogenomic dataset of 198 protein-coding genes and new microRNA complements sampled from all major arthropod lineages. The arthropods are considered in the next main unit, but of relevance to the present review, their phylogenomic analysis revealed both a paraphyletic Cycloneuralia and a monophyletic Panarthropoda, suggesting that the previous grouping of tardigrades and nematodes may have been the result of tree-reconstruction artefacts. Interestingly, the Scalidophora (Kinorhyncha + Priapulida) here appear as the sister taxon to an unnamed Nematoda (or presumably Nematoida) + Panarthropoda clade. Tardigrades and onychophores form a monophyletic lobopodia. Campbell et al. 2011 using two independent genomic datasets, arrived at a very similar phylogeny, except that onychophores and arthropods are now sister taxa and showing the tardigrade-nematode group to be a phylogenetic artifact resulting from long branch attraction, due to tardigrades' high rate of evolution. Their analysis strongly supported a monophyletic Panarthropoda including Tardigrada and suggest a sister group relationship between Arthropoda and Onychophora, in keeping with current morphological and fossil evidence. It also revealed a paraphyletic Cycloneuralia and a monophyletic Scalidophora. Their two molecular phylogeny is as follows:



Phylogenetic tree by < a href="references.html#Campbelletal2011">Campbell et al. 2011, using Bayesian analysis of molecular data, supports a monophyletic panarthropoda with tardigradesas the sister group of Onychophora + Arthropoda (defined as Lobopodia in this paper). This is in agreement with morphological and fossil evidence. Other findings shown here, such as a paraphyletic Cycloneuralia and monophyletic Scalidophora, Mandibulata, and Pancrustacea, are part of an emerging molecular consensus, although the Scalidophora may only be monophyletic as far as the crown group goes. The problem of a molecular and morphological Mandibulata and molecular-only Pancrustacea verses a fossil and morphological Schizoramia and Mandibulata will be addressed under Arthropods (next unit).

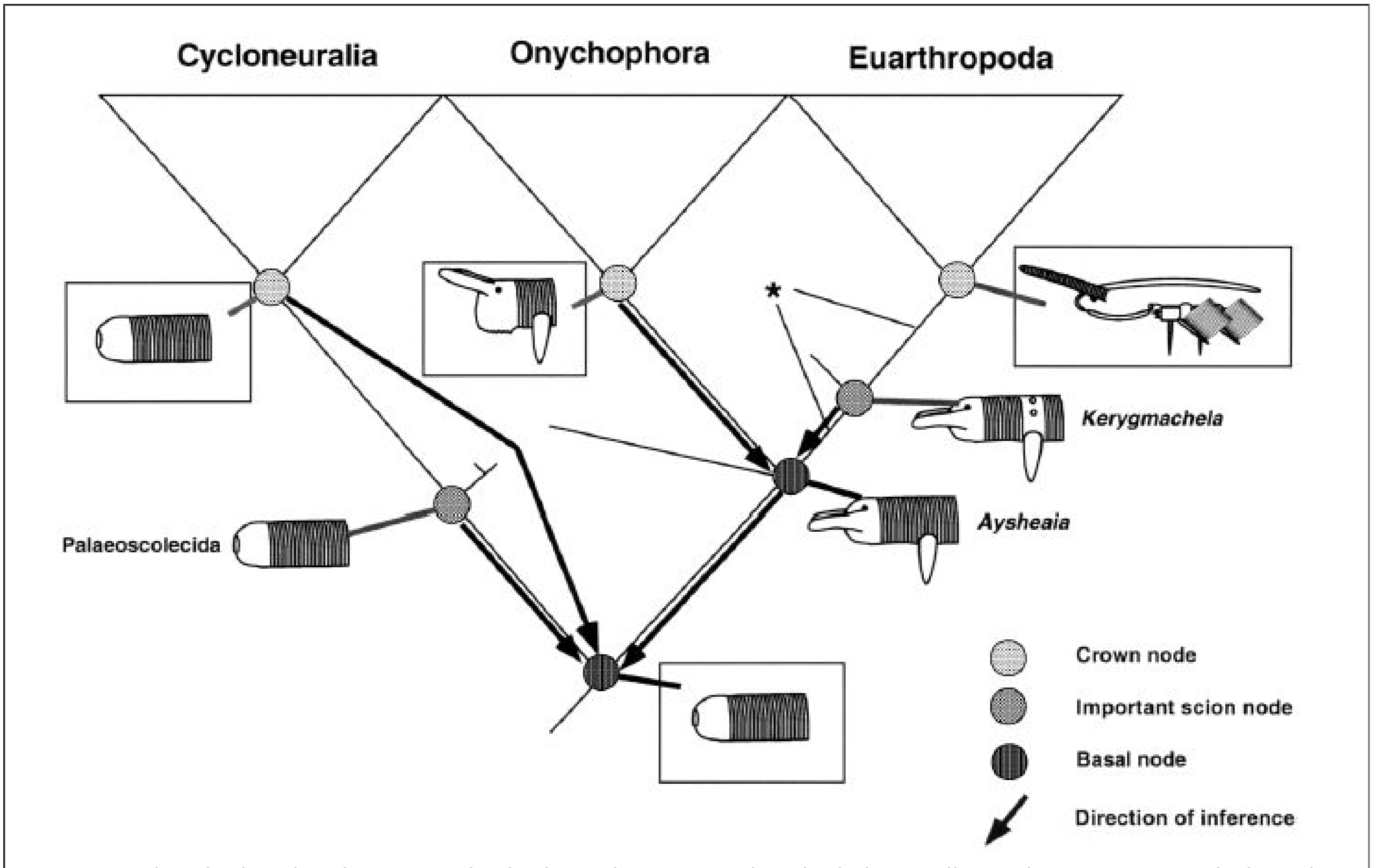


The tree on the left is part of a larger dendrogram from Edgecombe et al 2011 (abbreviations: E: Ecdysozoa; Ne: Nematozoa (= Nematoida); Sc: Scalidophora)

In the consensus tree suggested by Edgecombe et al 2011, not only are the Cycloneuralia paraphyletic, but the tardigrades are once again unresolved, resulting in the Panarthropoda also becoming a paraphyletic grouping leaving only Onychophora and the Arthropoda in a reduced (and unlabelled) Eu-Panarthropoda. We have however followed the phylogeny of both Molecular phylogeny according to Rota-Stabelli et al 2010 and Campbell et al. 2011, according to which the grouping of tardigrades and nematodes is an artifact of earlier phylogenomic analyses. As molecular phylogeny increasingly addresses the problem of Long Brabnch Attraction, a more accurate phylogenetic tree will certainlty emerge.

Which came first, the worm or the lobopod?

This is a bit like the story of *Archaeopteryx* and the deinonychosaurs, or perhaps lampreys and ostracoderms. Did evolution follow a simple ascending path of greater complexity and specialisation? Or did the more advanced form evolve first, from earlier unknown primitive ancestors, and then , througha sort of reverse evolutiobn, give rise to more primitive or degenerate (or in the case of *Archaeopteryx*, flightless longer tailed) descendants?

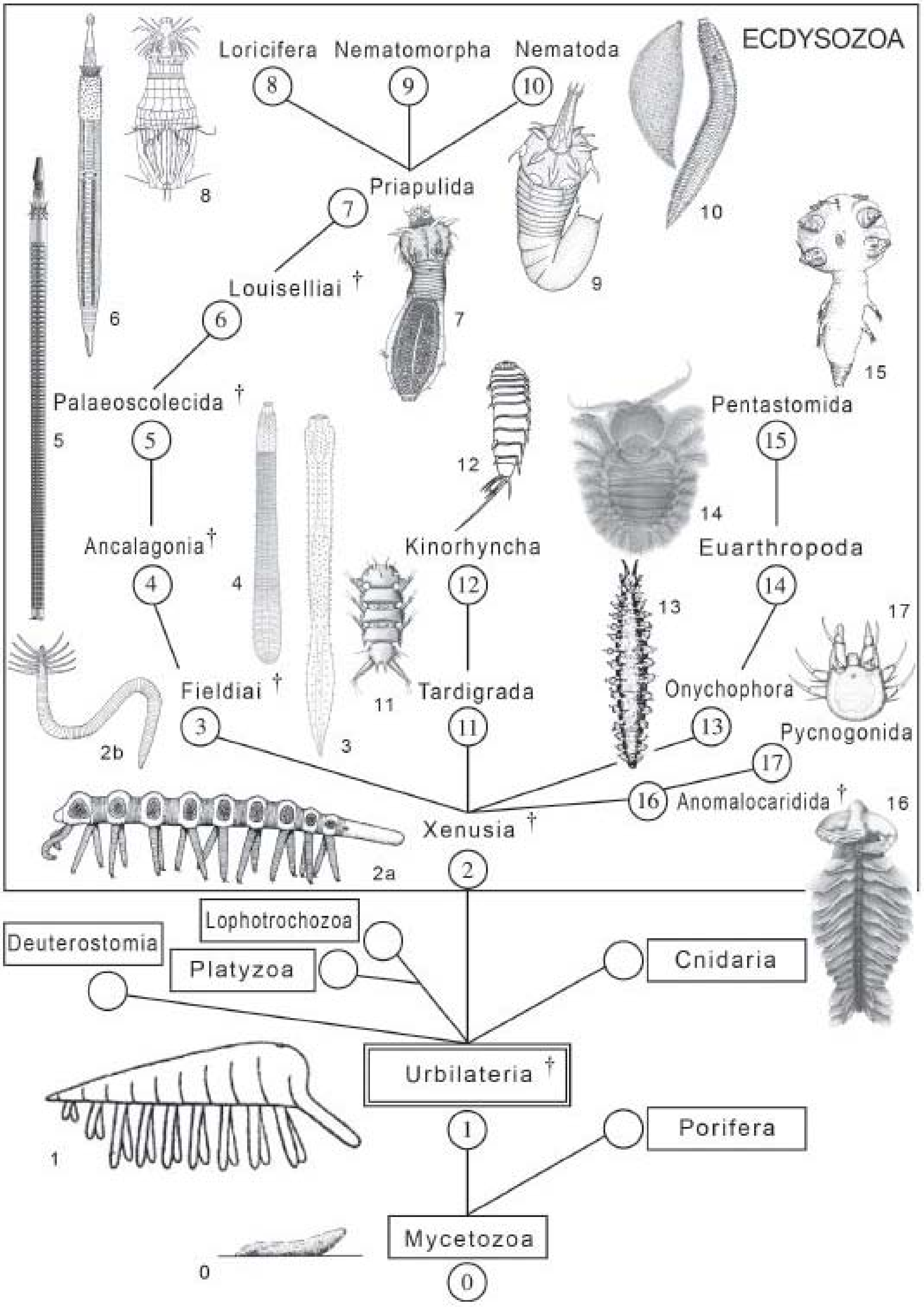


Reconstructing the basal and crown nodes in the Ecdysozoa. Nodes shaded according to key. Important plesions that are essentially metataxa (i.e. their character states cannot presently be distinguished from their respective plesion node) are shown. Reconstructed character states are shown inside boxes. Inference of character states at different nodes shown by bold arrows. Diagram and caption by Budd 2001

In considering the evolution of the Ecdysozoa, we naturally think that the ancestral form was a worm-like organism. This is illustrated by the cladistic diagram presented by Budd 2001 (*left*). Here an ancestral, worm-like form (shown as the basal node, at the bottom of the diagram) gives rise to the Cycloneuralia (shown on the left of the diagram) and the panarthropod clades (the Onychophora and Arthropoda are shown on the right; the position of the tardigrades is shoiwn by the asterix but not more precisely indicated because of its uncertain phylogenetic placement,. A later paper by Budd & Telford (2009), in keeping with developments (and new ambiguities) since the first paper was written, has a low resolution consensus phylogeny, with an unresolved panarthropoda(paraphyletic lobopoda) arising from an unresolved ecdysozoa (paraphyletic cycloneuralia). Our understanding is a bit better now because as we have seen, molecular phylogeny now places onychophores and arthropods as sister taxa, with tardigrades as an early off-shoot. The "worms came first" hypothesis is also This is supported by paleontological research into early armoured worms called, palaeoscolecids as well as lobopods (Dzik & Krumbiegel 1989, Liu et al 2008, Conway Morris & Peel 2010, Steiner et al 2012)

Going in the opposite direction, to more rather than less speculation is a rather exotic phylogeny by Zhuravlev et al 2011, according to which nematoida and related taxa are minaturised and simplied relatives or descendents of a lobopod-like ancestor. The authors provide this richly detailed diagram:

General phylogeny of the



Ecdysozoa **0**.migration slag of amoebozoan *Dictyostelium discoideum* Raper, extant; **1**.Urbilaterian, hypothetic (modified from van Beneden, 1891); **2a**.xenusian *Microdictyon sinicum* Chen, Hou and Lu, Lower Cambrian (modified from Hou and Bergstrom, 1995); **2b**.xenusian *Facivermis yunnanicus* Hou and Chen, Lower Cambrian (modified from Delle Cave and Simonetta, 1991); **3**.*Fieldia lanceolata* Walcott, Middle Cambrian (modified from Conway Morris, 1977); **4**.*Ancalagon minor* Walcott, Middle Cambrian (modified from Conway Morris, 1977); **5**.palaeoscolecid *Cricocosmia jinningensis* Hou and Sun, Lower Cambrian (modified from Han et al., 2007); **6**.*Louisella pedunculata* Walcott, Middle Cambrian (modified from Conway Morris, 1977); **7**.priapulid larva *Halicryptus spinulosus* von Seibold, extant (modified from Malakhov and Adrianov, 1995); **8**.loriciferan larva *Pliciloricus ornatus* Higgins and Kristensen, extant (modified from Malakhov and Adrianov, 1995); **9**.nematomorph larva *Gordionus senkovi* Malakhov and Spiridonov, extant (modified from Malakhov and Adrianov, 1995); **10**.nematodes *Greeffiella* (left) and *Criconema* (right), extant (modified from Brusca and Brusca, 2003); 11.tardigrade *Stygarctus abornatus* McKirdy, Schmidt and McGinty-Bayly, extant (modified from McKirdy et al., 1976); **12**.kinorhynch *Centroderes eisigii* Zelinka, extant (modified from Malakhov and Adrianov, 1995); 13.onychophoran *Peripatopsis moseleyi* (Wood-Mason), extant (modified from Ruhberg in Monge-Najera and Hou, 1999); **14**.larval euarthropod *Ascalaphus* sp., extant; 15.larval pentastomid *Boeckelericambria pelturae* Walossek and Muller, Upper Cambrian (modified from Maas and Waloszek, 2001); **16**.anomalocaridid *Anomalocaris saron* Hou, Bergstrom and Ahlberg, Lower Cambrian (modified from Hou et al., 1995); **17**.protonymphon larva of pycnogonid *Anoplodactylus* sp., extant (modified from Maxmen et al., 2005).. Caption and diagram by Zhuravlev et al 2011.

Although the idea of a lobopodous ur-bilaterian may be rather implausible, the possibility that wormlike ecdysozoan phyla are highly derived (and in the case of nematodes etc miniaturised and simplified) lobopods is not as incredible as it seems. Especially in the case of primitively parasitical nematoida, this would not be very different to the the case of the highly specialised and parasitic pentastomids, once believed to be a distinct phylum, but now almost unanimously agreed to be derived crustaceans. Whether evolution really did go that way regarding the wormlike and mostly microscopic cycloneuralia cannot be known for sure as yet. Although the majority view has the panarthropods as a specialised line (or convergent lines, if the tardigrades are distinct), derived from worm-like ancestors, it may also be that worm-like ecdysozoa gave rise to early lobopods, some of which in turn evolved into neo-worms, whilst other worms - for example the large priapulids which are better understood as primitive burrowers - never went through a lobopodous stage. This would be equivalent to a compromise maniraptoran hypotheiss, in which early coleurosaurs evolved into archaeopterids, some of which became neo-flightless theropods and others advanced birds. Fornow however we have followed a more traditional phylogeny. MAK120418

Molecular versus fossil phylogenies

It is no doubt obvious that the molecular phylogenies on this page differ quite markedly from the paleontological morphology and ecomorphic-based scenarios. The reasons for this are both methodological and the result of the differeing data each one incorporates. Molecular phylograms use branching trees with no actual ancestors and without reference to stratigraphic, ecological, or functional factors (the same applies to cladograms, hence molecular and morphology-based phylogenies are often grouped together and even synthesised, despite the molecular phylogenies contradicting obvious morphological evidence). Paleontological morphology-based scenarios in contrast examine the fossil record (especially exceptionally preserved fossils) to understand the groundplans and traits of actual ancestral groups, as well as the evolutionary and morphofunctional trends and processes leading to the development and emergence of new types of organisms. Because molecular evolution is based, obviously, only on extant taxa, it is limited to isolated lineages that are generally very far from their ancestral states (the exception would be currently evolving and diverging taxa that are still undergoing an adaptive radiation, e.g. bovid mammals, a very diverse group whose evolution only began in the Miocene). Long branch attraction, homoplasy, and other artifacts may result in the appearance of artificial clades, such as the Cyclostomata among basal vertebrates, the pleistomollusca (gastropods + bivalves) among molluscs or the tetracoronata/pancrustacea (Crustaceans + Insects) among arthropods, clades that in each case are well represented on molecular grounds but make little or no morphological sense. In all these instances there is the assumption that the phylogenetic signal in molecular sequencing is superior to that in morphology-based cladistics or morphofunctional or paleontologfical-morphological approaches, when no empirical evidence has been offered for this (although to be fair neither has any for the converse premise, that molecules have a less reliable phylogenetic signal)

When considering fossil evidence, even from lagerstätten, we need to be sensitive to the fact that very little data remains, relative to the great wealth of data (morphological, genomic, developmental, etc) available for extant taxa. It is easy for the faint phylogenetic signal to be swamped by the neontological noise. This is why additional emphasis should be given to these precious relics and clues from the past. Hence unique transitional taxa like *Kerygmachela*, *Markuelia*, *Mureropodia*, and *Sirilorica*. The most likely picture that emerges is of a paraphyletic assemblage, or evolutionary grade, of worm-like forms at the base of the ecdysozoan family tree. The isolated extant clades such as cycloneuralia, scalidophora, nematoida, and panarthropda, that emerge through molecular phylogeny are either of a phylogenetically limited sample of recent only forms, or the highly derived descendents of these early worms, or both. And because transitional types such as *Mureropodia* and *Facivermis* bridge the gap between scalidophoran worms and panarthropods, it seems likely that Scalidophora and Cycloneuralia, rather than being monophyletic clades, are paraphyetic assemblages (and hence, cladistically speaking, synonyms of Ecdysozoa). In this scenario, both the large and complex lobopods and arthropods on the one hand, and small and simple nematoids on the other, evolved as specialised, albeit astonishingly successful (specifically,m the arthropods and nematodes) side branches from the original priapozoan stem. MAK120422 revised 120429

Descriptions

Ecdysozoa: bugs > slugs

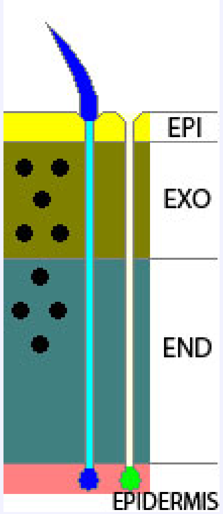
Range: Fr ECambrian

Phylogeny: Protostomia **:** Lophotrochozoa + * **:** Scalidophora (syn. of Ecdysozoa?) + (Nematoida + Panarthropoda)

Characters: thick three-layered cuticle composed of organic material (see diagram of arthropod cuticle, right), which is periodically molted as the animal grows (ecdysis); no surface locomotory cilia [n1], ciliary feeding mechanisms, or ciliated larvae; generally amoeboid sperm; embryos do not undergo spiral cleavage (Wikipedia); ; gut, if present, with anus ; coelom present only

A cicada in the process of shedding its skin. Photo by LiquidGhoul, Wikipemia, Gnu open source license / Attribution-ShareAlike

embryonically or absent; ventral nerve cord; usually gonochoristic (Cavalier-Smith (1998)); molting is controlled by characteristic hormones called ecdysteroids; the cuticle has 3 layers: epicuticle, exocuticle, and endocuticle; epicuticle is trilaminate, alpha-chitin in inner layer (Harvey et al. (2010)); primitively, triradiate pharynx (retained in tardigrades, pycnogonids and nematodes), homonomous annulation (priapulids and panarthropoda) (Daley et al 2009 cladogram, supplement fig S3) MAK120424



Comments: The moulting animals, one of the most successful and diverse clades of life on Earth. First proposed on molecular grounds by Aguinaldo et al 1997; since then a number of morphological synapomorphies have been discovered. Budd tentatively reconstructs the ecdysozoan common ancestor as a large worm-like form with a terminal mouth (Budd 2001); if Cycloneuralia are paraphyletic it may also have possessed a cycloneuralian brain and an introvert feeding mechanism. It is even possibile that the ecdysozoan ancestor was segmented. The similar deployment of homologous genes ("segment polarity" or "pair rule" genes) in arthropods and kinorhynchs would imply common ancestry of segmentation within the group. Telford et al 2008 MAK120415

Note: [n1] Although this would seem to follow from the occurrence of a thick cuticular covering, Telford et al. (2008) and Edgecombe et al. (2011) note that Gastrotricha (a phylum in the Spiralia) does have both a thick cuticle and a body covered by cilia. - Jack R.HoltDiversity of Life - Ecdysozoa

Links Introduction to the Ecdysozoa; Jack R.Holt Diversity of Life - Ecdysozoa; The Ecdysozoa: true taxon or molecular mirage? Brian K. Penney; Ecdysozoa photos; Ecdysozoa - Wikipedia; Reaching creationists: here's the toolbox, do you know how to use the tools? - PZ Myers (includes discussion of Edgecombe 2009)

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Ecdysozoa: Classification

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--Protostomia
   |--SPIRALIA
   |
   `----ECDYSOZOA = paraphyletic Scalidophora?
      |==Palaeoscolecida
      |==Priapozoa
      |  |--Kinorhyncha
      |  `--+--Priapulida
      |     `-- Loricifera
      `--+--Nematoida
         |   |--Nematoda
         |    `--Nematomorpha
         `--Panarthropoda
            |--Tardigrada
            `--+--Onychophora
                `--+--Dinocaridida
                   `--ARTHROPODA
```

Contents

As Ecdysozoa is a molecular phylogenetic and cladistic concept (see dendrogram page), there is little in the way of Linnaean-evolutionary based systematics. One of the few systematists still using a rank-based and paraphyletic/evolutionary (ancestral taxa) classification system is Thomas Cavalier-Smith, the Canadian microbiologist who has created a comprehensive revised classification of the kingdoms of life on Earth (Cavalier-Smith (1998)). He presents the Ecdysozoa as folows (our comments in square brackets):

- Infrakingdom 3. Ecdysozoa
  - Superphylum 1. Haemopoda [= Panarthropoda]
    - Phylum 1. Arthropoda
      - Subphylum 1. Cheliceromorpha
        - Infraphylum 1. Pycnogonida
        - Infraphylum 2. Chelicerata
      - Subphylum 2. Trilobitomorpha
      - Subphylum 3. Mandibulata
        - Infraphylum 1. Crustacea
        - Infraphylum 2. Myriapoda
        - Infraphylum 3. Insecta [= Hexapoda]
    - Phylum 2. Lobopoda [= Lobopodia]
      - Subphylum 1. Onychophora
      - Subphylum 2. Tardigrada
  - Superphylum 2. Nemathelminthes [= Cycloneuralia]

Phylum Nemathelminthes
  Subphylum 1. Scalidorhyncha [= Scalidophora]
    Infraphylum 1. Priapozoa (classes Priapula, Loricifera).
    Infraphylum 2. Kinorhyncha
  Subphylum 2. Nematoida
    Infraphylum 1. Nematoda
    Infraphylum 2. Nematomorpha

Whereas the standard consensus has around 38 animal phyla (including 8 in Ecdysozoa alone), Cavalier-Smith is concerned to reduce the excessive number of phyla that he considers are the result of taxonomic inflation. Hence he has has only 23 phyla, of which only three belong to the Ecdysozoa. While agreeing with the need to reduce the number of high rank taxa, we would not be quite so radical. The following classification is based mostly on Cavalier-Smith's, with some terminological adjustment to bring it line with our current coverage. Because there are only five phyla here, we have removed intermediate ranks such as Scalidophora (= Cephalorhyncha = Nemathelminthes = Scalidorhyncha) and Panarthropoda Nielsen, 1995 (= Haemopoda Cavalier-Smith 1998 = Aiolopoda Hou and Bergström, 2006);, thus allowing Protostomia to retain infrakingdom status and avoiding the need for additional high level ranks like "branch" (between sub and infrakingdom, or infrakingdom and phylum) . In keeping with the evolutionary-linnaean arrangement, this includes a large number of paraphyletic grades MAK120425

Kingdom Animalia (cont.)
  Subkingdom Bilateria (cont.)
  Infrakingdom Protostomia (cont.)
    Superphylum Ecdysozoa Aguinaldo et al. 1997 (moulting animals; Camb - Rec)
      incertae sedis
          (*Markuelia*, Camb)
      Phylum Priapozoa Cavalier-Smith 1998 (larva or adult with cuticular lorica; Camb-Rec).
        Subphylum Priapula (Priapozoa *sensu stricta*)
          Class undertermined - various Cambrian forms
          Class Palaeoscolecida (armour-plated priapozoans Camb-Sil)
          Class Priapulida (Penis worms, Camb or Carb to Rec)
        Subphylum Loricifera (tiny or microscopic, with lorica Camb-Rec)
      Phylum Kinorhyncha Reinhard 1887 (tiny or microscopic, segmented; without lorica - no fossil record).
      Phylum Nematoida Rudolphi 1808 (primitively parasitic worms, many free-living and microscopic, v poor fossil record)
        Subphylum Nematoda Gegenbaur 1859 (Roundworms - Carb to Rec)
        Subphylum Nematomorpha Vejovsky 1886 (Horsehair worms, - no fossil record).
      Phylum Lobopodia Snodgrass, 1938 (= Protarthropoda Lankester, 1904 = Lobopoda Cavalier-Smith 1998 ; soft cuticle; unjointed limbs with terminal claws ; both muscles and hydraulic pressure involved in locomotion; evolutionary grade, Camb-Rec).
        Subphylum Tardigrada Doyère 1840 (water bears, e.g. *Echiniscus*. Microscopic.Camb-Rec).
        Subphylum Onychophora Grube 1853 (velvet worms, e.g. *Peripatus*, Cambrian? or Carb to Rec)
                    Class Xenusia Dzik & Krumbiegel, 1989(Paleozoic lobopods, traditionally included under Onychophora - paraphyletic/ancestral panarthropod grade - Camb-Sil)
            Class Euonychophora Hutchinson, 1930 (terrestrial onychophora, crown and some stem group taxa - Carb-Rec)
        Subphylum "Protarthropoda" (used here as paraphyletic bridging taxon between lobopods and arthropods)
            Class Dinocaridida Collins, 1996 (paraphyletic grade of swimming and gilled lobopods, include Anomalocaridid superpredators Camb to Dev)
      Phylum Arthropoda von Siebold and Stannius 1848 (jointed exoskelton Camb-Rec).
        Subphyla unspecified
            Class Megacheira Hou and Bergström 1997 ("Geat Appendage" Arthropods - Camb)
             Class Marellamorpha - (monotypal for *Marella* and co, probably should be included under another higher rank taxon - Camb-Dev)
        Subphylum Arachnomorpha Størmer 1944
          Infraphylum Trilobitomorpha Størmer 1944 (trilobites and related forms - Camb - Perm).

Infraphylum Cheliceromorpha Boudraux 1978

Superclass Pycnogonida Latreille 1810 (sea spiders, e.g. *Nymphon* Camb-Rec).

Superclass Chelicerata Heymons 1901 (Horseshoe crabs (*Limulus* and co), eurypterids, arachnids Camb-Rec).

Subphylum Crustacea Pennant 1777 (e.g. copepods, ostracods, barnacles, crabs, shrimps, Cambrian to Rec).

Subphylum Atelocerata (= Uniramia, unranched limbs, (monophyletic according to morphology of fossil & recent froms, polyphyletic according to molecular phylogeny)

Superclass Myriapoda Leach 1814 (centipedes, millipedes, symphylans, pauropods; Sil to Rec).

Superclass Hexapoda (insects and related primitive forms; Dev to Rec)

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Ecdysozoa: Dendrogram

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--Protostomia
   |--SPIRALIA
   |
   `----ECDYSOZOA = paraphyletic Scalidophora?
      |==Palaeoscolecida
      |==Priapozoa
      |  |--Kinorhyncha
      |  `--+--Priapulida
      |     `-- Loricifera
      `--+--Nematoida
         |   |--Nematoda
         |    `--Nematomorpha
         `--Panarthropoda
            |--Tardigrada
            `--+--Onychophora
                `--+--Dinocaridida
                   `--ARTHROPODA
```

Contents

Traditional Ecdysozoan phylogeny. This phylogeny is almost certainly incorrect, in view of Scalidophora as most likely equivalent to stem Ecdysozoa (Dzik & Krumbiegel 1989,Budd 2001, Conway Morris & Peel 2010), and intermediate forms like *Facivermis* (Liu et al 2006) and *Mureropodia* (Vintaned Gamez et al 2011). bridging the worm-panarthropod divide, but has been left unrevised for now. MAK120423

```
BILATERIA
|--DEUTEROSTOMIA
`--Protostomia
   |--SPIRALIA
   |
   `----ECDYSOZOA
           |--SCALIDOPHORA
           |  |-- Markuelia
           |  |==Palaeoscolecida
           |  `--+--Kinorhyncha
           |     `--+--Sirilorica
           |        `--+-- Loricifera
           |           `--Priapulida
           `--+--NEMATOIDA
              |    |--Nematoda
              |    `--Nematomorpha
              `--PANARTHROPODA
                   |--Mureropodia
                   `--+--Aysheaia
                      `--+--Tardigrada
                         `--+--Xenusiidae
                            |--Orstenotubulus
                            |--+--Antennacanthopodia
                            |  `--Euonychophora
```

```
|     |--Helenodora
|     `--+--Peripatopsidae
|         `--Peripatidae
`--+--Microdictyon
    |--Archonychophora
    |  |--Hallucigenia
    |  `--Luolishaniidae
    |--Diania
    `--+--Megadictyon
       `--+--Kerygmachela
          `--+--Pambdelurion
             `--+--Opabinia
                `--+--Anomalocarididae
                    |  |--Hurdia
                    |  `--+--Anomalocaris
                    |     `--Laggania
                    `--+--Schinderhannes
                       `--ARTHROPODA
```

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Ecdysozoa: References

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--Protostomia
   |--SPIRALIA
   |
   `----ECDYSOZOA = paraphyletic Scalidophora?
      |==Palaeoscolecida
      |==Priapozoa
      |  |--Kinorhyncha
      |  `--+--Priapulida
      |     `-- Loricifera
      `--+--Nematoida
         |   |--Nematoda
         |    `--Nematomorpha
         `--Panarthropoda
            |--Tardigrada
            `--+--Onychophora
               `--+--Dinocaridida
                  `--ARTHROPODA
```

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Ecdysozoa: Nematoida

Abreviated Dendrogram

```
ECDYSOZOA
|--SCALIDOPHORA
|
`--+--NEMATOIDA
   |--+--Nematoda
   |  `--Nematomorpha
   `--PANARTHROPODA
```

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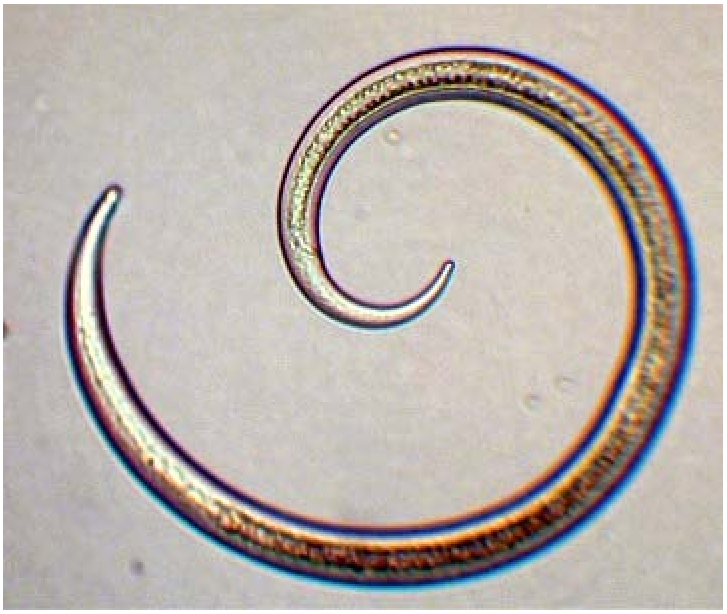

An unidentified free-living nematode found in marine sediments. The simplicity of a hydrostatic skeleton is evident
Image and caption from Reefkeeping and Sharon Taxonomy

Of all the metazoan clades to have evolved since the Cambrian explosion, three in particular stand out as extraordinary for their abundance and diversity (each with a million or more species). These are the nematodes, the mites (acari) and the insects. Interestingly, all three are ecdysozoans, and two of the three are mostly microscopic, whilst the third includes a majority of forms built to a tiny scale. But of these three, the nematodes win out as the most numerous animals on Earth, being found in all environments, both free living and parasitic, and even deep under the Earth. Closely related to the nematodes.are the nematomorpha, a small phylum of parasitic worms. They mostly infect terrestrial insects and other arthropods, but reproduce in aquatic environments. Around 300 species are known.

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Nematoida

Abreviated Dendrogram

```
ECDYSOZOA
 |--SCALIDOPHORA
 |
 `--+--NEMATOIDA
    |--+--Nematoda
    |  `--Nematomorpha
    `--PANARTHROPODA
```

Contents

The horsehair worm *Gordionus violaceus*

Taxa on This Page

Nematoida (= Nematoidea, Nematozoa)

Range: poor fossil record, but the group almost certainly would have evolved during the earliest Cambrian

Phylogeny:

Phylogeny: Ecdysozoa **:** Panarthropoda + Scalidophora + * **:** Nematoda + Nematomorpha

Comments: includes two related phyla of rather featureless worms, one of which is a rather small group, the other one of the most successful forms of life on Earth. MAK120416

The term Nematoida was coined by Schmidt-Rhaesa 1996 and 1998 and adopted by Cavalier-Smith 1998 and Peterson & Eernisse 2001. It seems to have edged out Nematoidea (Ehlers et al. 1996) and Nematozoa (Zrzavy et al. 1998), although it was first used in a different context in 1808. (see ToL - Guide to Names Used in the Higher Classification of Animals for a list of these and other taxon and clade names, also Taxonomicon) Nielsen (2001) and Telford et al 2008 list five morphological synapomorphies, although molecular support, though present, is weak. Our phylogeny presents a generally-accepted view of Nematoida as sisters to the Panarthropoda. The likely explanation for their loss of morphological complexity (though not a concomitant loss in developmental life history complexity) is that the Nematoida sprang from a parasitic group. Indeed, the Nematomorpha is entirely parasitic and many of the Nematoda also are parasitic. The free-living nematodes may have become so secondarily. Jack R.Holt Diversity of Life - Ecdysozoa (text slightly modified) MAK120418

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Nematomorpha - Gordians

By
Christopher Taylor

Abreviated Dendrogram

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ECDYSOZOA
|--SCALIDOPHORA
|
`--+--NEMATOIDA
   |--+--Nematoda
   |  `--Nematomorpha
   `--PANARTHROPODA
```

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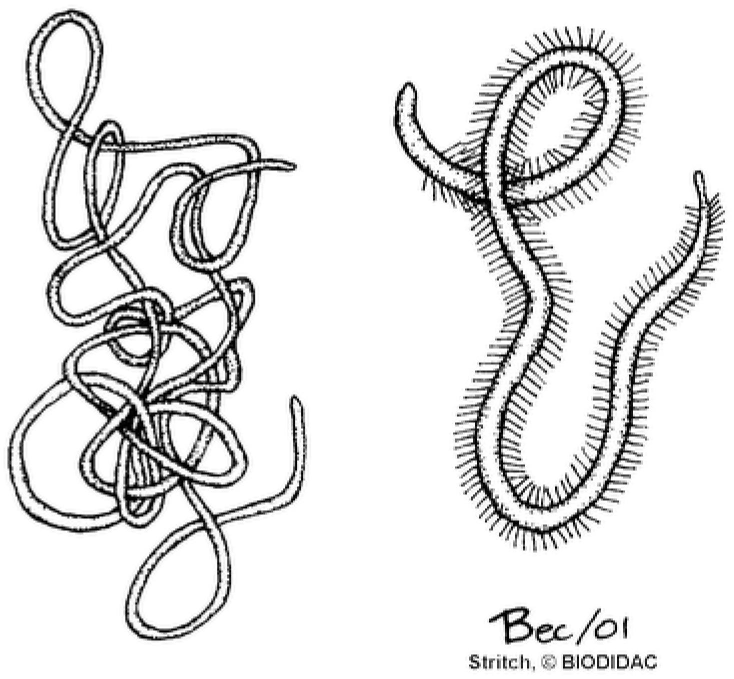
The following is reprinted from the Diversity of Life blog by Christopher Taylor (MAK):

Long-term followers of this site may recall this video, linked to over four years ago:

The animal emerging from the unfortunate cricket in the video is a Gordian or horsehair worm, Nematomorpha. Gordian worms spend most of their lives as internal parasites: either of insects (in the freshwater/terrestrial order Gordiida) or of shrimps and crabs (in the marine genus *Nectonema*). Of the two commonly used vernacular names for this group, 'Gordian worm' refers to the famed Gordian knot, and is derived from the appearance of mating tangles of these elongate animals. 'Horsehair worm' refers to the long-held belief (again, inspired by appearance) that the adult worms developed from horse hairs decaying in water. So persistent was this belief that Leidy felt compelled to report in 1870 on an attempt to generate horsehair worms by this method, explaining that, "I need hardly say that I looked at my horse-hairs for many months without having had the opportunity of seeing their vivification". He also scuttled the fear, which even Linnaeus had reported as fact, that a horsehair worm could inflict a nasty bite on anyone careless enough to handle one. In fact, Gordian worms (being internal parasites absorbing nutrients directly from the host when young and not feeding as adults) do not even possess a mouth. Instead, the males of many species possess a bifurcated tail end, used in copulation, that may have been mistaken for jaws. The complete absence of active feeding has the interesting side effect that adult Gordians may completely lack an internal bacterial flora (Hudson & Floate 2009).



Representative nematomorphs: Gordius *(Gordiida) on the left and* Nectonema *on the right, from* Biodidac.

The primary division within the Nematomorpha between the marine *Nectonema* and the terrestrial Gordiida is universally agreed upon. The two branches are ecologically, morphologically and molecularly divergent (Bleidorn *et al.* 2002). Adults of *Nectonema* have dorsal and ventral double rows of swimming bristles, while those of Gordiida lack bristles (except for, in some species, minute patches of bristles in front of the cloacal opening). Mature adults of Gordiida emerge from their insect host when the latter approaches or enters water. It has been suggested that the worm is able to cause its host to actively seek out water, but it seems more likely that the worm simply causes erratic but non-directional behaviour that may make the host more likely to come into contact with water than if it had remained in its preferred microhabitat (Thomas *et al.* 2002). Once the host does come close to water as a result of random movement, the worm may be able to induce a last suicidal jump; alternatively, it may simply be that the addled host does not recognise the water as dangerous and makes no attempt to avoid it.

Female Chordodes *wrapped around a stick, laying a white egg string. Photo from the Hairworm Biodiversity Survey.*

Once in the water, the adult Gordians will mate with any others present; when multiple adults emerge in close proximity, they may begin mating before they have even finished emerging from their host (Hanelt & Janovy 2004). The females lay their eggs in long strings: one female may lay nearly six million eggs, making them one of the potentially most fecund animals on the planet. The larvae that hatch from the eggs look nothing like their parents, being kind of sausage-shaped with an eversible, spiny proboscis. A larva will find itself an aquatic animal host such as an insect larva or mollusc to burrow into and form a cyst. If the aquatic secondary host is then eaten by a suitable terrestrial primary host (for instance, after an aquatic insect larva matures into a terrestrial adult), the cyst will hatch out and the Gordian will complete its development within the terrestrial host. The Gordian larva may also bypass the secondary host if a primary host drinks water containing Gordian larvae. The larva or mode of transmission of *Nectonema* remains unknown,but, as *Nectonema* adults live in the same habitat as their primary host, they probably do not require a secondary host.

Larva of Chordodes *encased in a cyst, from the Hairworm Biodiversity Survey.*

Phylogenetically, Gordians have usually been regarded as related to nematodes, with which they share a number of morphological features. However, a molecular analysis by Sørensen *et al.* (2008) suggested a relationship between Gordians and loriciferans (albeit with support that was not overwhelming). The Gordian larva (which has no equivalent in the direct-developing nematode life-cycle) does bear a vague resemblance to an adult loriciferan, though it is debatable whether the resemblance is more than superficial. Loriciferans have not appeared in many phylogenetic analyses to date, and further investigation is required to establish whether it is the adults or the larvae of the Gordians that hold the clues to their affinities. CKT110509

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Nematoda

Abreviated Dendrogram

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   `--PANARTHROPODA
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The Nematodes - Lifestyles of the small and simple

> "If all the matter in the universe except the nematodes were swept away, our world would still be dimly recognizable, and if, as disembodied spirits, we could then investigate it, we should find its mountains, hills, vales, rivers, lakes and oceans represented by a thin film of nematodes. The location of towns would be decipherable, since for every massing of human beings there would be a corresponding massing of certain nematodes. Trees would still stand in ghostly rows representing our streets and highways. The location of the various plants and animals would still be decipherable, and, had we sufficient knowledge, in many cases even their species could be determined by an examination of their erstwhile nematode parasites."

--N.A.Cobb

It is a strange psychological quirk that humans love (or at least are impressed by) big things. We get excited by fifty inch flat panel TV screens and mile-long imperial battlecruisers. The bigger a prehistoric

monster is, the more it fascinates. Every paleo geek loves *Tyrannosaurus rex*, but no-one cares about Parasite rex, despite the latter being without doubt the more deadly of the two (and far more impervious to anything human ingenuity could throw at it; resurrected dinosaurs wouldn't last five seconds against modern firearms). You would never see a thirty meter long nematode rising from the river like a mutaed alligator from the sewers, and it is precisely becaus eof their minute size, lack of complexity, and primitely parasitic habits that nematodes are the most abundant form of multicelluar life on Earth

Picture credits: Nematoda - photo © 2001, CSIRO Australia

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A quick tour of nematode diversity and the backbone of nematode phylogeny

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Abreviated Dendrogram

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ECDYSOZOA
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Contrary to textbook dogma, nematodes are not only highly diverse, but often also complex and biologically specialized metazoans. Just a few of the many fascinating adaptations are reviewed in this chapter, as a prelude to a quick tour through phylogenetic relationships within the phylum. Small Subunit rDNA sequences have confirmed several controversial prior hypotheses, as well as revealing some unexpected relationships, resulting in a recent proposal for revised classification. Three major lineages exist within the phylum: Chromadoria, Enoplia and Dorylaimia. The exact order of appearance of these lineages is not yet resolved, which also leaves room for uncertainty about the biology and morphology of the exclusive common ancestor of nematodes. Enoplia and Dorylaimia differ considerably in many respects from *C. elegans*, which is a member of Chromadoria. The latter group is extremely diverse in its own right, for example in ecological range, in properties of the cuticle and in structure of the pharynx. The formerly relatively widely accepted class Secernentea is deeply nested within Chromadoria, and has therefore recently been relegated to the rank and name of order Rhabditida. Within this order, closer relatives of *C. elegans*include strongylids, diplogasterids and bunonematids. Tylenchs, cephalobs

and panagrolaimids are also members of Rhabditida, albeit probably more distantly related to *C. elegans*

1. Nematodes are highly diverse, complex and specialized metazoans

Nematodes are the haiku among multicellular animals, combining endless variation with a deceptively simple underlying anatomical pattern. In the search for maximally informative models, this reputation for underlying simplicity has sometimes caused *C. elegans* to be erroneously described as a typical representative of all nematodes, or as a typical example of a simple metazoan (e.g., Nelson et al., 1982). However, simplicity lies very much in the eye of the beholder: nematodes are highly diverse in almost every respect, including for example morphology (Figure 1). A small sampler of some of the many other kinds of remarkable nematode adaptations will further illustrate this point.

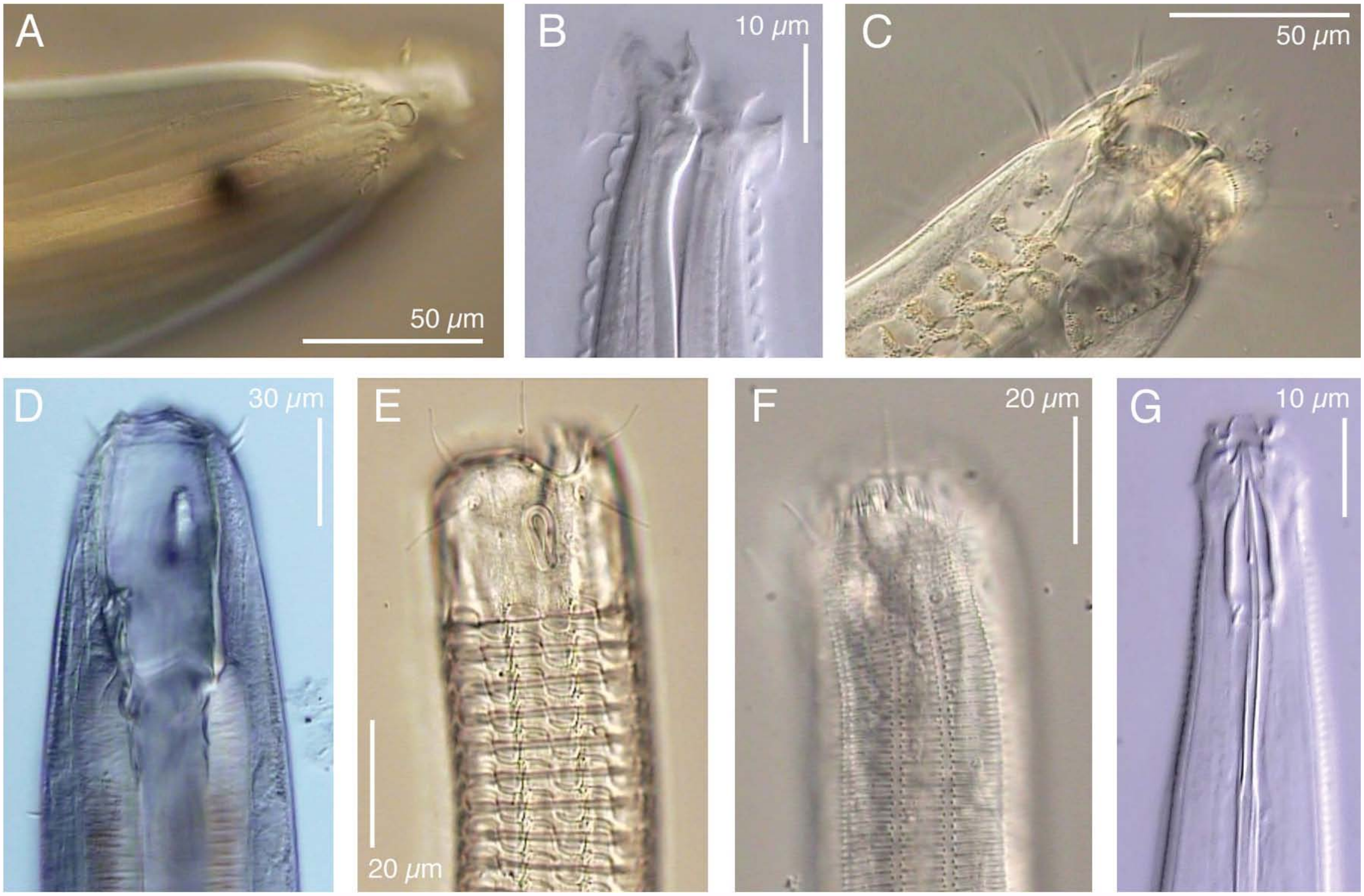

Figure 1. Examples of divergence in anterior morphology of some freeliving nematodes. A. *Thoracostoma* sp (Enoplina). B. *Acromoldavicus mojavicus* (Tylenchina: Cephalobomorpha). C. *Enoploides* sp. (Enoplina). D. *Pontonema* cf. *parpapilliferum* (Oncholaimina). E. *Ceramonema* sp. (Plectida). F. *Latronema* sp. (Chromadorida). G. *Actinca irmae* (Dorylaimida). Click on a picture to open a small video clip (200–600 Kb), or on a letter to open a large clip (2–5 Mb) of the depicted nematode. Use the left and right arrow keys on your keyboard to focus up and down. These clips were produced with Video Capture and Editing microscopy as described in De Ley & Bert (2002).

Two *Cryonema* species permanently live at freezing point inside lacunae in arctic ice; one of them preys on other lacunary nematodes (Tchesunov & Riemann, 1995). Nematodes of the subfamily Stilbonematinae are covered with a dense "fur" of species-specific ectosymbiotic sulfur-oxidizing bacteria, allowing them to thrive at the redox boundary layer in sulfur-rich marine sediments (Nussbaumer et al., 2004). *Oncholaimus* mates by traumatic insemination: males inject sperm through the female cuticle, females then develop specialized internal structures for sperm transfer to the reproductive system - or for evacuation of excess sperm into the intestine (Coomans et al., 1988). The entomopathogen *Steinernema tami* produces dimorphic sperm, with 50–100 μm wide megaspermatozoa functioning as self-propelled spermatophores carrying the 2 μm wide microspermatozoa on their surface (Yushin et al., 2003). *Mehdinema alii* uses male crickets as vectors for transmission between female cricket hosts, female nematodes give birth to fully formed dauers while males have a motile copulatory claw extruding through a separate postcloacal opening (Luong et al., 2000). The millipede gut inhabitant *Zalophora* is an intra-intestinal predator and cannibal of other gut nematodes (Hunt & Moore, 1999).

Some recent discoveries in nematodes extend the range of biological processes and properties known for all Metazoa. For example, mitochondrial mRNA transcription in *Teratocephalus lirellus* involves insertional editing of polyA motifs, a process otherwise only known in protists (Vanfleteren & Vierstraete, 1999). Mitochondrial DNA of the potato cyst nematode *Globodera pallida* is arranged in at least six different mini-circles, each of which carries only a subset of the mitochondrial genome, resembling conditions occurring in some plants and fungi but not other metzoans (Armstrong et al., 2000). Conversely, closer scrutiny of increasingly distant relatives of *C. elegans* has revealed a number of aspects in which some nematodes are much less different from other Metazoa than *C. elegans* is. A very recent case in point is the discovery that early development in *Tobrilus diversipapillatus* passes through a classical metazoan coeloblastula stage, unlike any other nematode species studied so far (Schierenberg, 2005). Clearly, our appreciation of nematode diversity will continue to change as we explore the biology of more species that have so far received little attention, and as we encounter more of the potentially vast number of unknown species.

2. Changing perspectives in nematode phylogeny and classification

In the face of overwhelming diversity, a phylogenetic framework is needed to underpin meaningful comparisons across taxa and to generate hypotheses on the evolutionary origins of interesting properties and processes. Our understanding of nematode relationships has a varied and at times turbulent history, reflecting not only wider developments in phylogenetics, but also the expertise and perspectives of those few systematists who produce comprehensive classifications. Until recently, the data for most nematode phylogenies consisted of relatively few morphological characters derived primarily from light microscopy and often by individual effort of the lone taxonomist. Molecular phylogenetics, bioinformatics and digital communication technologies have substantially altered the dynamics of nematode systematics, creating conditions where collaborative strategies are much more productive than individual effort. This approach was exemplified by the analyses of Blaxter et al. (1998) based on small subunit (SSU) rDNA sequences of 53 nematode species.

Just seven years later, SSU rDNA sequences are available in public databases for more than 600 nematode species. The basic topology obtained by Blaxter et al. (1998) appears to remain quite robust, although a number of important groups remain to be included. Also, it is increasingly clear that some important aspects of nematode phylogeny cannot be resolved by SSU data alone. Two of the major features of SSU analyses have independently confirmed suspicions held by several proponents of earlier morphological systems, i.e., that many important anatomical features have arisen repeatedly during evolution, and that one of the two traditional classes (Secernentea) is deeply phylogenetically embedded within the other (Adenophorea). In an effort to translate the implications of SSU rDNA sequences into classification, De Ley & Blaxter (2002, 2004) proposed a system based primarily on the molecular backbone of SSU phylogenies (Figure 2), but also incorporating other characters. The result combines elements from many previous systems, and introduces some new features with respect to ranking (e.g., use of infraorders; Figure 3). For the sake of convenience, we will follow the nomenclature of this system here, in order to outline the major features of SSU-based nematode phylogenies.

3. The backbone of the nematode tree

The molecular data published to date confirm the presence of three early nematode lineages, corresponding to the previously recognized subclasses Chromadoria, Dorylaimia and Enoplia (Lorenzen, 1981; Inglis, 1983). The exact order of appearance of these three lineages is not yet resolved (Figure 2). It seems likely that Enoplia appeared first, and it is even possible that Dorylaimia and/or Chromadoria could have originated within Enoplia. On the other hand, SSU data also allow for the possibility that Dorylaimia diverged first, which is an intriguing possibility because all known Dorylaimia are absent from marine habitats. A “Dorylaimia first” topology would therefore imply that the ancestor of all nematodes was perhaps a freshwater organism, and not a marine animal as more commonly assumed (De Ley & Blaxter, 2004).

Within Chromadoria, a number of clades have arisen in a series of successive bifurcations and radiations. These clades are classified as separate orders, including for example the predominantly marine Chromadorida and

Desmodorida, as well as orders that have also diversified extensively in freshwater sediments (e.g., Monhysterida) and moist soils (e.g., Plectida). In addition, the chromadorian monophylum also includes the clade formerly ranked as class Secernentea, a hugely successful radiation of predominantly terrestrial nematodes. SSU phylogenies place this taxon at the crown of Chromadoria and as sister group to the order Plectida. For this reason, De Ley & Blaxter (2002, 2004) classified it instead as order Rhabditida, thereby greatly expanding the contents of this taxon compared to all previous systems.

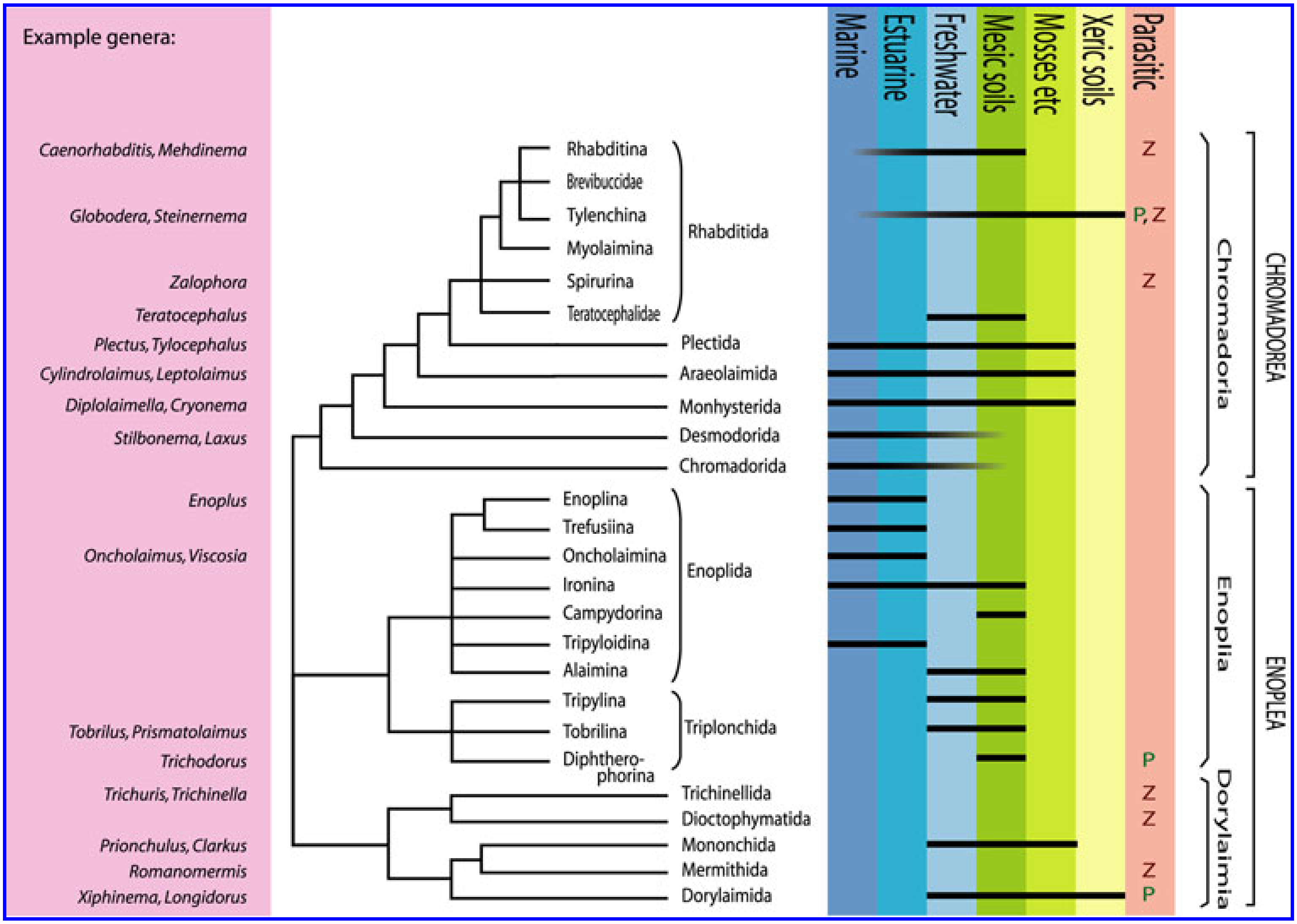

Figure 2. Summarized SSU phylogeny of Nematoda with example taxa, ecological range and higher classification (adapted from De Ley & Blaxter, 2002). P = phtypoarasitic, Z = zooparasitic.

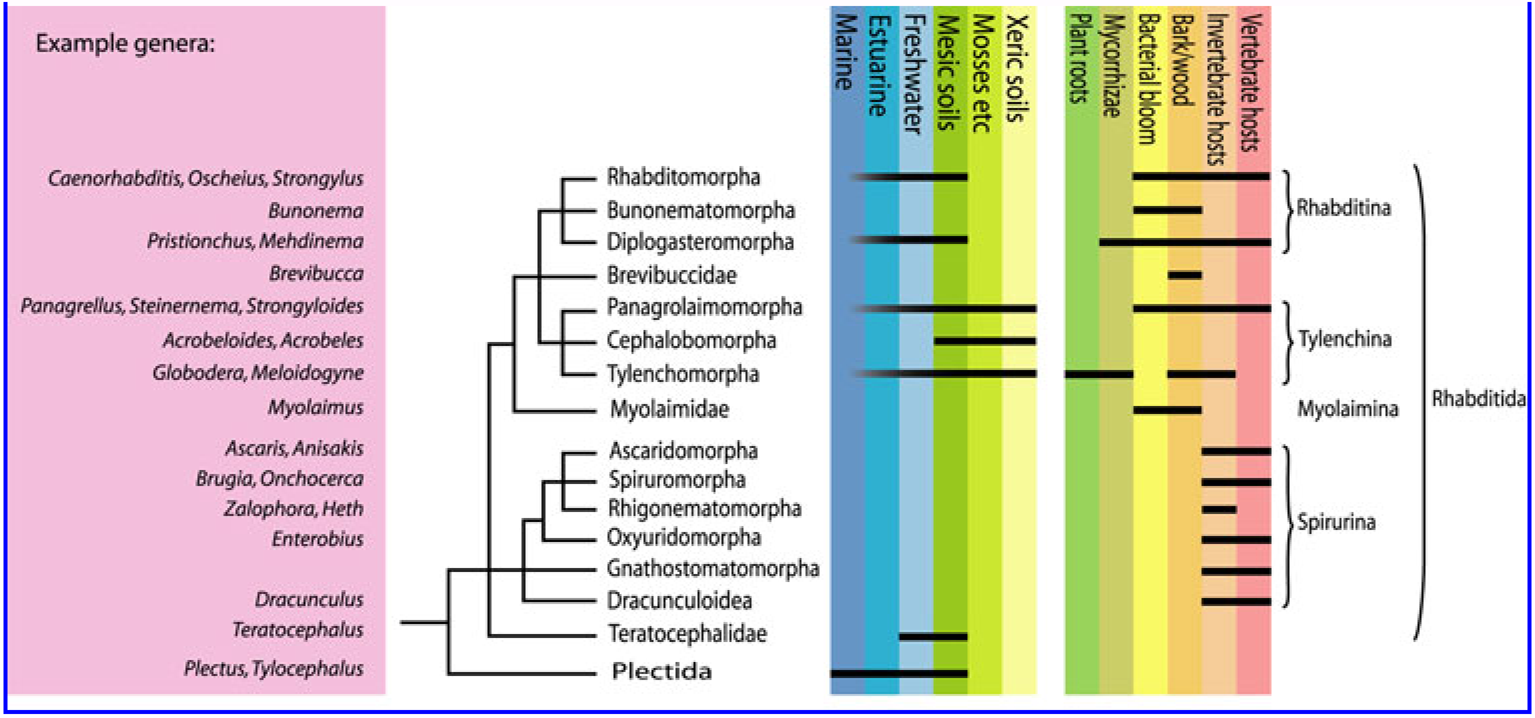

Figure 3. Summarized SSU phylogeny of Rhabditida with example taxa, ecological range and higher classification (adapted from De Ley & Blaxter, 2002). Note the use of infraorder names (ending in -omorpha).

4. Major features of Enoplea

The phylum Nematoda occurs in an incredibly wide spectrum of ecological habitats and natural histories, ranging from e.g., deep sea sediments to arid deserts, or from interstitial bacterivores to obligate parasites with multiple intermediate hosts. Several of its constituent clades cover a large subset of this ecological spectrum, but interestingly none of them appears by itself capable of covering the full ecological range of the phylum, especially so within the class Enoplea (Figure 2). This suggests that the evolution of ecological adaptations within each nematode taxon was constrained by limitations on the rates of change in genes and ecophysiology, or by competitive exclusion from habitats previously colonized by other taxa, or both.

The non-marine occurrence and the present diversity of Dorylaimia both suggest that these could have been the first nematodes to conquer freshwater and terrestrial habitats. Such an early origin could explain the great diversity within this subclass, which includes not only the mostly freeliving Doryaimida and Mononchida, but also remarkable animal parasites such as Mermithida and Trichinellida. Mermithids are highly unusual among metazoan parasites in that they actually leave the host before reaching adulthood - a property otherwise only found in the phylum Nematomorpha. The present existence of such exceptional biologies hints at much greater past diversity. The most successful surviving clade within Dorylaimia, however, is the order Dorylaimida. This includes many species of large predators/omnivores, as well as the plant-parasitic family Longidoridae, of which some species transmit plant viruses. The evolutionary radiation of dorylaims appears to have resulted in large part from functional diversification of the odontostyle, a protrusible, hollow and often needle-like tooth used for puncturing and emptying food items (e.g., Figure 1G). Although predation or plant feeding are well documented for larger dorylaims, the food sources of most smaller species (with much smaller odontostyles) remain unknown.

Enoplia are especially diverse in marine habitats, but multiple lineages are also found in freshwater sediments and/or moist soils (Figure 2). One of these lineages includes marine, freshwater and terrestrial taxa, suggesting that early Enoplia were characterized by much greater osmotic tolerance than early Dorylaimia. Most enoplian clades include large predators with big hooks or teeth in more or less complex arrangements (Figure 1C,D), as well as interesting sensory structures such as eyespots (Figure 1A,D) and a unique type of stretch receptors (= metanemes; Lorenzen, 1994). Enoplia are especially interesting phylogenetically because of the occurrence of features that are presumably ancestral within nematodes, such as a highly indeterminate mode of development (Justine, 2002) and retention of the nuclear envelope in mature spermatozoa (Lee, 2002). No Enoplia are known to have adapted to terrestrial environments subject to extreme temperatures, nor are there any surviving lineages that parasitize animals (with the possible exception of a few enigmatic taxa of uncertain position). The one enoplian order that has clearly undergone extensive evolution in soils is the order Triplonchida, which includes plant parasites such as *Trichodorus*. These are convergent with dorylaims in a number of respects, e.g., they also have a protrusible tooth for feeding (called an onchiostyle) and several species are known to act as virus vectors. Molecular data have shown that the triplonchid clade includes freeliving nematodes such as *Tobrilus* and *Prismatolaimus*, even though these are morphologically quite divergent from trichodorids.

5. Features and diversity of Chromadorea

The Chromadoria include at least four lineages that have attained greater habitat breadth than all Enoplia and most Dorylaimia. Chromadoria are common in marine sediments, but they have also flourished in terrestrial habitats e.g., those subject to frequent episodes of rapid de- and rehydration, such as mosses and lichens or extremely xeric and/or cryogenic soils. Throughout Chromadoria, cuticular structure has undergone a wide range of evolutionary modifications, sometimes resulting in strikingly decorative ornamentations (Figure 1E, F). A key adaptation within the order Rhabditida was the development of a chemically impermeable cuticle, which clearly contributed to their success as parasites, colonizers and extremophiles. Another subject of striking modification in Chromadoria is the pharynx, which is structurally much more diverse in this subclass than in Enoplia or Dorylaimia. This diversity revolves mostly around the evolution of one or more rounded muscular bulbs, which has apparently allowed for more compact body designs. Freeliving Chromadoria are on average noticeably smaller than Enoplia and Dorylaimia, correlated with a greater preponderance of rapidly reproducing bacterial feeders. As a possible corollary, many species (such as *C. elegans*) have also evolved compressed generation times and other adaptations for rapid dispersal and efficient colonization of eutrophic environments. Several chromadorian lineages have independently evolved curved, swiveling teeth in can-opener-like arrangements. These are used to e.g., pry open the silicate frustule of diatomaceous algae, or to slice the cuticle of other nematodes. Some of these species are among the smallest known predatory nematodes. The most distant relatives of *C. elegans* that can presently be efficiently cultured with *C. elegans*-like methods are certain bacterivorous species of the orders Monhysterida and Plectida (De Ley & Mundo-Ocampo, 2004).

Within the order Rhabditida, a major factor has been the development of a modified juvenile stage specifically adapted to long-term survival. A true dauer stage is rarely reported outside of the suborder Rhabditina (which includes *C. elegans*) but a “proto-dauer” actually occurs in several other lineages, including some panagrolaims as well as the morphologically bizarre genus *Myolaimus*. Appearance of a proto-dauer in the early evolution of Rhabditida probably set the stage for subsequent specialization into the non-feeding, highly modified and highly dispersive dauer stage of Rhabditina. True dauers are often capable of seeking out and hitching rides phoretically on larger animals, which has in turn allowed multiple invasions of the internal organs of other animals. At least three Rhabditida lineages have independently evolved major zooparasitic radiations. A fourth lineage has not only given rise to zooparasitic species, but also radiated into the most diverse group of plant parasites and fungal feeders among nematodes. These are the tylenchs, equipped with a protrusible stomatosylet that is convergent with, but clearly different from, the odontostyle of dorylaims and the onchiostyle of trichodorids. SSU sequences have confirmed the previously unpopular hypothesis that their closest relatives are the morphologically very dissimilar cephalobs (Siddiqi, 1980). Both groups are therefore now united in the suborder Tylenchina (Figure 3) - another example of a more drastic change induced by the new phylogenies.

Analogous to zooparasitic Rhabditida, the life cycle of some parasitic tylenchs includes an infective juvenile stage. However, most tylenchs and cephalobs do not have one single dispersive and enduring stage, but are instead capable of surviving harsh conditions throughout most of their life cycle. This has enabled them to compete very successfully with dorylaims in even the driest and coldest terrestrial environments. One secret to this success could be constitutive postembryonic expression of traits that first evolved and appeared in the proto-dauer stage only: tylenchs and cephalobs are in some respects quite dauer-like throughout their life cycles. Interestingly, some cephalobs have also developed strikingly complex labial structures, presumably for collecting and ingesting scarce bacteria in poor soils (Figure 1B).

The third major lineage within Tylenchina are the panagrolaims, a less clearly circumscribed amalgam of freeliving opportunists, fermentation specialists, insect pathogens and animal parasites. Although there are numerous morphological intermediates between panagrolaims and cephalobs, robust molecular resolution is still missing. One interesting character that supports monophyly of Tylenchina is axis determination in the early zygote, which does not depend on sperm entry in these nematodes (contrary to Rhabditina; Goldstein et al., 1998). Parthenogenesis appears to be much more common in Tylenchina than hermaphroditism, and Goldstein et al. (1998) speculated that this could in fact be linked to the mechanism of axis determination.

Within the suborder Rhabditina, diversity segregates into four major groups: strongylids, diplogasterids, bunonematids and rhabditids (*sensu stricto*). The latter group includes *C. elegans* as well as many other species that differ morphologically in details of the male and female reproductive system. Strongylids were traditionally placed in their own order, on the basis of their importance as animal parasites and their morphological complexity as adults. However, they actually arose from within rhabditids, as is clear from SSU sequences (Sudhaus & Fitch, 2001), juvenile morphology and male genital characters. Compared to rhabditids, diplogasterids are characterized by a shift of pharyngeal pumping function to the median bulb, with concomitant muscle and valve reduction in the basal bulb. This arrangement is superficially very similar to the pharynx of Tylenchina, but ultrastructural and molecular data strongly indicate that the resemblance is purely convergent (Blaxter et al. 1998; Baldwin et al., 2001). The group includes the "satellite model" *Pristionchus pacificus*, in a colorful array of bacterivores, fungivores, animal parasites and "can-opener" type predators (Fürst von Lieven & Sudhaus, 2000). The closest relatives of diplogasterids appear to be certain species that exhibit the morphology typical of rhabditids (Sudhaus & Fitch, 2001), but also the truly perplexing bunonematids (Fürst von Lieven 2002). The latter include some of the most unusual anatomies among nematodes, with complex cuticular ornamentations arranged in dorsoventral symmetry,*i.e.* at right angles to the bilateral symmetry of the internal organs. They appear to be specifically adapted for life along surfaces within decomposing material, and provide a most appropriate conclusion to this chapter's quick tour through nematode diversity.

6. Acknowledgements

I am indebted to Dr. Jay Burr for providing several of the specimens included in Figure 1, and to Dr. Irma Tandingan De Ley and Mrs. Melissa Yoder for assistance with Video Capture and Editing microscopy as described in De Ley & Bert (2002), in the course of collaborative research supported by National Science Foundation awards DEB-0228692 and DEB-0315829.

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[*] Edited by David H.A. Fitch. Last revised April 5, 2005. Published January 25, 2006. This chapter should be cited as: De Ley, P. A quick tour of nematode diversity and the backbone of nematode phylogeny (January 25, 2006), *WormBook*, ed. The *C. elegans* Research Community, WormBook, doi/10.1895/wormbook.1.41.1, http://www.wormbook.org.

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It's Nematodes All the Way Down

By
Christopher Taylor

Abreviated Dendrogram

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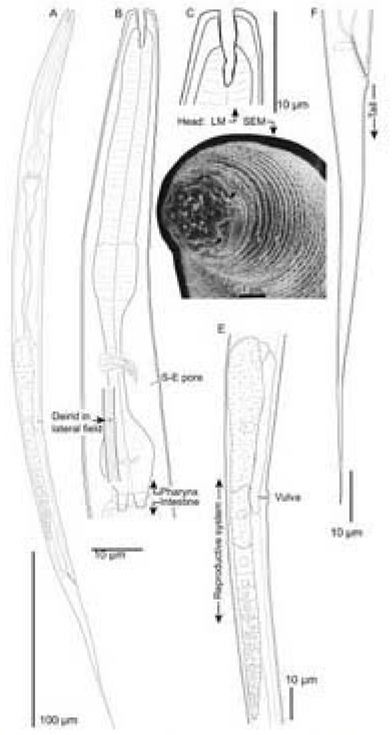

Supplementary Figure 5. General morphology of *Halicephalobus mephisto* n. sp.: LM drawings of female holotype and SEM photograph of head. A: Entire body; B: Neck region; C: anterior region; D: SEM *en face* view; E: reproductive system; F: tail.

Halicephalobus mephisto, as illustrated by Borgonie *et al.* 2011.

It has to be said, nematodes are not among the most loved of organisms. For the most part, the only nematodes that get any press are either the developmental model animal *Caenorhabditis elegans* or the small proportion of species that affect us economically as parasites of ourselves or our food sources. There are not thriving clubs of amateur nematologists, there are no news-groups where nematode spotters eagerly spread the news of their latest desmoscolecid sighting. So it suggests something out of the ordinary may be going on when a new nematode species makes its debut in the pages of *Nature*, as one did today (Borgonie *et al.* 2011).

Appearance-wise, *Halicephalobus mephisto* is fairly ordinary (most nematodes are). It does have a higher-than-usual temperature resistance, being able to live in temperatures up to 41°C, but this is not extreme. Nor is the new species' ability to tolerate low oxygen concentrations, a common ability among minute animals such as nematodes and tardigrades. What is unusual about *H. mephisto* is where it was found: some 1.3 km beneath the surface of the Earth. *Halicephalobus mephisto* was recovered from fracture water (that is, water that was sitting in a fracture within the rock) in South Africa that had been isolated from the rest of the world for somewhere between 3000 and 12000 years, before being broken into by the Beatrix gold mine.

The presence of living organisms at this depth was not unexpected: bacteria had been found in fracture water previously. Nevertheless, this is the first time that a multicellular animal has been found at this depth. A samples taken in another mine at a depth of 0.9 km also recovered nematodes: one belonging to a previously known species, *Plectus aquatilis*, and one belong to an unidentifiable species of the family Monhysteridae. A sample taken at a depth of 3.6 km in a third mine did not recover any specimens, but did allow the recovery of nematode DNA suggesting their possible presence. Samples from the soil surrounding the boreholes from which the water samples were taken, as well as samples of the water used in drilling the mines themselves, were tested to establish that the nematodes were indeed from the original fracture water and not recent contaminants, but these control samples were nematode-free.

Halicephalobus mephisto lives a life completely isolated from the surface world, presumably feeding on the bacterial biofilms growing along the edge of the fracture. It would not be abundant: in the Beatrix mine sample, 6480 litres of water were filtered but only a single nematode was recovered (thankfully, the parthenogenetic nematode was successfully raised and bred in the lab, providing the necessary specimens for the species description). But it provides further support for the principal that where there is liquid water, there is life.

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| Unit Back: Scalidophora | Clade Down (none) | Ecdysozoa Dendrogram | Nematoida References | Unit Next: Panarthropoda |

Nematoida: References

Abreviated Dendrogram

```
ECDYSOZOA
|--SCALIDOPHORA
|
`--+--NEMATOIDA
   |--+--Nematoda
   |  `--Nematomorpha
   `--PANARTHROPODA
```

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Scalidophora

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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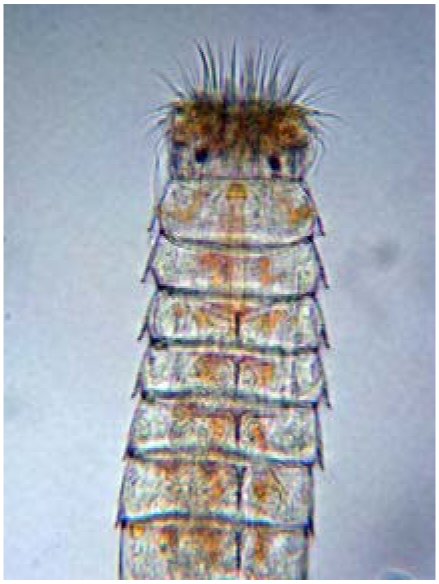

Interstitial kinorhynch collected off Florida .
Photo © Rick Hochberg via Encylopedia of Life, Creative Commons Attribution Non-Commercial Share Alike

The Scalidophora are a clade represented today by three rather distinct phyla. Although relatively unimportant now, were numerous and diverse during the early Paleozoic. During the Cambrian, they were far more common and diverse. Whilst some taxa, such as the Cambrian Priapulids have hardy changed, other groups, like the

Palaeoscolecida, represent quite distinct taxa that may or may not be related to modern forms. Although usually portrayed as a monophyletic assemblage, they may be a paraphyletic or ancestral grade of Ecdysozoa, especially when Cambrian forms are cons9idered. If this is so, then Scalidophora in the broad sense would be equivalent to Ecdysozoa.

Pending a more complete coverage, this unit will basically be a collection of holding pages with only a brief description. MAK120420

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Scalidophora

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
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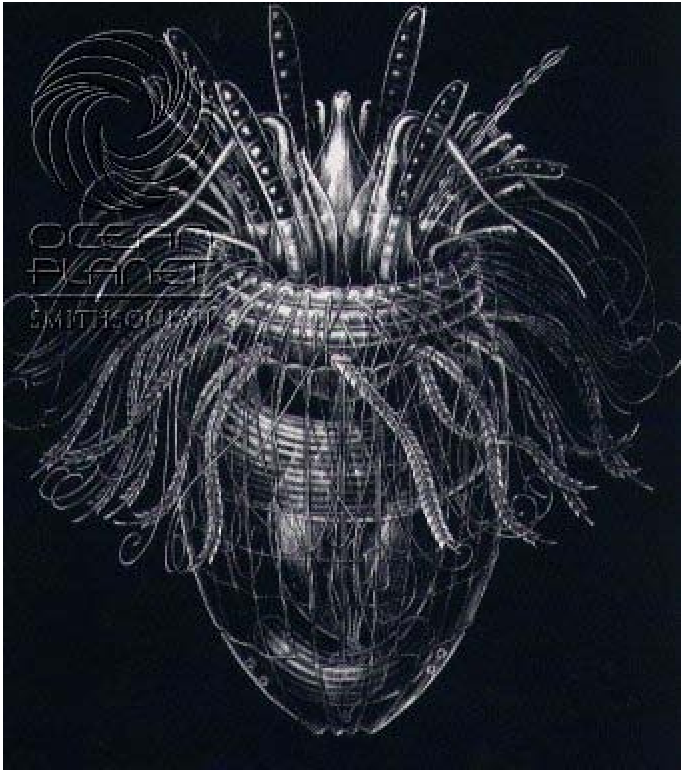


Pliciloricus enigmatus Higgins & Kristensen, 1986 (Loricifera, Nanaloricida, Pliciloricidae). Actual size is about one-quarter of a millimeter.,
EM image from nasa.gov via wiki.en Wikimedia Commons. Public domain

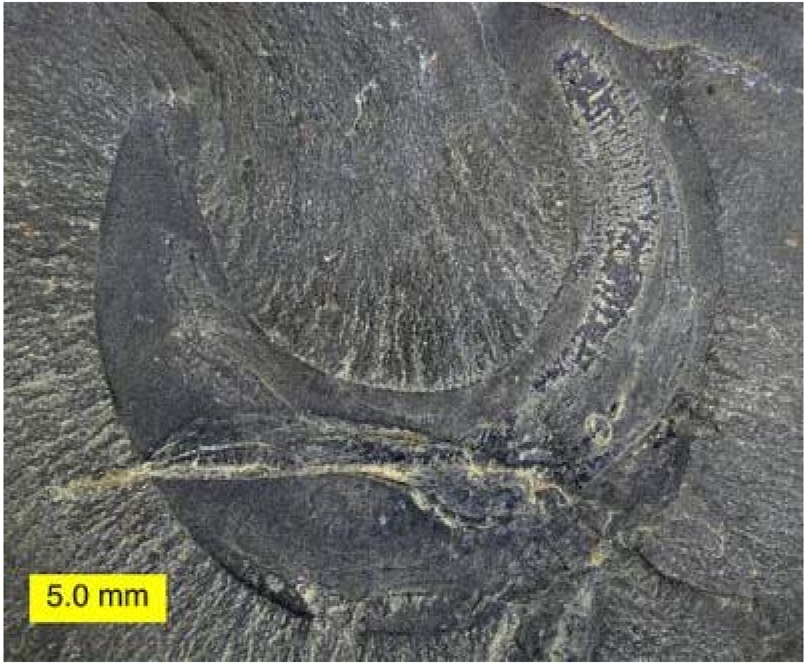
Introduction

The Scalidophora are a group of marine pseudocoelomates (animals lacking a true body cavity), consisting of the three phyla Kinorhyncha, Priapulida, and Loricifera. The members of this group share a number of characteristics, including introvert larvae and moulting of the cuticle (ecdysis). Kinorhyncha and Loricifera are both minute meiofaunal predators, while Priapulida can reach (for a worm) reasonably large sizes. They were originally included in the phylum Aschelminthes, along with other taxa now placed in the Lophotrochozoa, which is now known to be a polyphyletic taxon. They are now considered to either constitute one of the two or three clades of the Ecdysozoan superphylum, or to be a paraphyletic assemblage of generalised Ecdysozoans, from which more specialised lineages like the Panarthropoda (which may themselves be paraphyletic or ancestral, although we have here more parsimoniously treated them as monophyletic) are derived. Wikipedia, updated MAK120420

Fossil record

Scalidophora have a fairly extensive fossil record for a soft-bodied clade, particularly in the Cambrian. Indeed, scalidophorans seem to have been the major infaunal predators in the Cambrian fauna, only later being replaced by the annelids. While fossil scalidophorans such as *Palaeoscolex* and *Ottoia* are often referred to as priapulids, most of them lie outside the priapulid crown group and may not have exactly resembled modern species. The name *Priapulida* is better retained for the crown group, with *Priapozoa* used for the wider group including the Cambrian taxa.

Palaeoscolex and its close relatives were covered in an armour of small plates, and disarticulated plates are commonly found as microfossils. The Palaeoscolecida were regarded as probable annelids for many years, until Conway Morris reidentified them as priapulid relatives. CKT061014



Ottoia prolifica from the Walcott Quarry of the Burgess Shale (Middle Cambrian) near Field, British Columbia, Canada.
Photo by Mark A. Wilson, Wikipedia, public domain

Descriptions

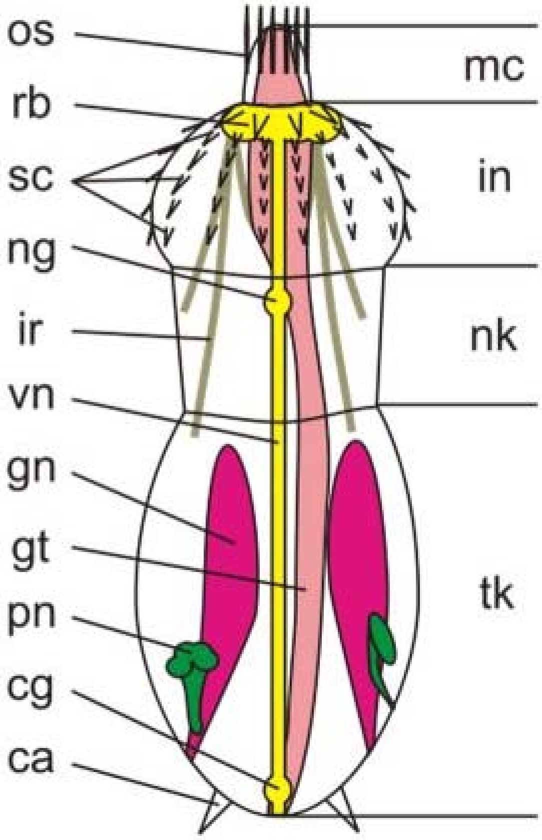
Scalidophora (= Cephalorhyncha) *Markuelia*

Range: Fr ECambrian

Phylogeny: Ecdysozoa : Panarthropoda + Nematoida + * : *Markuelia* + Palaeoscolecida (paraphyletic) + (Kinorhyncha + (Loricifera + Priapulida)

Comments: The Scalidophora is based on shared details of the introvert in priapulids, kinorhynchs and loriciferans (Edgecombe et al 2011). This grouping has been recovered as monophyletic by molecular studies (Halanych 2004). Nielsen (2001) used the name *Cephalorhyncha* for this clade (see also (UCMP) link, below), but in its original usage it also included the Nematomorpha. Based on new molecular data and analyses, Sørensen et al. (2008) concluded that the Loricifera and Nematomorpha appear to be sister taxa, which would make the Scalidophora (or Cephalorhyncha sensu Nielsen 2001) clade paraphyletic. Conversely some paleontological morphological analysis locates them between the Kinorhyncha and Priapulida (Dong et al 2004 and later papers, e.g. Dong et al 2005 and Harvey et al 2010). The implication is that either the moloceular or the morphological characters are convergent. For now we have followed the latter, pending further analyses

As of 2010, relationships among phyla within the Ecdysozoa remain poorly resolved, so it is difficult to know which groups will eventually win wide acceptance by specialists as



Anatomy of a stylised scalidophoran. ca - caudal appendages; cg - caudal "ganglion"; gn - gonad; gt - well, in - central part of an introvert; ir - introvert retractor; mc - mouth cone; ng - neck ganglion; nk convincingly monophyletic and deserving of a name. - Leo Shapiro, EoL EoL (Attribution-NonCommercial-ShareAlike); MAK120415

- neck; os - oral stylet (arming) pn - cluster of protonephridia (left side: vinctiplicatan variant, right: kinorhynch) rb - ring-brain, sc - scalids; tk - in trunk; vn - ventral nerve cord.
Diagram by Kuzia from Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

For now, we have followed the traditional phylogeny (based on molecular studies). However, it may be that the priapulida (or, more correctly, the priapozoa) are primitive, and that kinorhynchs and loriciferans represent more derived ancestors, with the kinorhynchs being the most specialised, rather than the most basal, of all. The apparently basal position of these miniaturised forms would be due to their highly derived nature, and loss of traditional synapomorphies. Or it may be that the priapulids *sensu latu* are a paraphyletic assemblage, with some Cambrian priapulids (or priapozoa), such as *Ancalagon* and *Fieldia*, occupying a basal position, near *Markuelia* (Dong et al 2004, cladogram, fig 3b; Dong et al 2005 cladogram, fig 3a.) MAK120420

Link: Introduction to the Cephalorhyncha (UCMP)

Image scalidophoran external and internal structures, by Kuzia by-sa 3.0 / gnu Wikipedia

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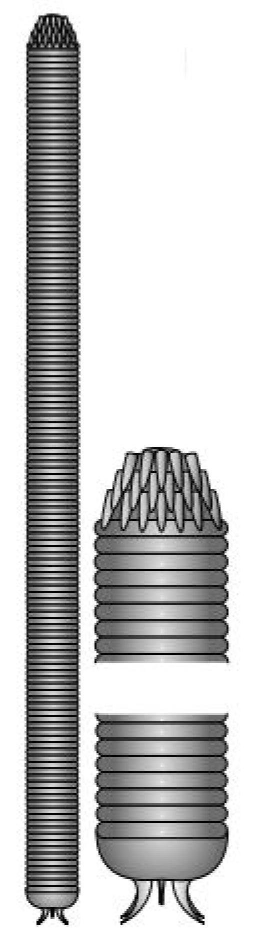

Markuelia

Range: Cambrian

Phylogeny: Basal Scalidophora

Comments: Known only from fossil embryos. Wikipedia: X-ray tomographic microscopy has been applied to splendidly preserved, uncrushed Markuelia fossils found in Hunan province in southern China and in eastern Siberia. When details in features smaller than one micrometre across can be observed, these fossils are seen to represent many developmental stages, from the first cell divisions to the time of hatching; therefore they offer a unique opportunity to study the development of Early Cambrian animals.

Image Reconstruction of the embryo of *Markuelia hunanensis* unfurled, Dong et al 2004 fig 3a. This species is from the Late Cambrian Bitiao Formation in Wangcun, Hunan, south China; the earliest record of the genus is Early Tommotian (earliest Cambrian) (Dong et al 2004 p.239)

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Scalidophora: Kinorhyncha

Abbreviated Dendrogram

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BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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Light microscopy image of unspecified kinorhynch.
Photo © Alvaro Esteves Migotto via Encylopedia of Life, Creative Commons Attribution Non-Commercial Share Alike

The Kinorhyncha are a small phylum of tiny segmented pseudocoelomate marine invertebrates that live between mud or sand grains, feeding on organic matter or diatoms. Although most species are marine, some have been found sandy beaches and brackish estuaries, while others live on hydrozoans, bryozoans, or sponges. In the past they have been grouped with rotifers, but it is now known that the two phyla are only very distantly related (both being protostomes).

The fact that kinorhynchs are now placed in the scalidophoran clade of Ecdysozoa shows that the old category of Pseudocoelomates is a polyphyletic one; the pseudocoelomate condition having evolved a number of times as a side effect of minaturisation. It is quite possible also that the ancestral ecdysozoan was segmented, and kinorhynchs, like tardigrades and arthropods, retain this primitive condition (lost in nematodes and priapulids). Kinorhynchs do not have a fossil record, although as the related Priapulida extend back to the Cambrian (and possibly the Loricifera as well) it is likely that they also have a long evolutionary history. MAK120416

Links: Mud Dragon (Kinorhyncha) - Encyclopedia of Life; Kinorhyncha - Wikipedia; Kinorhyncha - Tree of Life Web Project

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Scalidophora: Loricifera

Abbreviated Dendrogram

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BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `--  Loricifera
      `--+--NEMATOIDA
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Light microscopy image of the undescribed species of *Spinoloricus* (Loricifera; stained with Rose Bengal). Scale bar is 50 µm.
From Danovaro et al 2010, via Wikipedia, Creative Commons Attribution 2.0 Generic

The Loricifera are one of several newly discovered and still rather obscure phyla of mostly microscopic marine invertebrates consisting of only a handful of species. They may or may not be minaturised descendents of larger Cambrian forms such as *Sirilorica carlsbergi*, a wormlike burrowing animal which may be close to the common ancestor of loricates and priapulids (Peel, 2010), hinting at a greater diversity and ecological importance for this group during the early Paleozoic. In the last few years, the discovery of three-dimensional "Orsten"-like fossil Loricate larvae from the Middle Cambrian limestone of northern Australia (near Mt Isa, Queensland) have pushed back the antiquity of the group (Maas et al 2009). Several extant species are unique among metazoa in being able to live entirely in an anearobic (oxygen-free) environment. MAK120420

Links: Loriciferans - Encyclopedia of Life; Loricifera - Wikipedia; Loricifera: Larger life without oxygen; Loricifera - Wired Science; Loricifera - Tree of Life project MAK120416

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Palaeos

ECDYSOZOA

PALAEOSCOLECIDA

PALAEOSCOLECIDA

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Scalidophora: Palaeoscolecida

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |  |--Maotianshania
      |  `--+--Cricocosmia
      |     `--Palaeoscolex
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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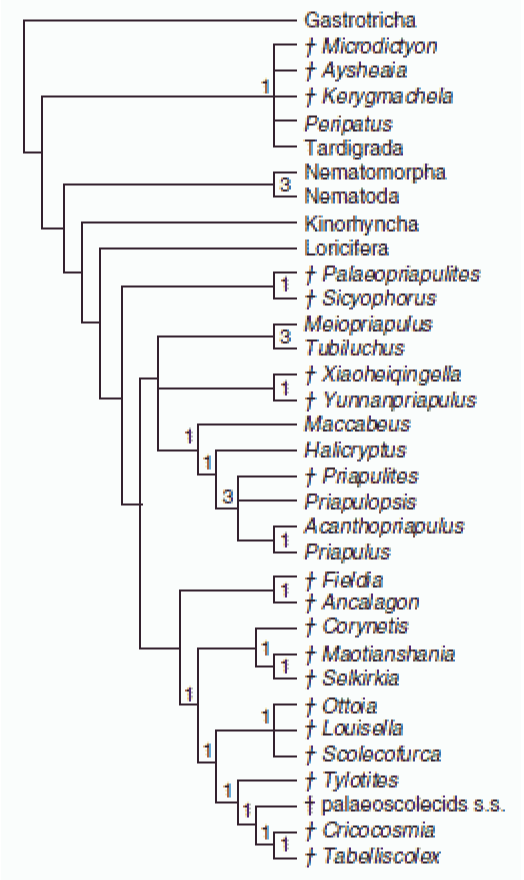
3. Palaeoscolecida X
4. *Palaeoscolex* X

Palaeoscolecidans were a successful group of burrowing worms in the early Palaeozoic, when they were probably even more significant than the annelids. Originally interpreted as annelids, the segmented appearance is apparently only superficial, and results from alternating bands of larger and smaller plates (Ivantsov & Wrona, 2004). Well-preserved specimens from the Chengjiang Fauna possess an anterior spiny proboscis like that of the modern priapulids, and palaeoscolecidans have most often been regarded as priapozoans. Other authors have suggested relationships with the modern nematomorphs, or as stem-

Holotype of *Tabelliscolex hexagonus* comes from Han et al., 2007..

panarthropods (Han et al., 2007). At the very least, a position within the Ecdysozoa, the clade uniting these three groups, seems well-established. - CKT080122

Dzik & Krumbiegel 1989, Budd & Jensen 2000, Budd 2001, Conway Morris & Peel 2010 propose a palaeoscolecid-like form as the common cycloneuralian or ecdysozoan ancestor. Harvey et al 2010 using a traditional cladistic morphological approach, tested and rejected the hypothesis that palaeoscolecids reresent ancestral ecdysozoans and found them instead to be standard Priapulids. Their detailed analysis recovered a monophyletic Cycloneuralia and Panarthropoda, with the Loricifera occupying a transitional position between the Kinorhyncha and the Priapulida (see also the cladograms in Dong et al 2005). Their cladogram, which includes many fossil taxa, is shown at the right.

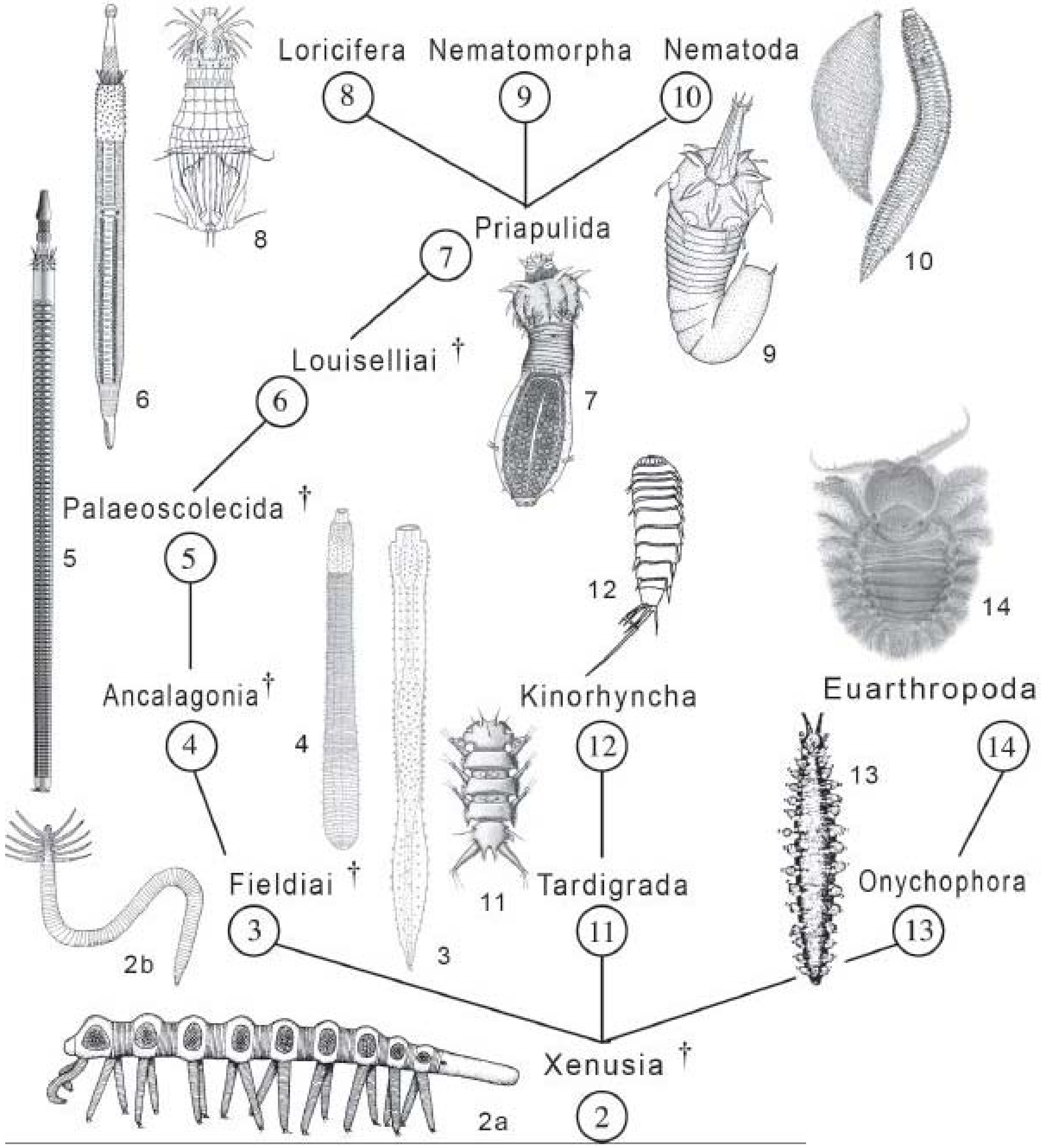


Parsimony analyses of priapulids and related fossil and extant cycloneuralians by Harvey et al 2010 This cladogram gives the strict consensus of most parsimonious trees. Numbers reflect Bremer support for respective nodes as determined by the Double Decay Analysis..

With studies of this kind however there is always the problem of distinguishing between primitive and derived features. Palaeoscolecids may well share primitive or ancestral ecdysozoan traits with priapozoans, causing the two to cluster together in morphological analyses, or for one to be subsumed under the other (seeing how they may both be paraphyletic or even polyphyletic groups this would not be unlikely). Without knowledge of soft parts (although some information can be retrieved from lagerstatten) or genome information and other characters well represented in extant taxa, determining the basal relationships between these early worms is always going to be problematic. Not surprsingly, researchers in this field arrive at very different conclusions, this being even more the case when different methodologies and starting assumptions are used.

For example Zhuravlev et al 2011 note that on the one hand the palaeoscolecidans possess Cephalorhynchan (= Scalidophora + Nematoida) characteristics such as a terminal mouth and an anus, an invertible proboscis with pointed scalids, a thick integument of diverse plates, sensory papillae and caudal hooks. But they also share a number of features with Cambrian lobopods (the paraphyletuic class Xenusia), such as a thick integument of diverse plates. They argue that cephalorhynchs are descendents of xenusians, which lost walking appendages and acquired a retractable proboscis and worm-like body as an adaptation to a burrowing lifestyle. The Cambrian *Facivermis* might represent an intermediate semi-burrowing form, in the process of losing its limbs. Tardigrades, onychophorans and anomalocaridids (making up a paraphyletic panarthropoda, leading to the arthropods) represent other xenusian descendents, which evolution interstitial, surface-dwelling and swimming lifestyles, respectively. This is illustrated by the following diagram (some taxa have been removed, specifically .anomalocarids as ancestors to pycnogonids, which makes less sense then the hypothesis that they represent a paraphyletic assemblage leading to the true arthropods):

General phylogeny of the Ecdysozoa
2a.xenusian



Microdictyon sinicum Chen, Hou and Lu, Lower Cambrian (modified from Hou and Bergstrom, 1995); **2b**.xenusian *Facivermis yunnanicus* Hou and Chen, Lower Cambrian (modified from Delle Cave and Simonetta, 1991); **3**.*Fieldia lanceolata* Walcott, Middle Cambrian (modified from Conway Morris, 1977); **4**.*Ancalagon minor* Walcott, Middle Cambrian (modified from Conway Morris, 1977); **5**.palaeoscolecid *Cricocosmia jinningensis* Hou and Sun, Lower Cambrian (modified from Han et al., 2007); **6**.*Louisella pedunculata* Walcott, Middle Cambrian (modified from Conway Morris, 1977); **7**.priapulid larva *Halicryptus spinulosus* von Seibold, extant (modified from Malakhov and Adrianov, 1995); **8**.loriciferan larva *Pliciloricus ornatus* Higgins and Kristensen, extant (modified from Malakhov and Adrianov, 1995); **9**.nematomorph larva *Gordionus senkovi* Malakhov and Spiridonov, extant (modified from Malakhov and Adrianov, 1995); **10**.nematodes *Greeffiella* (left) and *Criconema* (right), extant (modified from Brusca and Brusca, 2003); 11.tardigrade *Stygarctus abornatus* McKirdy, Schmidt and McGinty-Bayly, extant (modified from McKirdy et al., 1976); **12**.kinorhynch *Centroderes eisigii* Zelinka, extant (modified from Malakhov and Adrianov, 1995); 13.onychophoran *Peripatopsis moseleyi* (Wood-Mason), extant (modified from Ruhberg in Monge-Najera and Hou, 1999); **14**.larval euarthropod *Ascalaphus* sp., extant; Caption and diagram by Zhuravlev et al 2011.

Alternatively, the palaeoscolecidans may simply be a separte line of early minearlised ecdysozoa, and the similarities with teh priapulids may be shared primitive ecdysozoan features. Palaeoscolecidans, priapulids, lobopods, and other groups would be different lineages in a rich early flowering of Cambrian ecdysozoans, equivalent to, say, the great diversity of early Paleozoic arachnomorphs (trilobites, tribitomorphs, and chelicerates) in comparison with teh impoverised fauna of the late Paleozoic through to recent. MAK120420

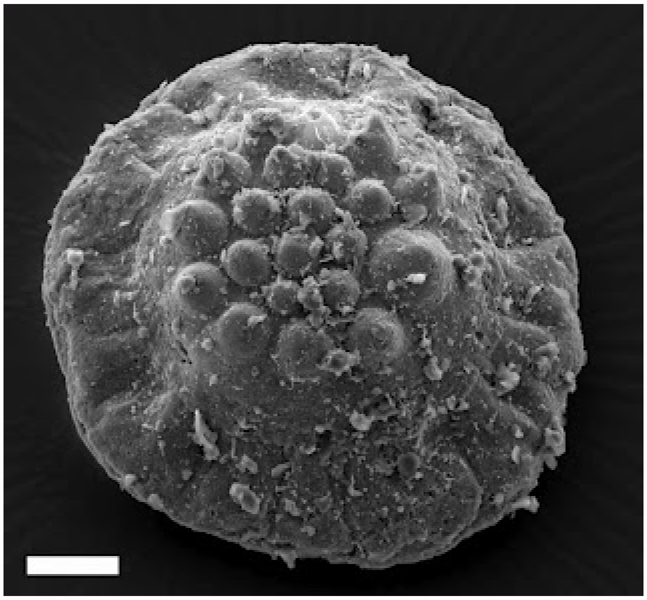
Descriptions

Palaeoscolecida: Conway Morris & Robinson, 1986 **:** *Palaeoscolex*, *Cricocosmia*, *Tabelliscolex*, etc

Range: Early Cambrian to late Silurian

Phylogeny: Basal or stem Priapozoa/Scalidophora/Ecdysozoa? Paraphyletic or polyphyletic? **:** *Maotianshania* + (*Cricocosmia* + *Palaeoscolex*)

Characters: spiny introvert, segmental array of sclerites in organised bands (Conway Morris & Peel 2010)



Comments: Palaeoscolecids bear an annulated trunk ornamented with circular patterns of phosphatic tesselating plates; a layered cuticle; and an armoured proboscis. They are usually a few centimetres in length. There is no one character that unites the palaeoscolecids as a clade (indeed they are likely paraphyletic), and few individual specimens contain all characteristic palaeosolecid traits. (Harvey et al 2010) - Wikipedia.

Note: Comment: Unlike other animals known from isolated armour plates (scleritomes) , the Palaeoscolecida were actually known as entire animals long before their dermal armation was described, but the said armation was described as isolated problematic fossils before a connection was made between the animal and its armour (Ivantsov & Wrona, 2004) The photo at the right shows one of the isolated sclerites, originally described under the name *Hadimopanella*. Palaeoscolecid sclerites are round and button-like, with a central array of nodules that vary in different species from low and rounded to higher and pointed. Opinions on the nature of these microfossils (to appreciate how small they are, the scale bar on the photo above represents 0.03 mm) varied from some sort of dermal armour to the remains of reproductive cysts (Repetski, 1981). The dermal armour theory, of course, won out when the connection was made between the isolated sclerites and ornamentation on the compressed body fossils almost simultaneously by different authors in 1989 (Ivantsov & Wrona, 2004). CKT080122

Maotianshania cylindrica**:** Sun & Hou, 1987

Horizon: Early Cambrian of China (Chengjiang)

Phylogeny: Palaeoscolecida **:** (*Cricocosmia* + *Palaeoscolex*) + *

Comments: May be intermediate between priapozoa and palaeoscolecids because in addition to a typical proboscis, this species has a trunk with numerous small sclerites. But unlike palaeoscolecidd these have a rather uniform distribution, unlike the organised bands represnetative of most palaeoscolecidans. (Conway Morris & Peel 2010). It may well be therefore that this species belongs to a different group, which may or may not be related to true palaeoscolecids MAK120422

Cricocosmia jinningensis Hou & Sun, 1988

Horizon: Early Cambrian of China (Chengjiang)

Phylogeny: Palaeoscolecida **:** *Maotianshania* + (*Palaeoscolex* + *)

Palaeoscolex: *Palaeoscolex piscatorum* Whittard 1953 (Type species); *Palaeoscolex antiquus* Glaessner, 1979. (Early Cambrian of Australia) (Glaessner 1979); *Palaeoscolex sinensis* Hou & Sun, 1988 (Early Cambrian (Chengjiang) of China); Palaeoscolex lubovae Ivantsov & Wrona 2004, P. spinosus Ivantsov & Wrona 2004, (both Early Cambrian of eastern Siberia) (Ivantsov & Wrona2004)

Range: Early Cambrian of Australia, Bohemia, China, and Siberia

Phylogeny: Palaeoscolecida**:** *Maotianshania* + (*Cricocosmia* + *)

Comments: originally described as an annelid. A number of species, perhaps a wastebasket taxon?

Phosphatized palaeoscolecid cuticle fragments from the Early Cambrian Sinsk Formation of the (Siberian Platform) at the Achchagyy Tuoydakh fossil-Lagerstatte show remarkably well preserved arrays of plates and platelets identical to widely reported isolated sclerites assigned to *Hadimopanella*, *Kaimenella*, *Milaculum*, and *Utahphospha*. Some of the described cuticular trunks exhibit distinction between the dorsal and ventral sides: nodular sclerites occur on the dorsal and spiny sclerites on the ventral sides of the worm body, suggesting adaptation for a level-bottom, vagile benthic and probably epifaunal mode of life. Sclerites recorded with microplates accreted into the basal brim imply that the more complex sclerite structure bearing a series of nodes was derived from simple small sclerites with a single node. There is little biostratigraphic utility to these isolated sclerites, as the same morphology occur in different worms, and different sclerites may occur in one scleritome. - from the abstract by Ivantsov & Wrona 2004 MAK120422

Links: Marine Species, Palaeoscolex antiquus

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Scalidophora: Priapozoa

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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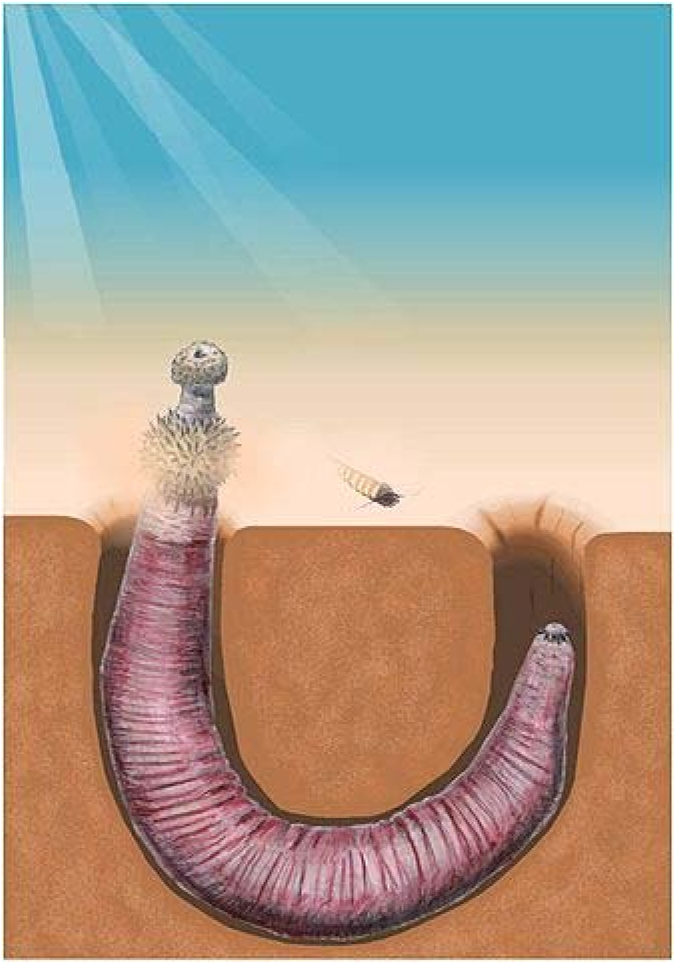
1. Priapozoa



Life restoration of *Ottoia prolifica* in natural environment with the hyolith *Haplophrentis*, a food source (Conway Morris 1977);. *Ottoia* was about 8 cm in length; it is a common representative of the Burgess shale fauna.
Artwork by Smokeybjb, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

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Descriptions

Priapozoa (incl. Archaeopriapulida) **:** *Ottoia*, *Palaeoscolex*, *Priapulus* etc

Range: fr the Cambrian

Phylogeny: monophyletic clade of stem and crown Priapulids; likely to be synonymous with Scalidophora or even Ecdysozoa as a whole, however a reduced definition, e.g. LCA of *Ottoia* and *Priapulus* and all its descendents, may mean the clade can still be retained. It is not clear whether or not some or all the palaeoscolecids would be included in this definition MAK120422

Comments: Priapozoa is here used to refer both to stem group Priapulids and associated taxa such as palaeoscolecidans that are classed with them, and extant priapulids and their immediate relatives. Most authors supporting this affinity have simply referred to palaeoscolecidans as "priapulids". The modern priapulids are a small, well-defined group of worms, while the various Palaeozoic taxa regarded as stem-priapulids show a much higher diversity of body plans (many of them, for instance, were far more elongate than any living priapulid, while no living priapulid possesses a dermal armour like that of palaeoscolecidans). adapted from CKT080122

In distinguishing early priapozoans from modern taxa, the paraphyletic term Archaeopriapulida might be used. This includes the assemblage of priapulid-like worms known from Cambrian lagerstatte (*Ancalagon, Fieldia, Louisella, Ottoia, Selkirkia*, etc). They may or may not be closely related to the palaeoscolecids. Despite a remarkable morphological similarity modern cousins, they fall outside of the priapulid crown group, which is not unambiguously represented in the fossil record until the Carboniferous. - adapted from Wikipedia

In any case, Priapozoa may simply turn out to be synonymous with Scalidophora or even Ecdysozoa. Dzik and Krumbiegel (1989) suggest a general priapulid grade as ancestral to panarthropods. Budd and Jensen 2000, Budd 2001, and Conway Morris & Peel 2010 propose a palaeoscolecid-like form as the common ecdysozoan ancestor; although this hypothesis has been rejected by Harvey et al 2010 on morphological cladistic grounds. Dong et al 2004 fig 3a features a cladogram in which some Cambrian priapozoans are basal Scalidophora, Harvey et al 2010 arrives at a somewhat different topology. The discovery of the early cambrian transitional form *Mureropodia*, with both priapozoan and lobopod (basal panarthropod) characteristics (Vintaned Gamez et al 2011), supports the hypothesis that panarthropods, and hence all derived ecdysozoa, evolved from a priapulan-like ancestor. MAK120422

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Scalidophora: Priapulida

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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The Priapulids

Priapulus caudatus, a penis worm (Priapulida - Priapulimorpha - Priapulimorphida - Priapulidae. Photo by BOLD, Biodiversity Institute of Ontario, Creative Commons Attribution Non-Commercial Share Alike

There are fewer than 20 described living species of Priapula (or Priapulida), although additional species are known that await formal description. Priapulans are free-living benthic marine worms with an eversible proboscis. They range in size from 1 mm (early instars may be as small as 50 µm) to more than 40 cm in length . They can be found from polar seas to the tropics and from ocean trenches to the intertidal zone. Some species can occur in extremely high densities. Sexes are separate and in at least one family sexual dimorphism is evident. Males spawn first, then females; fertilization is external. Nearly all species have a non-swimming benthic larval stage, which apparently may last as long as one to two years. Larvae live in mud and are probably detritivores. The body of a priapulan is cylindrical and includes an introvert (retractable and invertible proboscis), a neck-like collar, a trunk, and sometimes a "tail". The introvert has spines resembling those on the introvert of kinorhynchs and loriciferans. Large priapulans burrow actively in relatively fine marine sediments, primarily in boreal and cold temperate seas. A few species construct tubes. Small priapulans burrow or live interstitially among sediment particles. Priapulans are relatively common in the fossil record and may have been important predators in Cambrian seas. Most priapulans today live in soft sediments and feed on soft-bodied invertebrates such as polychaete worms and other priapulans. During feeding, a portion of the toothed pharynx is everted through the mouth at the end of the extended introvert, then retracted together with the prey item. (Brusca and Brusca 2003; Shirley 2009 and references therein; Margulis and Chapman 2010).

The Priapula are believed to be closely related to the Kinorhyncha and Loricifera, with which they are often grouped in a clade referred to as Scalidophora; some authors include the Nematomorpha as well in a clade referred to as Cephalorhyncha (Aleshin et al. 1998 and references therein; Halanych 2004 and references therein). Sørensen et al. (2008) present data that they argue supports a sister relationship for Loricifera and Nematomorpha, which would render the Scalidophora paraphyletic. As of 2010, relationships among phyla within the Ecdysozoa remain poorly resolved, so it is difficult to know which groups will eventually win wide acceptance by specialists as convincingly monophyletic.- text © Leo Shapiro (Creative Commons Attribution Non-Commercial Share Alike)

Descriptions

Priapulida: *Ottoia*, *Palaeoscolex*, *Priapulus* etc

Range: fr the Carboniferous

Phylogeny: Priapozoa **:::** *

Comments: The Priapulida or penis worms (the shape says it all) are a small phylum of marine worms that burrow in mud in relatively shallow water. Unlike many other ecdysozoan phyla, they never underwent minaturisation, nor have they diverged much in form from their Cambrian ancestors. These ancestral types filled the marine ambush preditor role in the Cambrian sea floor. Phylogeneticaly (in mapping out the evolutionary tree) we might distinguish the recent or crown-group Priapulids such as *Priapulus*, shown above, and their immediate fossil ancestors from the larger grouping that includes various Cambrian or stem-priapulids such as *Ottoia prolifica*, which show a much greater range and diversity of morphologies and adaptations. Both crown and stem groups together can be referred to as Priapozoa, although there is the question of whether the priapozoa are even distinct from ecdysozoa as a whole. MAK120420

Links: Priapulida - Tree of Life Web Project; Penis Worm (Priapulida) - Encyclopedia of Life (overview text reproduced above under open source license); Priapulida - Wikipedia; Priapulida - Infoplease.com

Image: Encyclopedia of Life. Scale bar (bottom right), 1 mm

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Ecdysozoa: Dendrogram

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |==Palaeoscolecida
      |--Kinorhyncha
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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Note: the following dendrogram is a slightly modified version of a dendrogram drawn by CKT for Palaeos org, which itself is based strongly on Dong et al 2004, cladogram, fig 3b; extant priapulids follow Mikko's phylogeny. This phylogeny is certainly less than satisfactory if the hypothesis of paraphyletic Priapozoa and Palaeoscolecida as ancestral ecdysozoans (e.g. Dzik and Krumbiegel 1989, Conway Morris & Peel 2010) , but we have retained it for now pending later revision MAK120422

EOL:Encyclopedia of Life
MH : Mikko's phylogeny
ToL Tree of Life

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA  (= Introverta, Nematozoa, Cycloneuralia)  = paraphyletic SCALIDOPHORA?
[Cephalorhyncha, Scalidorhyncha] =  paraphyletic Priapozoa? (stem "priapulida")
      |--Markuelia
      |--+--Ancalagon
      |  `--Fieldia
      |--+--Kinorhyncha [Echinoderida]  ToL  MH
      |   |   |--Homalorhagida
```

```
|   |   `--Cyclorhagida
|   `--+-- Loricifera ToL
|       `--+--Priapulida  ToL EOL  MH
|          |  |--Tubiluchidae
|          |  |  |-- Meiopriapulus
|          |  |  `-- Tubiluchus
|          |  `--+-- Maccabeus [Maccabeidae]
|          |     `--o Priapulidae
|          |        |-- Halicryptus
|          |        `--+-- Priapulites
|          |           `--+-- Priapulopsis
|          |              `--+-- Acanthopriapulus
|          |                 `-- Priapulus
|          `--+--Selkirkia
|             `--+--Palaeoscolecida
|                |  |--Maotianshania
|                |  `--+--Cricocosmia
|                |     `--Palaeoscolex
|                `--+--Ottoia prolifica
|                   `--+--Louisella pedunculata
|                      `--Scolecofurca
`--+--NEMATOIDA
   `--PANARTHROPODA
```

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dendrogram CKT070908, modified MAK120420

Scalidophora

Abbreviated Dendrogram

```
BILATERIA
|--DEUTEROSTOMIA
`--+--SPIRALIA
   |
   `--ECDYSOZOA = paraphyletic SCALIDOPHORA?
      |--Markuelia
      |--Kinorhyncha
      |==Palaeoscolecida
      |==Priapozoa
      |  `--+--Priapulida
      |     `--+--Sirilorica
      |        `-- Loricifera
      `--+--NEMATOIDA
         `--PANARTHROPODA
```

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Palaeoscolecida

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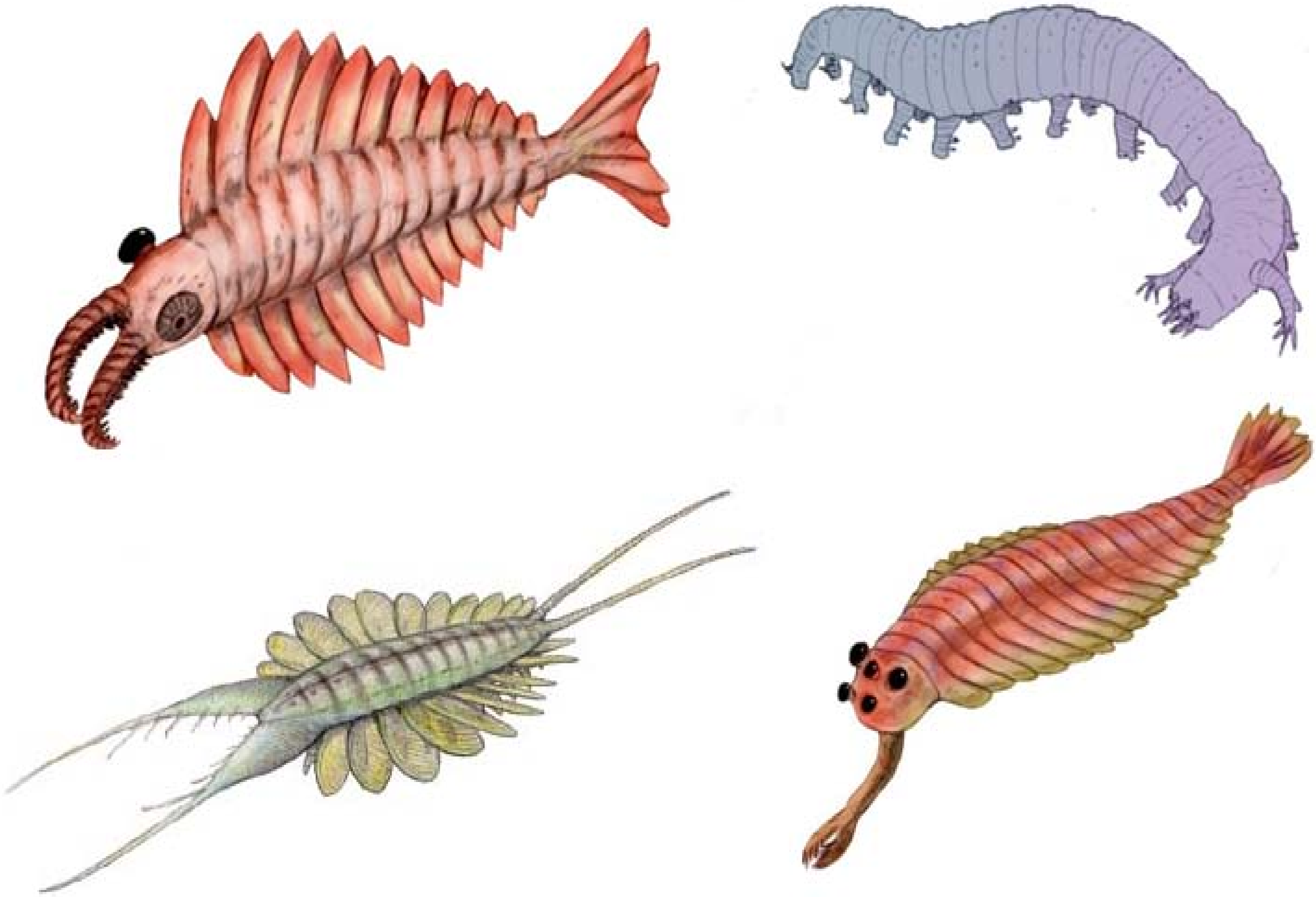
Ecdysozoa: Panarthropoda

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Luolishaniidae
                `--+==Siberiidae
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

Contents



A selection of Cambrian lobopodians and protoarthropods; "non-missing links" between worms and arthropods. Clockwise from upper left, *Anomalocaris*, *Aysheaia*, *Opabinia*. and *Kerygmachela*.
Artwork by Renato de Carvalho Ferreira via Wikipedia. Creative Commons Attribution-Share Alike

In this and the following several units we consider one of those fascinating instances of evolution, the transition from one body type; in this case, the soft-bodied ancestral worm; to a radically different type, the armoured and jointed skinned arthropod. Like the evolution of vascular land plants from green algae, brachiopods, annelids and molluscs from earliest Cambrian "coat of mail" ancestors, vertebrates from early deuterostomes, amphibians from fish, birds from dinosaurs, and mammals from reptiles, this is one of those extraordinary stories well documented through a convergence of the fossil record, comparative morphology (of both extinct and extant forms), and molecular phylogeny. It was also one of the most dramatic aspects of the Cambrian explosion, as the lobopodians and protoarthropods that resulted from this burst of evolutionary creativity were among the most spectacular creatures of their time; cruising superpreditors, five eyed aliens, and walking catuses are among some of the strange players of this evolutionary drama. For now our coverage is still rather scanty, but it is hoped that this can be adressed in future. MAK120419

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Panarthropoda: Lobopodia

Abbreviated Dendrogram

```
ECDYSOZOA
|--SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |  |--Xenusion
             |  `--Hadranax
             |--Microdictyon
             |--Orstenotubulus
             |--ONYCHOPHORA
            `--+--Hallucigenia
               |--Diania
               `--+==Siberiidae
                  `--+==DINOCARIDIDA
                     `--ARTHROPODA
```

Contents

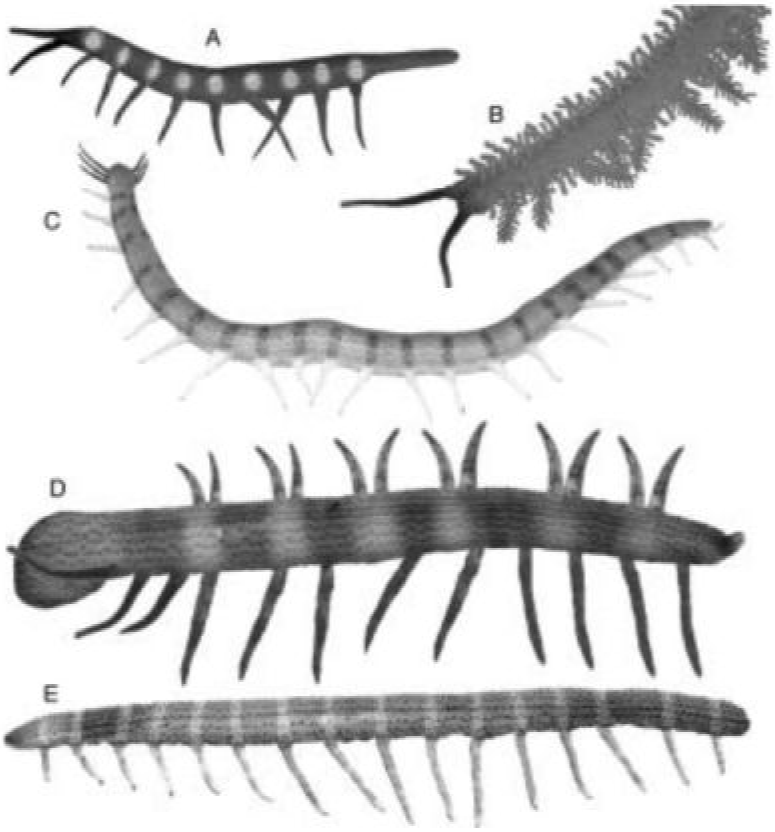
Taxa on This Page

1. *Hadranax*X
2. *Orstenotubulus* X
3. XenusiidaeX
4. *Xenusion*X

The Lobopodia or Lobopoda [1] are an evolutionary grade or phylum Cavalier-Smith (1998) of ecdysozoans, intermediate between the worm and the arthropod states. During the Cambrian period, they were very common and diverse, probably filling a range of ecological roles and guilds, although their soft bodies meant that they were rarely preserved, except for lagerstätten and a few rare impressions. This means that their numbers and importance would have been underestimated, as with their contemporaries and distant cousins the /priapozoan worms, another important Cambrian group. If we add the protoarthropods - essentially specialised swimming and gilled lobopodians, this becomes even more the case.

Because the conditions that allowed lagerstätten-type preservation were less common after the Cambrian, it seems that the early lobopodians [2] died out at the end of the Cambrian, but this was not the case, as rare instances have bene found at from the Ordovician and Silurian that hint at a greater diversity (Whittle et al 2009)

At some point though these early forms disappeared; perhaps a situation similar to the mid-Palaeozoic decline of trilobites and early echinoderms. Eventually, only two specialised lobopodian grade lineages remained, the onychophora, represented today by *Peripatus* and co, who took up a terrestrial lifestyle, and the tardigrades, enigmatic microscopic forms that independently evolved have many arthropod qualities. All three together are collectively known as "lobopods" or "lobopodians", and they differ from arthropods in not having evolved a hard jointed exoskeleton or efficient, articulated limbs.



Computer generated reconstructions of the fossil onychophorans. A: *Microdictyon sinicum*; B: *Onychodictyon ferox*; C: *Cardiodictyon catenulum*; D: *Hallucigenia fortis*; E: *Luolishania longicruris*. - artwork from Monge-Nájera & Hou (2002) (compare with the line art from Bergstrom and Hou (2001)). These were among the first life-like reconstructions of the variety of Cambriabn lobopodians. Yet while the body proportions and skin texture are probably realistic, Maas et al 2007 have since argued on the basis of the exceptionally preserved three dimensional *Orstenotubulus evamuellerae* that long-legged lobopodians could not have walked with legs straight such as are shown here (and in numerouis other reconstructions, especially of *Hallucinogenia*) but would instead have crawled with legs held mostly horizontally. (Ironically Monge-Nájera & Hou in this very paper addressed the problem of taphonomic distortion; the long-legged and straight legged lobopodians would be another example of this). Compare these reconstructions with the more stylised (yet still evocative) images offered by Jerzy Dzik (2011)

The onychophores and tardigrades will be described a little later. But it is the Cambrian forms (see illustration, right), such as the venerable Burgess Shale genera *Ayshenia* and *Hallucigenia*, as well as *Microdictyon* and a host of others recovered from the Chengjiang lagerstätte that are the focus of the present unit . Of these *Hallucigenia* is particulari;ly notorious, due to being spectacularly misinterpreted and reconstructed upside down, leading popular science writer Stephen Jay Gould in his *Wonderful Life* (on the Cambrian explosion) to wrongly conclude that the Cambrian was full of bizarre short-lived phyla, of which only a tiny perceptage survived. Significantly, several of the organisms Gould described - *Hallucigenia, Opabinia*, *Anomalocaris* - are bnow known to form a single evolutionary gradation of transitional forms (see cladograms below).

But while we can now be pretty confident of the big picture, the details elude us. Tardigrades, onychophores, and arthropods all evolved from lobopodians (the latter via protarthropods), but determining exactly which Cambrian lobopodians are related to which remains difficult. Moreover, many Cambriabn lobopodians seem not to be related to modern tardigrades and onychophores at all. A distinction is therefore made between recent onychophores and tardigrades (and their immediate and obvious fossil ancestors) and the range of Cambrian forms. The Class rank taxon *Xenusia*, which sounds like the name of an alien planet in a 1950s sci fi movie, was coined by Dzik & Krumbiegel, 1989 (from *Xenusion*) to distinguish the fossil forms from recent onychophores and tardigrades.

With the introduction of cladistic techniques and the study of new taxa, a more developed picture of Cambrian lobopodian morphology has taken shape, beginning with Ramsköld's work on the Chengjiang lagerstätte. In a recent write up, Ramsköld & Chen (1998) analyze the Cambrian lobopodia together with Recent Onychophora, and locate the extant onychophorans as ingroup Cambrian lobopodians on the basis of four synapomorphies. They named two new clades, Alphonychophora and Betonychophora, with extant onychophorans and the Carboniferous *Helenodorus* making up a third clade, Euonychophora. The three clades constitute an unresolved trichotomy, combined in a monophyletic Onychophora. They reject the possibility of tardigrade relationships. Their cladogram is as follows:

```
|--Hypanc
`--+--Betonychophora
   |  |--Paucipodia
   |  `--+--Cardiodictyon
   |     `--+--Microdictyon
   |        `--+--Hallucigenia sparsa
   |           `--Hallucigenia fortis
   |--Alphonychophora
   |  |--+--Xenusion
   |  |  `--Luolishania
   |  `--+--Aysheaia pedunculata
   |     |--Aysheaia prolata
   |     `--Onychodictyon
   `--Euonychophora
      |--Helenodorus
      `--Recent Onychophora
```

In this cladogram, instead of an outgroup taxon, a hypothetical ancestor (Hypanc) is used. This approach does not seem to be used by many workers.

Budd 1999 however argued that some of the characters considered by Ramsköld and Chen) were invalid or based on outdated concepts such as Articulata (worms + arthropods). For example, "suppression of external segmentation" is not a derived character because lack of external segmentation is a primitive feature shared by Cambrian lobopodians, and ecdysozoa inb general. The features of Cambrian lobopodians are either autapomorphies, such as the long defensive spines of *Hallucigenia*, or plesiomorphies, such as the annulated trunk and lobopod legs. This is also shown by the fact that proto-anomalocarids such as *Kerygmachela* and to a lesser extent *Pambdelurion*, demonstrate the retention of many lobopodian features up to the arthropod stem-group level (Budd 1999, summarised in Budd 2001 and Edgecombe 2009). Nevertehless Ramsköld & Chen (1998) remains an important study, with pertinant observations and critiques.

More recent cladograms depict the Xenusians as a grade of evolution rather than a natural group. The combination of characters revealed by the Cambrian forms provides the opportunity to break up the long branch between recent onychophorans (which are entirely terrestrial) and arthropods (Edgecombe 2009). Nevertheless there is little agreement about actual relationships between the various taxa, as shown by the following series of cladograms

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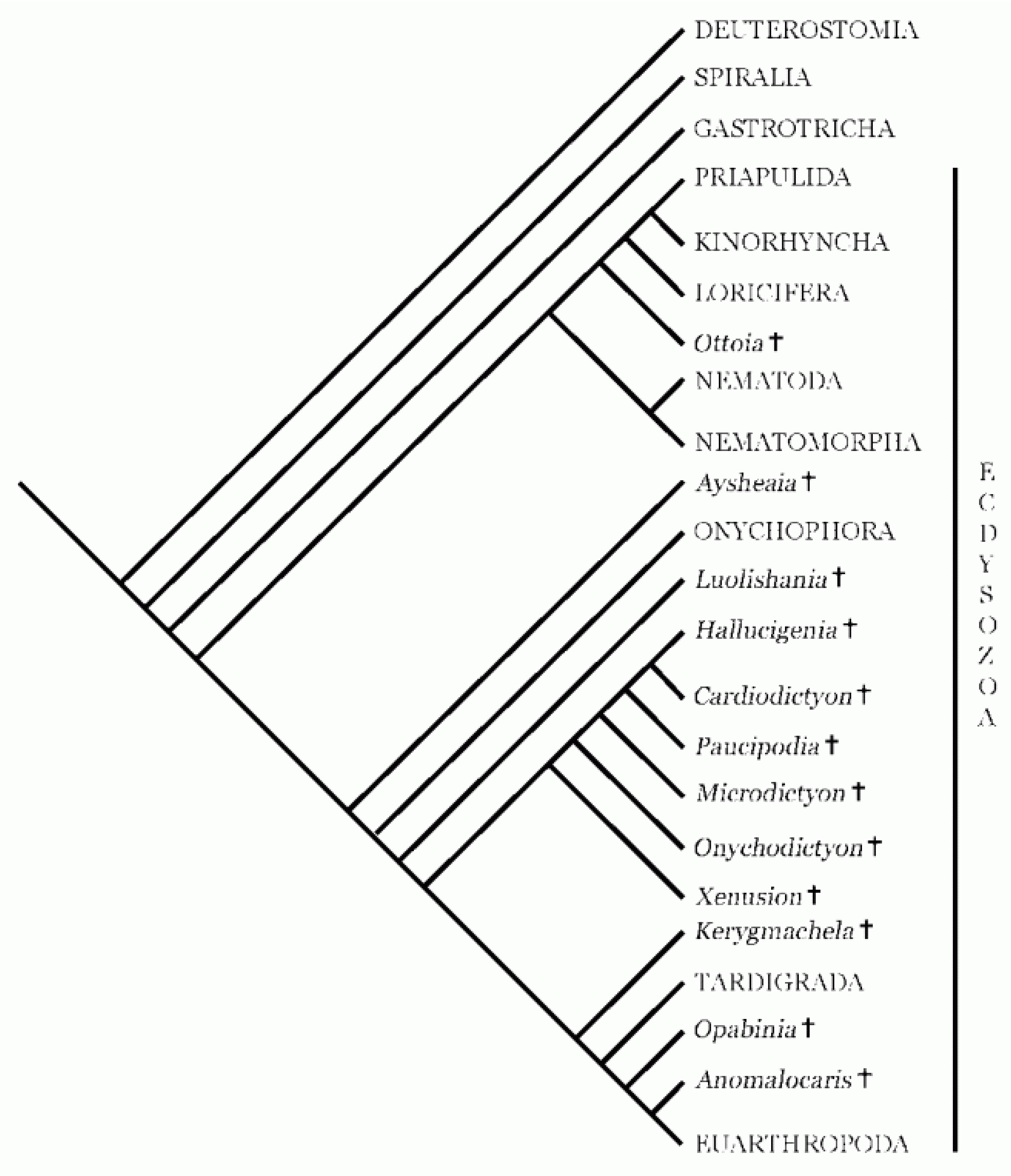
Eriksson et al 2003:

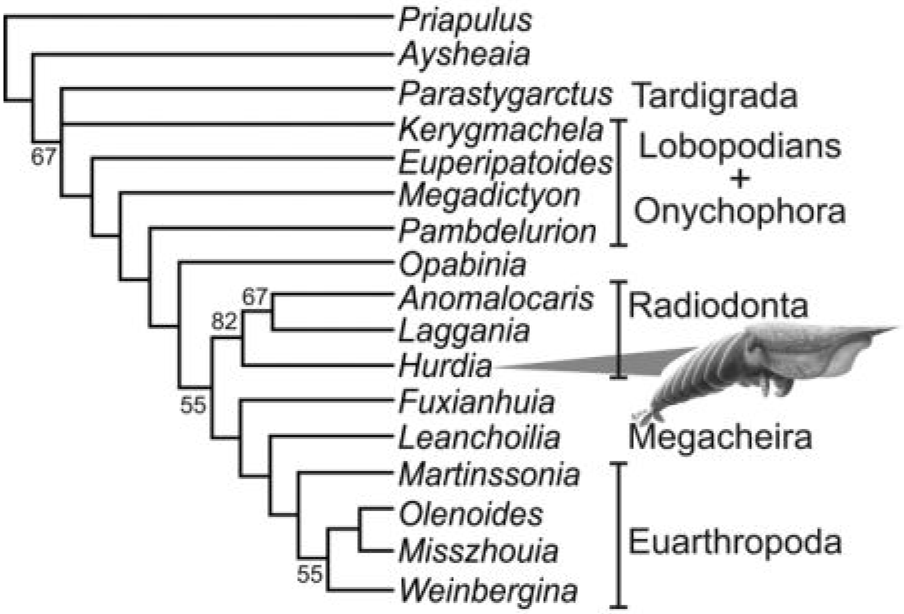
Tree by Eriksson et al 2003 showing possible



relationships among extinct and extant ecdysozoans. Extant clades are shown in capitals. Based on Schmidt-Rhaesa et al. (1998), Budd (1996, 1999), and Budd and Jensen (2000). . This innovative cladogram rejects the idea of a monophyletic lobopodia, although most lobopodians still form a single clade. Here Ramsköld & Chen (1998)'s "Betonychophora" constitute the most derived taxa, forming a monophyleticc clade, whilst members of their Alphonychophora make up stem taxa. In keeping with Budd's findings, *Ayshenia* here occupies a very basal position (Graham Budd, an important and seminal theorist in proto- arthropod development, is co-author of both this paper and the following, see also this earlier mentioned synopsis). In contrast to other phyloggenies shown here, Onychophora is placed beneath (stemward, more primitive than) all other Cambrian lobopodians. The crownward position of the tardigrades shown here (tardigrades as sister taxon of arthropods) is based on Nielsen,1995's influential work, but finds little support in later phylogenetic analyses (Edgecombe 2010).

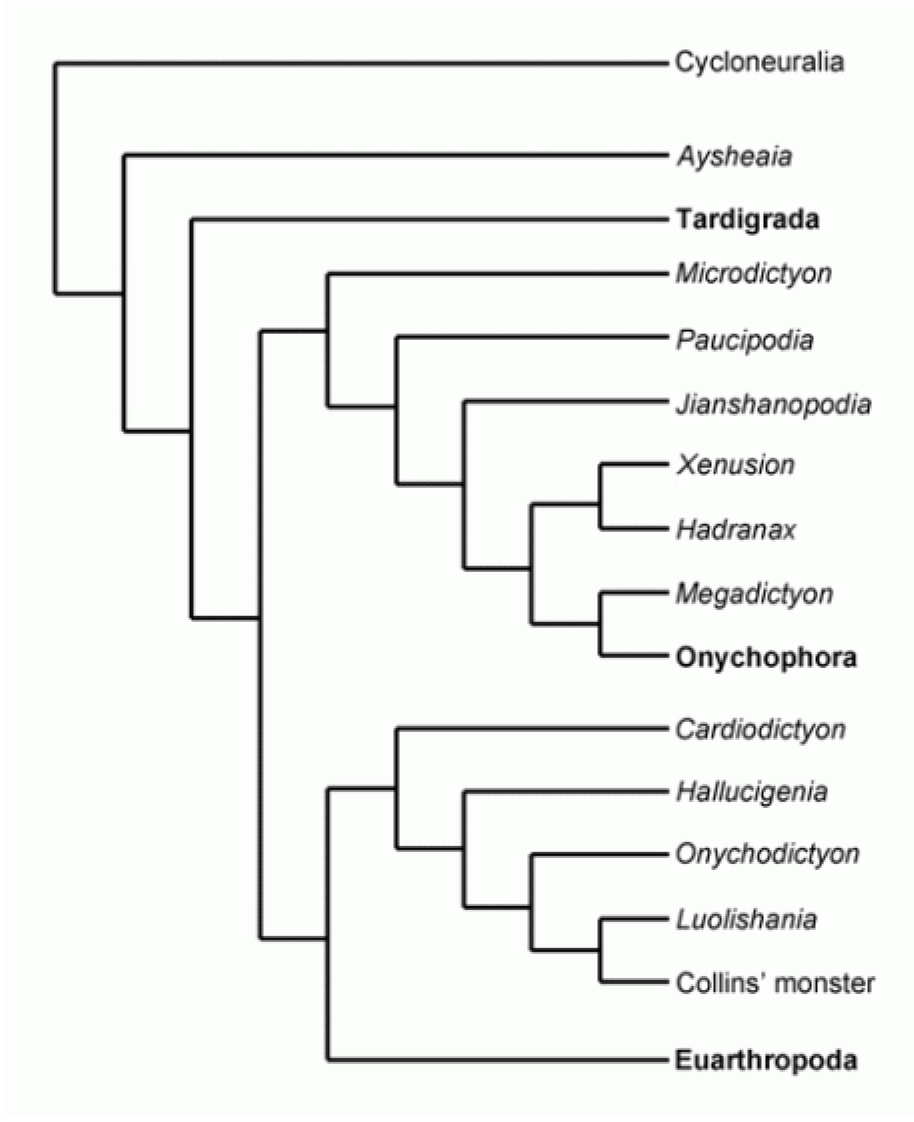
Daley et al 2009:

Cladistic analysis of selected stem and



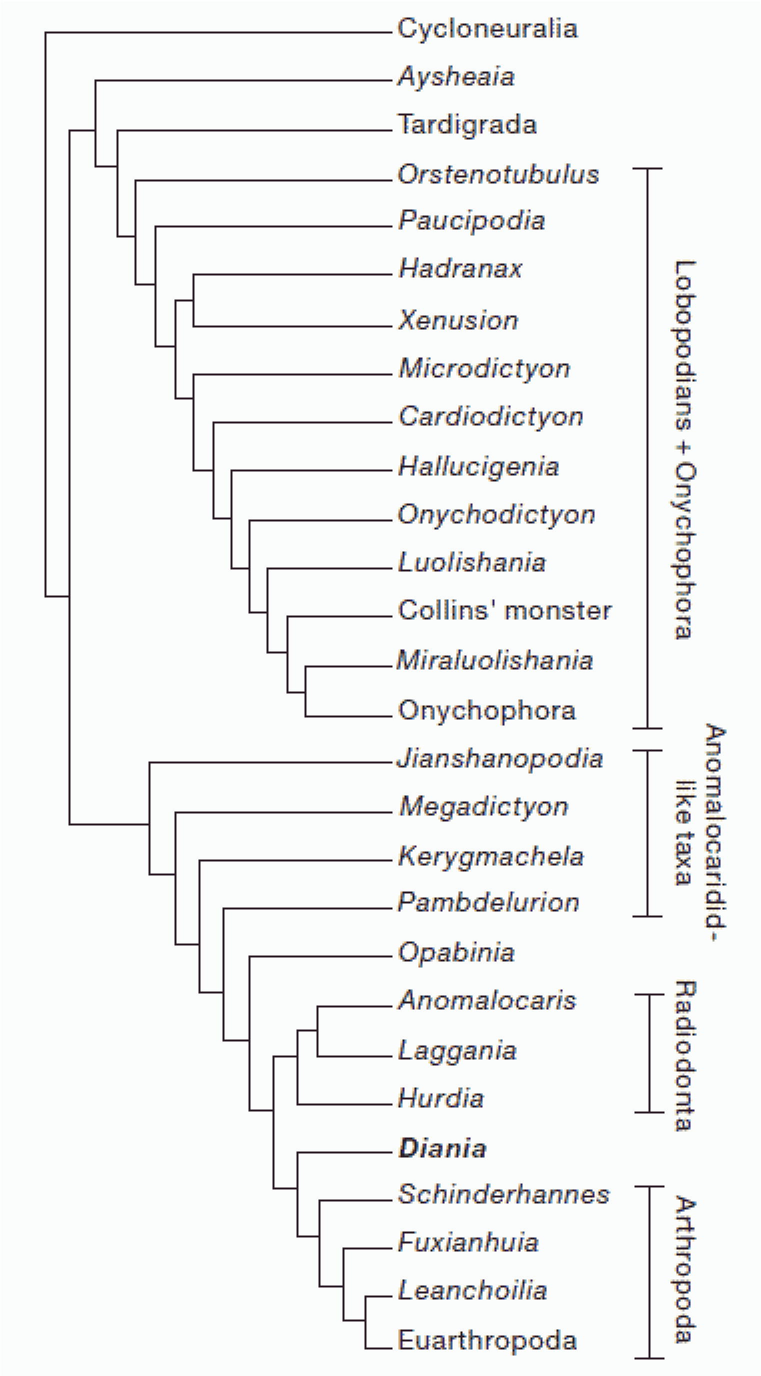
crown group arthropods, strict consensus of three trees, from Daley et al 2009's study of the Burgess Shale Anomalocaridid *Hurdia victoria* (illustrated). An abbreviated version of this cladogram is given by one of the co-authors of this paper, Edgecombe 2009 fig.3 (Although for the sake of convenience only the senior author's name is given, each of the papers featured here has about half a dozen co-authors, more or less). In keeping with the phylogeny provided by Eriksson et al 2003, *Ayshenia* occupies the basal placement. Several very interesting new taxa put in an appearance here, including the transitional lobopod-protoarthropods *Megadictyon* and *Pambdelurion* And although this study mostly features protoarthropods rather than lobopodians proper, it is distinguished by the fact that the lobopod-anomalocarid non-missing link *Kerygmachela* is here placed even stemward of the onychophora, based on the premise that the ventrally placed mouth (an advanced feature) only evolved once. But in view of the otherwise more advanced features of *Kerygmachela*, it is more parsimonious to assume that this at least happened twice, once with onychophores (perhaps an adaptation or preadaptation to terrestrial lifestyle) and once with the protoarthropods.

Ma et al 2009:



Phylogenetic relationships between Cambrian lobopodians and extant panarthropods from Ma et al 2010, modified from Ma et al 2009. Extant taxa shown in bold. From an analysis of the lobopodian *Luolishania longicruris*, this cladogram is similar to Ramsköld & Chen 1998 in featuring a large number of lobopodians, and like those authors dividing the lobopodians into several clades, although as with other phylogenies shown here the protoarthropods are also included. Here, apart from Tardigrades and *Aysheaia*, all lobopodians form two distinct clades. In contrast to Ramsköld & Chen the recent onychophora constitute the crown group of the more stemward of one of these clades (tentatively efferred to as Onychophora). The protoarthropods (anomalocarids etc) and true arthropods constitute sister clades (in contrast to other phylogenies in which they form a single gradation) which is then paired with the more crownward lobopod clade, here called Archonychophora. However, the relationship of the taxa of these two lobopodian clades shows no concordance with either Ramsköld & Chen 1998 or Eriksson et al 2003. The primitive genera *Hadranax* and *Xenusion* are also occupy a clade intermediate between the two proto-anomalocaridid-like genera *Jianshanopodia* and *Megadictyon*, perhaps due to shared primitive features common to large lobopodians. The sister taxon of the crown group Onychophora is here *Megadictyon*, which is elsewhere unanimously considered either a basal protoarthropod or a transitional form between lobopodians and protarthropods. Since Euonychophores and *Megadictyon* are not particularily similar, this makes one think the anomolous result here is an artifact of statistical cladistic method which breaks down when dealing with poor data and numerous homoplasies, as is the case with Cambrian lobopodians. Less controversially, *Kerygmachela* here returns to a more conventional position at the base of the stem arthropods, above the lobopodians.

Liu et al 2011



Cladistic analysis of all Cambrian lobopodians and some arthropod stem group taxa, from Liu et al 2011's paper on the "walking cactus" *Diania cactiformis*, which here resoves as the sister taxon to true arthropods. In contrast to other studies, fossil and recent lobopodians other than *Diania* here form a single pectinate clade, with extant Onychophora as the most derived member. *Ayshenia* is the most basal lobopodian, but no longer a basal panarthropod. As with Ma et al 2009, *Hadranax* and *Xenusion* are here sister taxa (family Xenusiidae). Ma et al (2009)'s "Archonychophora" is here incorprated with the same order of taxa, except that it is now a paraphyletic group, leading to crown Onychophora. The sister taxon of the Onychophora is *Miraluolishania* (which Ma et al 2009 had earlier argued was a synonym of *Luolishania*. , *Megadictyon* is here returned to the protoarthropods, just beneath *Kerygmachela*. Ironically, Ma et al (2009)'s sister taxon to the protoarthropods becomes here the sister taxon to the extant onychophora, and vice versa. These strangely inverse placements are clearly the result of lack of obvious synapomorphies, and support Ramsköld & Chen (1998) hypothesis of a number of distinct lineages, and euonychophora not being derived from currently known Cambrian lobopodians.

A new taxon, *Orstenotubulus*, makes a cladistic debut, it here occupies a position just above the tardigrades, perhaps because of small size. In other respects, *Orstenotubulus* appears to be a rather typical xenusian lobopodian, with features in common with tardigrades, euonycxhophores, and spiny xenusian lobopodians.

But the most unusal and controversial placement in this cladogram is *Diania* itself, which apart from its armoured exoskeleton, otherwise resembles a standard vanilla Cambrian lobopodian, is here anomalously placed even above the proto-arthropods. It's elevated position is no doubt due to Liu et al 2011 's premise that arthropodisation and jointed legs only occurred once. But if we assume, like the ventral mouth of onychophores and arthropods, that this occurred several times, *Diania* would then be located in a more stemward position. Liu et al 2011's analysis was criticised by Mounce & Wills 2011 and Legg 2011, but both critics used a strict consensus approach which resolted in an unresolved polytymy or "star" diagram and which, as Liu et al. 2011b pointed out in their counter-reply, did not provide much meaningful information. In

> any case, apart from *Diania*, the protoarthropods and arthropods appear in a pectinate series such as was first proposed by Graham Budd in the late 1990s

A characteristic of various lobopodian and protoarthropod cladograms is that whereas there is generally a degree of consensus regarding the latter, there is almost none at all regarding the former. Various taxa are arranged in totally different ways with each analysis. The problem is that lobopodians in general are highly plesiomorphic, and quite likely homplastic, with few obvious distinguishing features, or at least few that are preserved as fossils. Add to that the unreliability of even those characteristics that do appear in fossils. Although lagerstätten (sites of exceptional fossil preservation) such as Chengjiang and the Burgess Shale provide a unique window into the past, by revealing even the soft-bodied organisms and even impressions of internal organs, taphonomic factors inevitably introduce distortion that needs to be considered when reconstructing the anatomy of these ancient craetures. The absence of bucal parts, adhesive-expelling organs, gonopore, eyes, legs, claws, annulation and papillation in fossils may not represent their absence in the actual animals. Leg thickness and claw orientation can also be unreliable, while the apparent presence of certain structures may simply be the result of tissue decomposition (Monge-Nájera & Hou (2002))

An interesting feature of many Cambrian lobopodians, and perhaps a primitive condition for panarthropoda as a whole, are the paired sclerites or minature armour plates,s ymmetrically arranged along the trunk, mostly in pairs dorsally positioned to the walking limbs. These show a general net-like microstructure, which has been described for *Hallucigenia, Onychodictyon* and *Microdictyon*, and also found in other genera such as *Cardiodictyon*, *Luolishania* (= *Miraluolishania*?), and "Collins monster"). These may have been a supportive structure for secretive or sensory papillae that may have had tactile, chemosensory or secretory functions, as well as protecting the soft-bodied trunk. Steiner et al 2012 p.121. In support of the lobopodians from worms hypothesis, lobopodian sclerite microstructure is comparable to a similar microstructure in paired trunk sclerites of the (Cricocosmiid palaeoscolecidans *Cricocosmia* and *Tabelliscolex*. The net-like trunk sclerites of lobopodians are interpreted as having carried numerous sensory or secretory papillae. Duplicates of trunk sclerites in *Microdictyon* and *Cricocosmia* also are evidence of a moulting of the external cuticle. Steiner et al 2012

Some Cambrian lobopodians were well armoured or defended. *Hallucigenia sparsa* was eqipped with what seem to be long defensive spines. Hou & Bergström 1995 reconstruct *Onychodictyon* as resembling a stout spiny onychophore. While *Diania cactiformis* actually did resemble a walking cactus. Jerzy Dzik (2011) reconstructs many lobopodians as prickly customers covered in an array of defensive scleroites, rather like the halwaxiid "coat of mail" animals, and in view of their success in the early Cambrian oceans, it may indeed be that these soft-bodied creatures were well protected against whatever preditors may turn up. MAK120427

Notes:

[1] The taxon Lobopodia was coined by the renowned arthropod morphologist Robert Evans Snodgrass in 1938, to refer to intermediates between annelids and arthropods. The equally brilliant Thomas Cavalier-Smith in 1998 made this the phylum Lobopoda (without the "i"), perhaps to avoid confusion with lobopodia as the technical term for the lobose pseudopods of amoeboid protists.

[2] Grammatically, the unwieldly "lobopodian" is more correct than "lobopod", and hence has bene used here. As explained by Hou & Bergström 2006, a *lobopod* is the unsegmented, not sclerotised locomotory limb of many panarthropods (or *aiolopods* to use those authors preferred term), whereas a *lobopodian* is the animal itself, a panarthropod with lobopod limbs (similarily "pseudopod" is not a taxon but an amoeboid extrusion). For any number of reasons, the term lobopod has taken on the colloquial meaning as shorthand for lobopodian (or lobopodan, or lobopod-bearing animal, depending on your preferred terminology), even appearing in the scientific literature (e.g. Budd 1993 Liu et al 2008). For one thing "lobopodian" can be confusing because the suffix implies it is an adjective (so there would be no way other than context to distinguish it from the noun in the singular). I"Lobopod" has the advantage of being easily and intuitively used, by analogy with arthropod(a) and tetrapod(a), the suffix of the taxon lobopodia in this case is -ia rather than just -a. There is also the convenience, why use five syllables when you can make do with three? With vertebrates by convention we drop the -ia suffix to get the common name, so "Dinosauria" becomes "dinosaur". For now we have chosen to go with the pedantic spelling found in most of the literature, annoying as it may be. Of course there is always the option of adopting Cavalier-Smith's spelling ("lobopoda") to avoid any further grammatical problems and bring lobopod in line with tetrapod, gastropod, and so on MAK120505

Descriptions


Aysheaia pedunculata, from photo by Claire H., Wikipedia/Flikr, Creative Commons Attribution-Share Alike

Aysheaia pedunculata Walcott 1911

Horizon: *Bathyuriscus-Elrathina* Zone, Burgess Shale of British Columbia (middle Cambrian). A related species, *A. prolata* is found in the contemporary Wheeler Formation of Utah

Phylogeny: Panarthropoda **:** *Mureropodia* + ((Tardigrada + (Onychophora + (Xenusiidae + *Orstenotubulus* + *Microdictyon* + Onychophora + (*Paucipodia* + Archonychophora + *Diania* + (paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))))) + *)

Comments: Specimens of *Aysheaia pedunculata* average about 1 to 6 cm in length, with ten body segments, each of which has a pair of spiked, annulated legs. There are six finger-like projections around the centrally-located mouth and two grasping legs on the "head" (in front of the first pair of trunk appendages). Based on association with sponge remains, it is believed that Aysheaia was a sponge grazer and may have protected itself from predators by seeking refuge within sponge colonies, perhaps using its claws to cling to the sponge (adapted from Wikipedia)

Aysheaia was the first of the Cambrian lobopodians to be recognised as such. It was originally described by Walcott in 1911 as an annelid, along with *Canadia* (now *Hallucinogenia*) *sparsa*. The genus name commemorates a mountain peak named "Ayesha" (originally Aysha) north of the Wapta Glacier, after the heroine of Rider Haggard's 1887 novel *She* Similarities between *Aysheaia* and extant onychophora were pointed out to Walcott almost immediately, and Hutchinson in 1930 assigned *Aysheaia* to its own monotypal order Protonychophora, within the Onychophora (this contains only the monotypal family Aysheaiidae). As a result, and due to overall similarity to the modern day *Peripatus*, *Aysheaia* has traditionally been included as an early representative of the modern phylum Onychophora. Whittington (1978) helped popularise the genus in the paleontological community. Other features however, such as cebntrally-located mouth and the ornament of the trunk are distinct from modern onychophorans (Liu et al 2008 p.280),. Simonetta, A. M. & Delle Cave. 1975 pointed out similarities with tardigrades, considering *Aysheaia* intermediate between Tardigrades and Onychophores (Ramsköld & Chen (1998) p.110). And according to Budd, *Aysheaia* must be considered a metataxon, as it possesses no currently identified autapomorphies that would distinguish it from the arthropod crown node (Budd 2001 p.274). This is another way of saying that it represents the condition of a common ancestor of that group (in this case panarthropoda). In cladograms by Budd and co-workers, and all later researchers in this field, *Aysheaia* consistently is located benath the Tardigrade-Onychophore-Arthropod divide, the only exception being Liu et al 2011, for whom *Aysheaia* is the basalmost member of a monophyletic Lobopodia. (see above cladograms). Featured in many older paleontology books, *Aysheaia* has since been dethroned by the more charismatic *Hallucinogenia*, and more recently the range of Chengjiang forms. But the generalised (ancestral) nature of this genus means that it has an important position in the evolutionary history of the panarthropods.

Aysheaia therefore is more primitive then any onychophoran, or even most lobopodians. Such was the rate of evolution at this time that even as early as the Middle Cambrian, *Aysheaia* wa s a "living fossil", coexisting alongside its more advanced descendants. A parallel may be made with quaternary and recent Monotremes in Australasia, who survive by virtue of specialised morphology and lifestyle. *Aysheaia* may have had a similar strategy, in this case, as a sponge specialist, it was able to continue in a particular ecological niche long after its contemporaries had disappeared.

We have however placed *Aysheaia* above *Mureropodia* because it still is a full-fledged lobopodian, whereas the other two taxon have transitional priapulozoan features. The "half worm" *Facivermis*, considered a transitional form (Liu et al 2006), is here reinterprteted as a highly specialised filter feeder.MAK120425

Xenusiidae Dzik & Krumbiegel, 1989

Range: Early Cambrian

Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + ((*Paucipodia* + Archonychophora + *Diania* + (paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))) + *Orstenotubulus* + *Microdictyon* + Onychophora + * **:** *Hadranax* + *Xenusion*))

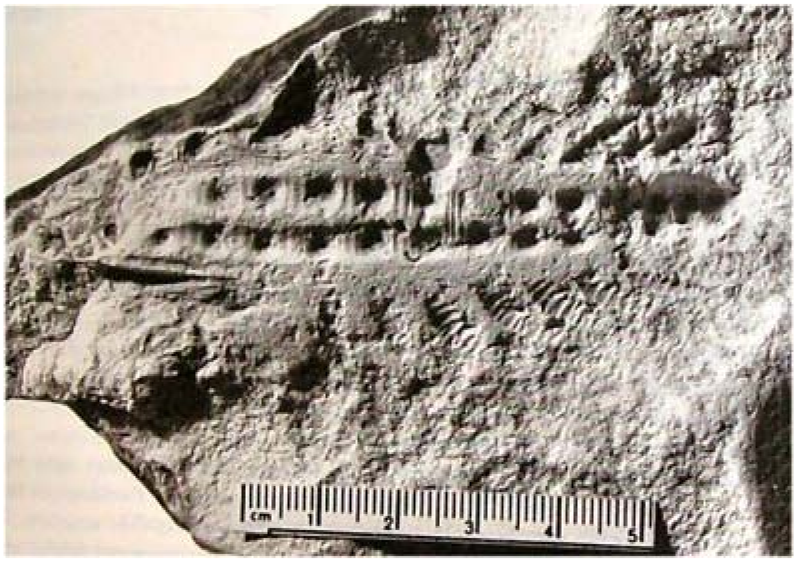
Characters: Large size, large nodes on the trunk, relatively wide, well-defined trunk annulations, lack of claws Liu et al 2011 although that last feature is likely to simply be due to poor preservation

Comments: large forms so far known only from the Early Cambrian of the baltic and Greenland; may be a small early clade (Liu et al 2011) or a paraphyletic ancestral grade (Dzik 2011). Poor preservation means it is not known whether features such as oral papillae (a feature of modern onychophorans.), a proboscis, or foot claws were present (Liu et al 2011)

Xenusion auerswaldae Pompeckj 1927

Horizon: Earliest Cambrian (Pleistocene drift), Germany

Phylogeny: Xenusiidae **:** *Hadranax* + *



Xenusion auerswaldae, impression Kalmarsundzandsteen, found near Sewekow in eastern Germany original url

Comments: Although *Aysheaia* was the first recognised lobopodian (Onychophora sensu latu), *Xenusion* followed not long after. It was discovered in glacial drift (a sandstone boulder carried by glaciers) in Germany, thought to have originated in Southern Sweden. More recently a second specimen was discovered, and described by Dzik & Krumbiegel, 1989. Both specimens were preserved as empty cuticles shed after moulting. Originally considered to be of Late Precambrian (Late Neoproterpozoic) age, *Xenusion* is now considered to be Earliest Cambrian. It was a large lobopodian with pairs of dorsal plates; From Wikipedia: "The specimens are not especially well preserved. The older specimen is 10 cm or so in length with a narrow, weakly segmented body. A depression runs up the bottom on all but the rearmost segments. There is a slightly bulbous tail, and each segment beyond that seems to have a single pair of tapering annulated legs similar to the modern onychophore, but without claws. Nine segments are present. There is a spine on each body bump and faint transverse parallel striations on the annulations on the legs. The legs of what is possibly the foremost segments are either missing or not preserved. The head is believed to be missing or is poorly preserved. " Although *Xenusion* was armed with spines, they were shorter than those of *Hallucigenia*. The original specimen would appear to be part of an animal about 20 cm in length, larger than most Cambrian species or extant onychophores.

Considered an ancestral form intermediate between Tardigrades and Onychophores by Dzik, who places it at the base of his dendrogram, largely also because of the date (earliest known lobopodian) (Dzik & Krumbiegel, 1989, Dzik 2011). Ramsköld & Chen (1998) argue that Dzik & Krumbiegel (1989)'s interpretation of the second specimen is incorrect, in that it should be interpreted as preserved from the ventral (bottom) rather than the dorsal (top) side. They also state that there is no evidence of a long, (priapulozoan-like) proboscis (although this does not mean it would have been absent, simply that it wasn't preserved), nor is the front of the trunk narrower than the rear.

The phylogenetic status of this taxon are debatable, as typical with the Xenusia as a whole, and so far cladistic analyses has failed to resolve the problem. Ramsköld & Chen 1998 include it in their Alphonychophora, along with *Luolishania*, *Ayshenia* and *Onychodictyon*. Dzik 2011 place it close to *Aysheaia* but not to the other two taxa. Eriksson et al 2003 consider it a stem-xenusian (in an unnamed clade), but more derived than recent onychophora. While according to both Ma et al 2009 and Liu et al 2011 it is a stem-onychophora, more derived than basal taxa such as *Paucipodia* but still fairly primitive in relation to recent onychophora (i.e. it it tends to resolve at about halfway up the cladogram). In view of all this uncertainty we have for now retained it as a general basal lobopodian. MAK120501.

References: Dzik & Krumbiegel, 1989; Ramsköld & Chen (1998)

Hadranax augustus Budd and Peel, 1998

Horizon: Early Cambrian Sirius Passet lagerstätte, North Greenland

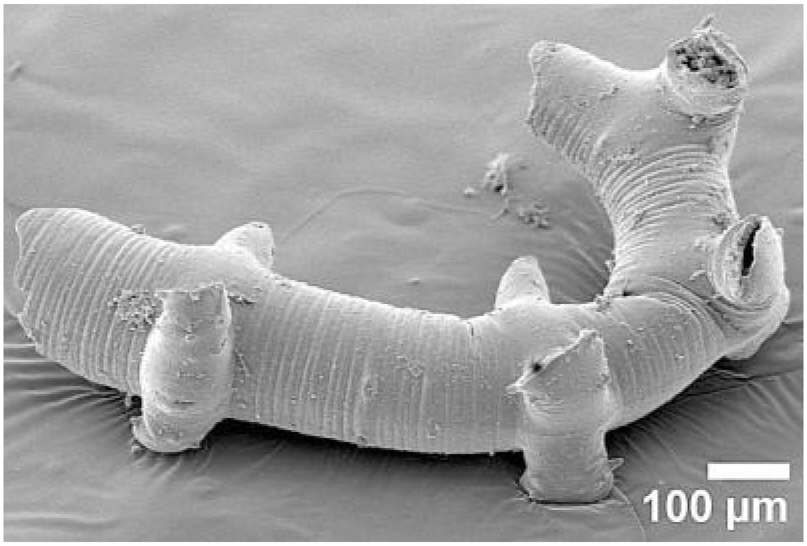
Phylogeny: Xenusiidae **:** *Xenusion* + *

Comments: A large lobopodian known from an incomplete specimen, it has strong appendages and dorsal tubercles; it seems to be related to *Xenusion* (Budd & Peel 1998)

Orstenotubulus evamuellerae Maas et al 2007

Horizon: "Orsten" beds, Västergötland, Sweden, Agnostus pisiformis Biozone (formerly zone 1 of the Upper Cambrian succession in Sweden).

Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + ((*Paucipodia* + Archonychophora + *Diania* + (paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda))))) + Xenusiidae + *Microdictyon* + Onychophora + *))



Orstenotubulus evamuellerae, the only lobopodian preserved in three dimensions (apart from Cambrian tardigrades which however are more derived forms). The exceptional preservation, down to the microscopic scale, make this the best understood of all the Cambrian armoured lobopodians. Photo © CORE Orsten Research. This photograph does not show the large spines (see sketch below left)

Comments: The first Cambrian lobopodian preserved in three dimensions, the exquisate micro-preservation of *Orstenotubulus* has provided many important insights about the early history and morphology of this group. Fossils are extracted by acid preparation and, as with all the orsten fossils, provide a degree of preservation down to the level of microscopic detail, providing an exception opportunity for study of the morphology of these ancient invertebrates.

All the Orsten fossils are tiny, on the millimeter scale or less. At 4 to 5 mm in length, and a diameter of about 100 to 200 microns, *Orstenotubulus* is only a tenth the linear dimensions of the better-known Cambrian lobopodians, although in oall ther respects very similar. There are 9 or 10 leg-bearing segments, and body and limbs are almost totally cylindrical. *Orstenotubulus* not only reveals the unscleratised, micro-annulated body and unjointed annulated limbs (shared with other Cambrian and recent lobopodians). The pattern of micro-annulated regions alternating with smooth regions also occurs in the Chengjiang lobopodians *Cardiodictyon* and *Microdictyon*. The micro-annulation indicates that the body of *Orstenotubulus* was only flexible in the regions between the limbs, whereas the smooth regions were most likely sclerotized. These give rise to tubular legs that extend laterally. In some segments, the smooth zones are dorsally drawn out into paired, conical humps or domes, extending into long spines. Such paired spines arranged in rows on conical humps or domes are characteristic of several Cambrian lobopodians, such as *Xenusion*, *Hallucigenia*, and *Luolishania*, possibly protecting the animal from predatorsand presumably possessing telescopic movability. Hallucigenia sparsa even had similar domes. Comparable dorsal outgrowths and telescopic spines occur in some Tardigrada but are absent in extant Onychophora, The legs are also equipped with spine-like outgrowths occur on short, conical sockets. These were probably telescopic and retractable. Similar features seem to occur in *Aysheaia*, *Xenusion*, *Luolishania*, and *Jianshanopodia* , but tardigrades and onychophorans lack such structures.

Towards the ventral midline of each leg, the spine-like outgrowths are accompanied by sets of outgrowths, or dermal papillae, consisting of several epidermal cells. They may also have had apical bristles (their absence here may be a preservational or preparational artifact), are similar to tubercles scattered over the body surface of *Aysheaia*, as well as to those of extant onychophora. These papillae might have had a sensory function, such as coordinating the retraction of spines during locomotion, and be an ancestral characteristic for panarthropods as a whole.

O. evamuellerae also shows strikingly similarities with recent tardigrades and onychophorans in the surface microstructure of its cellular-structured cuticle and the telescopic spines. The cuticle is annulated with a hexagonal surface microtexture like that of extant onychophorans.

The single ventral gonopore (genital opening), which indicates that this feature, also found in onychophorans, tardigrades, pentastomids, myriapods and insects, would seem to represent the plesiomorphic state for the panarthropoda. The paired state in chelicerates and crustaceans was then convergently achieved. (As with the general body plan and the plesiomorphic embryology of uniramia as opposed to more derived arthropoids, this shows that these lineages predate more specialised forms. Hence it is unlikely that the Pancrustacea hypothesis (insects evolved from Crustaceans) is correct)

Orstenotubulus is, like that of many other Cambrian forms, of the long-legged type, a morphotype with no extant equivalent. The specimens demonstrate that "ventral dangling" might not even occur after death, and its frequent occurance in other fossil lobopodians is the result of distortion due to two dimensional preservation, such as the animal being covered by sediment and its leg pairs pressed together, although lateral posture might be true of at least some short-legged forms, such as *Aysheaia* and *Jianshanopodia*. Hence walking on long, unsclerotized unjointed limbs, such as current reconstructions of *Hallucinoghenia* and *Micrtodictyon*, is not possible. This shows how misleading it can be to rely only on extant forms, such as onychophores, tardigrada, and arthropods, where changes in locomotory mechanisms have already taken place. The lateral orientation of *Orstenotubulus*' limbs. supported by anchoring spines pointing ventrolaterally, imply that most early lobopodians were crawlers rather than walkers MAK120427

Reference: the above is condensed from Maas et al 2007 and a few second-hand sources,a long with our own commenst ina few places.

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page uploaded 15 July 2002, checked ATW050625, revised MAK120419, 120501.

Lobopodia: Lobopodia (2)

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Paucipodia
                |--Microdictyon
                |--Archonychophora
                |  |--Cardiodictyon
                |  `--+--Hallucigenia
                |     `--+--Onychodictyon
                |        `--Luolishaniidae
                |--Diania
                `--+==Siberiidae
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

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Descriptions

Paucipodia inermis Chen et al., 1995

Horizon: Yuanshan Member, Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + (Xenusiidae + *Orstenotubulus* + Onychophora + ((paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))) + *Microdictyon* + Archonychophora + *Diania* + *)))

Comments Appears to be a very simple lobopodian, unarmoured, with only six, or alternatively nine, pairs of appendages (hence the name), and a proboscis-like head area (a primitive feature). Most cladograms place it in a basal position (although more derived than the apparently more complicated *Aysheaia*). But regularily spaced paired pigment patches along the presumed nerve cord could be ganglia, if they are not taphonomic artifacts. Their regular spacing in relation to the limbs is closer to the segmental ganglia of arthropods than to the unganglionated nerve cord of onychophorans. This would mean that *Paucipodia* is more derived than extant Onychophora, despite its otherwise primitive features (Edgecombe 2009 pp.185-6), an example of mosaic evolution. MAK120427

Microdictyon Bengtson et al. 1981 emend. Chen, Hou & Lu 1989 **:** M. effusum, M. rhomboidale, M. robisoni, M. sinicum, M. sphaeroides, M. tenuiporatum, etc

Range: Early Cambrian (Atdabanian to Toyonian), Cosmopolitan

Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + (Xenusiidae + *Orstenotubulus* + Onychophora + ((paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))) + *Paucipodia* + Archonychophora + *Diania* + *)))

Comments: an armoured lobopodian, very similar to, and perhaps closely related to *Hallucigenia* (Ramsköld & Chen (1998)) but without the spines. Isolated sclerites have long been known for example from Siberia as components of the small shelly fauna, and as with many such structures, their nature was puzzling. The discovery of *Microdictyon sinicum* (Chen, Hou and Lu, 1989) in the Chengjiang Lagerstätte (Early Cambrian Maotianshan Shale) of Yunnan China, solved the problem, as it was realised that the sclerites were attached to a lobopodian-like animal. *Microdictyon sinicum* is a typical lobopodian, with ten pairs of prominent net- or grate-like structure of flat trunk sclerites on the sides, matched to a pair of long slender limbs. The head and posterior are tubular and featureless (Wikipedia). Unlike other armoured lobopodians, in which there are generally an additional one or two limb pairs behind the head, in *Microdictyon* every limb pair is associated with a pair of sclerites. Ramsköld & Chen (1998), pointing out the similaritiy to *Hallucigenia*, note that if the first two sclerite pairs are removed, *Microdictyon* would have the same configoration of sclerites and limbs as *Hallucigenia*. So either these two taxa are closely related, as the authors argue, or else rthis is a shared primitive feature (p[lesiomorphy) of armoured lobopodians.

The suggestion that the sclerites may be eyes or eye-like structures, or a supportive structure for lateral paired eyes (Dzik 2003, Gehring 2012), is unlikely to be the case, as true small single eyes have been figured from *Miraluolishania*, *Hallucigenia* and *Cardiodictyon* (Steiner et al 2012 p.121, although this does not deny the possibility that arthropod compound eyes (as opposed to simple lobopodian eyes) may have developed from proto-arthropod sclerite-like structures (a bit like mammalian ear bones developing from therapsid jaw bones).

the following species are listed (Wikipedia), many from isolated sclerites, although no attempt here is made to work out their phylogeny

- Type species. *Microdictyon effusum* Bengtson, Matthews et Missarzhevsky, 1981; Early Cambrian, Atdabanian Stage, Kazakhstan; Atdabanian and Botomian Stages, Russia (Siberian Platform) and England; Early Cambrian, Sweden.
- *M. anus* Tong, 1989, Early Cambrian, upper Meishucunian Stage (= Atdabanian Stage), China (Shaanxi).
- *M. chinense* Hao et Shu, 1987, Early Cambrian, Qiongzhusi Stage (= upper Atdabanian-lowermost Botomian Stages), China (Shaanxi); Atdabanian through Botomian stages, Siberian Platform.
- *M. depressum* Bengtson, 1990, Early Cambrian, Atdabanian through Botomian Stages, South Australia.
- *M. fuchengense* Li et Zhu, 2001, Early Cambrian, upper Meishucunian Stage (Atdabanian Stage), China (Shaanxi).
- *M. jinshaense* Zhang et Aldridge, 2007, Early Cambrian, Qiongzhusi Stage (= upper Atdabanian Stage-lowermost Botomian), China(Shaanxi).
- *M. rhomboidale* Bengtson, Matthews et Missarzhevsky, 1986, Early Cambrian, upper parts of the

Atdabanian Stage, Kazakhstan; Atdabanian Stage, Canada, the United States (M. cf. rhomboidale).
- *M. robisoni* Bengtson, Matthews et Missarzhevsky, 1986, Middle Cambrian, Amgan Stage, the United States;
- *M. rozanovi* Demidenko, 2006, Early Cambrian, Toyonian Stage, Siberian Platform.
- *M. sinicum* Chen, Hou et Lu, 1989, Early Cambrian, upper Meishucunian Stage (= Atdabanian Stage) Stage, China (Yunnan.
- *M. sphaeroides* Hinz, 1987, Early Cambrian, Atdabanian Stage, Great Britain.
- *M. tenuiporatum* Bengtson, Matthews et Missarzhevsky, 1986, Early Cambrian, Atdabanian Stage, Siberian Platform.

Placed in the monotypal Family Eoconchariidae Hou & Shu 1987 (= Microdictyonidae Chen, Hou & Lu 1989) ref), in the monotypal Order Scleronychophora by Hou & Bergström (1995). Such taxonomic speculation does little to elucidate evolutionary relationships. The wide distribution of these tiny structures shows that lobopodians were an important element of early Cambrian faunas. Of course, not all need necessarily belong to the genus *Microdictyon* itself.

Microdictyon sinicum and the related *Paucipodia inermis* seem to have lived in close association with other animals like sponges or the enigmatic jelyfish ecomorph Eldonia. It is not clear whether they were parasitic on live*Eldonia*, feeding on carcasses of eldoniids on the sea bottom (Chen et al 2007), or had some other relation, perhaps mutualist or commensualist. MAK120427

Archonychophora Hou & Bergstrom, 1995 *sensu* Ma et al 2010

Horizon: Early to Middle Cambrian

Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + (Xenusiidae + *Orstenotubulus* + Onychophora + ((paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))) + *Paucipodia* + *Microdictyon* + *Diania* + * **:** *Cardiodictyon* + (*Hallucigenia* + (*Onychodictyon* + Luolishaniidae)))))

Characters: Differentiation of head from body, a set of anterior appendages ventrally at the base of the head (Liu et al 2011); trunk bears spine-shaped sclerites, which are often differentiated with regard to trunk tagmosis.

Comments Ma et al 2009 and 2010 distinguish two Cambrian lobopodian clades. *Microdictyon*, *Paucipodia*, *Jianshanopodia*, *Hadranax* and *Xenusion* (which would be family Xenusiidae), *Megadictyon*, and finally as the most derived forms extant onychophora, are placed in the first clade. The characteristics of this clade are more likely to be convergences or plesiomorphic. Large body size and tapering body shape are not features found in Microdictyon, Paucipodia, or extant onychophores. Limbs shortening towards one end of the body is found in both clades, The absence of spine-shaped sclerites in the Xenusiidae may be actual or simply be due to poor poreservation, while *Paucipodia* could be better understood as secondarily unarmoured. Lack of a distinct head and body tagmosis is a plesiomorphic feature, and in any case does not apply to *Jianshanopodia* or *Megadictyon*, both of which are transitional to protoarthropods. Their second clade, for which they used Hou & Bergstrom's taxon Archonychophora (but in a different definition) seems to be better defined. It includes *Cardiodictyon*, *Hallucigenia*, *Onychodictyon*, *Luolishania*, and the "Collins' Monster". and features many arthropodian and protoarthropodian characteristics. In contrast, Liu et al 2011 recognised only a single lobopodian clade, but consider *Jianshanopodia* and *Megadictyon* to be stem arthropods rather than stem euonychophora. For now we are tentatively positing a monophyletic Archonychophora intermediate between basal Xenusian klobopodians and Siberiid protodinocaridid lobopodians, but this may also be a paraphyletic grade, with some forms such as *Luolishania* and the "Collins' Monster" (= family Luolishaniidae) being mnore derived and arthropod-like than standard armoured lobopodians like*Cardiodictyon*, *Hallucigenia*, and *Onychodictyon*. The heavily armoured *Diania* may represent a third lineage, intermediate between these two. MAK120430

Cardiodictyon catenulum Hou et al., 1991

Horizon: Yuanshan Member, Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Archonychophora : (*Hallucigenia* + (*Onychodictyon* + Luolishaniidae)) + *

Comments This most elongate of all the Cambrian lobopodians, with 23 to 25 pairs of appendages on the trunk (more than twice the usual number), along with pairs of unique triangular sclerites that change in ontogeny from V-shaped in small adyults to shield shaped in large adults. The legs are finely and densely annulated, each with two curved, pointed terminal claws. There are at least one pair of set of anterior appendages at the base of the head (Ramsköld & Chen (1998), Liu et al 2011). The existence of head sclerites was reported by Hou & Bergström (1995), but Ramsköld & Chen (1998) found no evidence of any in the specimens they examined. MAK120501

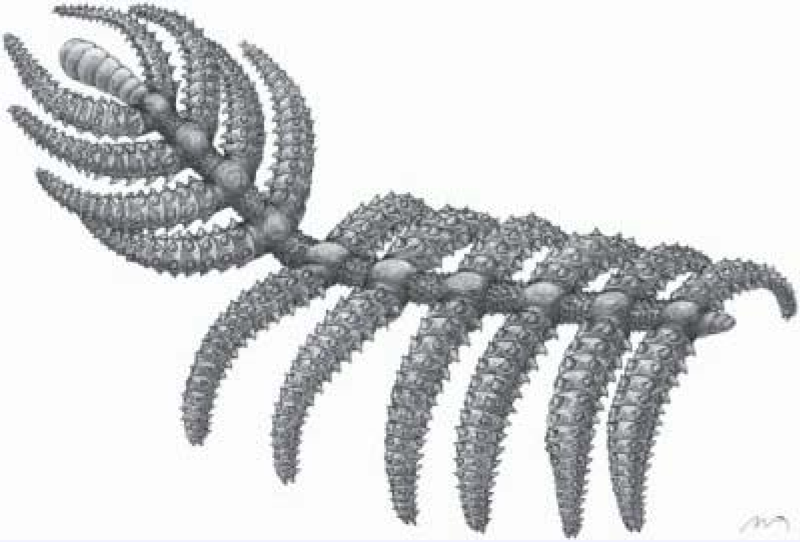
Onychodictyon ferox Hou, Ramsköld, and Bergström, 1991

Horizon: Yuanshan Member, Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Archonychophora **:** *Cardiodictyon* + (*Hallucigenia* + (Luolishaniidae + *))

Comments robust, short-limbed lobopodian, consisting of a head with large papillae and an elongate trunk. The trunk with 10 segments, each with a pair of dorsal round plates and lobe-like appendages on the ventro-lateral surface. Terminal claws prominent, indicative of an adapation to specific lifestyle in the epibenthos, perhaps climbing on algae or sponges. In addition to the standard trunk sclerites, head sclerites have been postulated by Ramsköld & Chen (1998). There are two species, the larger *Onychodictyon ferox* Hou, Ramsköld, and Bergström, 1991, 5 to 7 cm long, and the smaller *Onychodictyon gracilis* Liu et al 2008 upto 5 cm long, although it is possible these sexual dimorphs. (Liu et al 2008b). Although *Onychodictyon ferox* doesn't show any sign of anterior appendages, *Onychodictyon gracilis* shows one pair (Liu et al 2011) , so it is likely that the absense in *O. ferox* is due to poor preservation. As with *Hallucigінia*, elongated spines protruding from the plates, (Liu et al 2011). Hou & Bergström 1995 consider *Onychodictyon* to be the nearest to extant onychophorans of any of the other Cambrian lobopodians, and *Onychodictyon* is often reconstructed to look like a squat, spiny *Peripetus*. Subsequent cladograms and phylogenies place it near *Cardiodictyon*, *Hallucigenia*, and *Luolishania* (Ma et al 2009, Liu et al 2011, strict consensus of the latter's data by Mounce & Wills 2011 and Legg 2011 result in a (*Cardiodictyon* + (*Onychodictyon* + *Hallucigenia*)) clade with *Luolishania* resolving separately), despite the others all being long-limbed forms. It may in addition to (Dzik 2011) or apart from, those taxa also be close to *Diania*. MAK120427

Diania cactiformis Liu et al 2011



Horizon: Yuanshan Member, Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + (Xenusiidae + *Orstenotubulus* + Onychophora + ((paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))) + *Paucipodia* + *Microdictyon* + Archonychophora + *))))

Comments nicknamed the "walking cactus" because of its appearance. The generic name is from Dian, a linguistic abbreviation in Chinese of the Yunnan province, where the Chengjiang fossil Lagerstatte is located. The species name speaks for itself.

Although similar to other Cambrian lobopodians in most respects, *Diania* is remarkable in being densely covered on most of the trunk and espcially the limbs by numerous spinose sclerites. Sclerotization is usually not seen in the limbs of lobopodians except in the paired trunk sclerites and sclerotized claws. The microstructure of sclerites in *Diania* also differs from the net-like microstructure of trunk sclerites in other xenusian lobopodians

As well as a protective function, massive sclerotization of the outer cuticle enhanced body rigidity, and required the development of jointed legs. is the most basal panarthropod to possess articulated limbs (all other lobopodians had soft cuticle and hence naturally flexible limbs). Compared to puny limbs of *Hallucigenia* or *Hallucigenia*, or the stumpy ones of *Aysheaia* or recent onychophores the limbs are both exceptionally robust (in the illustration they appear to be as thick as or thicker than the trunk) and long, and it is easy to envisage this animal crowling along the sea floor.

In terms of limb morphology, *Diania* is closer to the arthropod condition than any other lobopodian known to date. Phylogenetic analysis by Liu et al (2011) empahsised the exceptional sclerotization and arthropod-like limbs of this taxon, and recovered it as the sister taxon to the Arthropoda proper, above ebven the dinocaridida (protoarthropods). The authors suggest that arthropodization (sclerotization of the limbs) preceded arthrodization (sclerotization of the body)., and that taxa such as Kerygmachela, Jianshanopodia, and Megadictyon1 constitute a paraphyletic series with different taxa expressing different grades of arthropodization. In their scenario the heavier sclerotization and partial arthropodization found in *Diania* led to the sclerotized exoskeleton of euarthropods.

Perhaps because of the obviously primitive grade of organisation of *Diania* in every way except arthropodisation, Liu et al (2011) were strongly criticised (by Mounce & Wills 2011 and Legg 2011, to which they responded Liu et al. 2011b. Other workers such as Ma et al 2009 and Dzik 2011 have provided alternative phylogenies in which different taxa (Archonychophora and Siberiidae respectively) represent uintermediate forms, although ironically each considers the others candidates much more basal for Ma et al 2009, siberiid lobopodians (although they did nort use that term as it had not yet been coined) were stem Euonychophora, whereas for Dzik 2011 archonychophora were derived Cambrian lobopodians,that either went nowhere or became pentostomids. We feel a more reasonable hypothesis than thes ethree is that there was a tremendous amount of parallelism among panarthropods, witha number of different lines evolving arthropodlike features while retaining various primitive traits. A similar situation can be seen with Permo-Triassic therapsids as they evolve from a reptilian to a mammalian condition. This makes determining phylogeny difficult. We have for now placed *Diania* as a standard lobopodian that independently aquired arthropodisation. It may or may not belong in the Archonychophora, a group taht culminated in the proto-arthropod-like Luolishaniid filter feeders. The Siberiids are another group that were independently evolving towards the dinocaridid and ultimately arthropod condition. For this reason we have placed *Diania* among the lobopodians rather than the protoarthropods. MAK120430

Reference and illustration: Liu et al (2011)

Ecdysozoa: Panarthropoda

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Mureropodia
      `--+--Aysheaia
         `--+--TARDIGRADA
             `--+--Xenusiidae
                |--ONYCHOPHORA
                `--+--Luolishaniidae
                   `--+==Siberiidae
                      `--+==DINOCARIDIDA
                         `--ARTHROPODA
```

Contents

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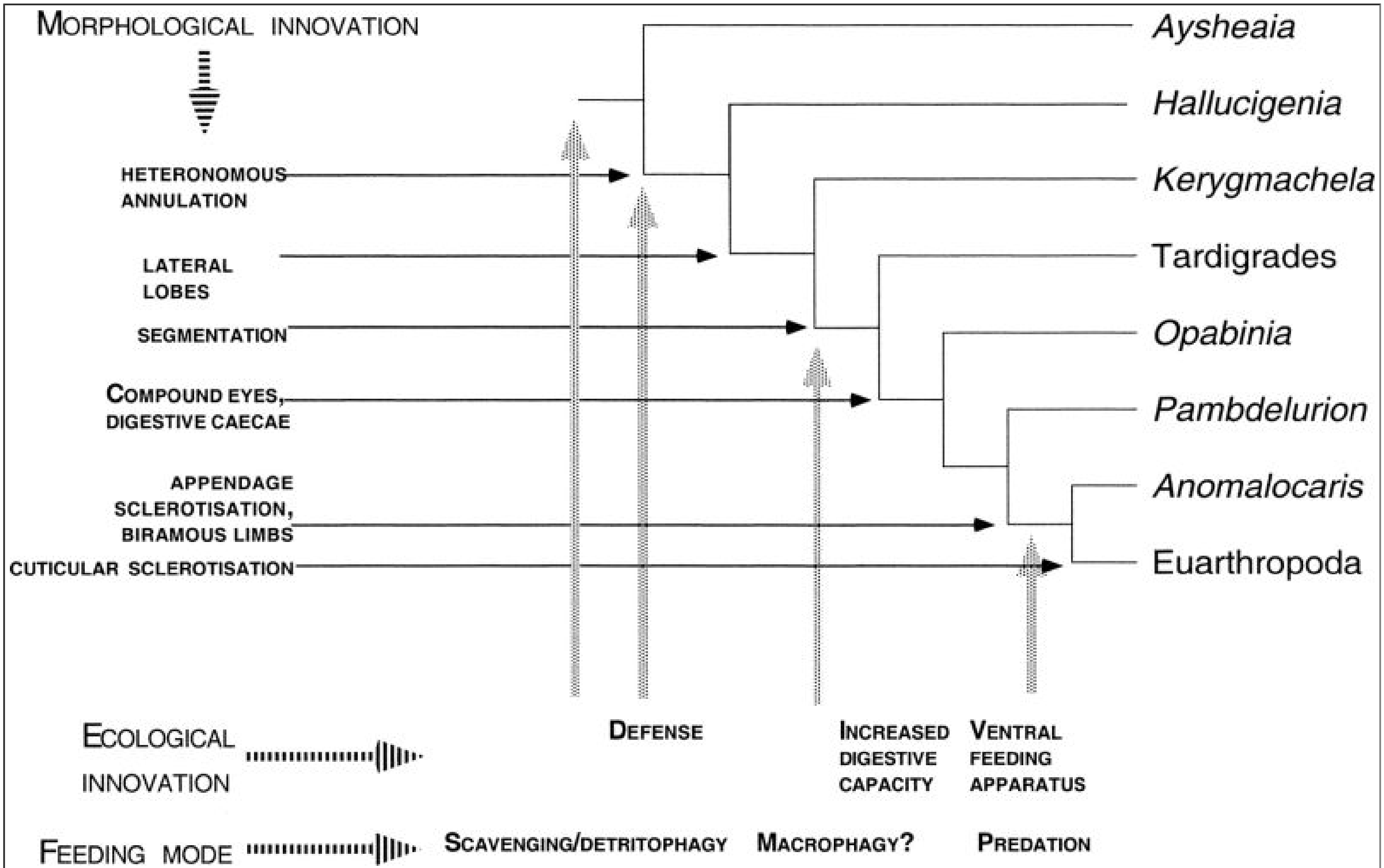
1. *Mureropodia* X
2. Panarthropoda

During the Cambrian period, ancestral Panarthropods were much more diverse than they were even during the later Paleozoic. There were several different lineages of lobopodians and proto-arthropods, including large carnivorous swimming forms like *Anomalocaris* and *Kerygmachela*, as well as smaller crawling types such as *Aysheaia*, *Hallucigenia*, and *Microdictyon*, and larger crawlers such Xenusion , *Jianshanopodia*, and *Megadictyon*. Whilst true arthropods, tardigrades and onychophorans are highly differentiated in form today, such was not always the case. During Cambrian Epoch 2, many transitional forms co-existed, and exciting new discoveries have come to light. Of particular interest are froms such as the aforementioned *Jianshanopodia*, *Megadictyon*, and *Kerygmachela*, which provide a link between lobopodians on the one hand, and anomalocaridids and arthropods. on the other. Another new anomalocarid-like taxon, *Pambdelurion* , indicates that the biramous arthropods actually arose from within the anomalocaridids (Budd 1997). After dominating the oceans for many millions of years, the big protoarthropods seem to have disappeared by the Mid Ordovician, their place as super-predators being taken by largecephalopod mollusks. However, medium-sized forms (still respectable in invertebrate standards) such as*Schinderhannes* continued to the Devonian at least. MAK020503, revised ATW050113 and MAK120505

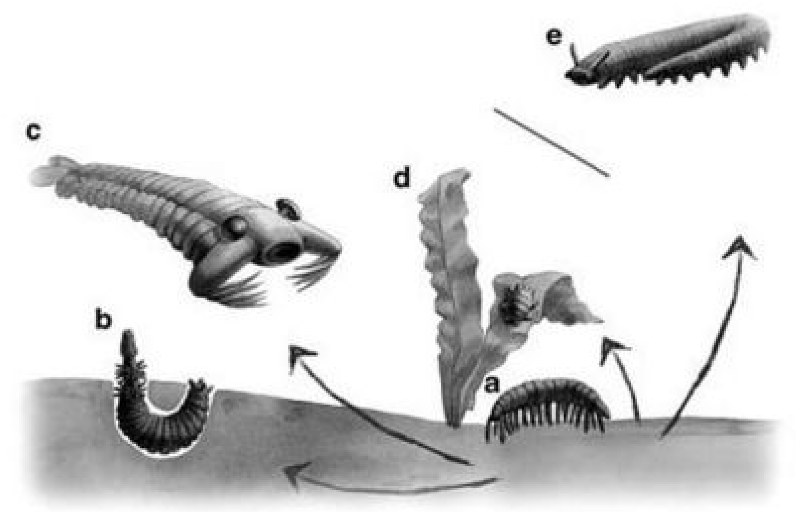


Graham Budd's scenario of panarthropod evolution, showing successive morphological innovations, and correlated functional and ecological shifts, with particular reference to feeding mode, from Budd 2003. Larger diagram. A version of this diagram (modified from Budd, 1996, 1999), is also at Species splitting)

Dzik and Krumbiegel (1989) hypothesize an origin from priapulid-palaeoscolecid-like worms through the development of segments and limbs. Complete specimens of *Facivermis yunnanicus*, showing both priapulid and arthropod characters, provide strong support for this proposed affinity. (ref Cambrian lobopods), although this could be taken the other way as well, *Facivermis* being a lobopodian in the process of losing its limbs (see also the discussion on worms and lobopodians).. We have followed Dzik 2011 in making *Facivermis* a specialised end-taxon far from the original ancestral lobopodian condition. Better evidence may be had in the discovery of a new, priapulozoan-like lobopodian, *Mureropodia apae*

The bauplan of early panarthropods (paraphyletic class or phylum Xenusia) includes a vermiform body; a proboscis or mouth cone; paired lobopods with claws; a cuticle displaying a repeated anatomical patterning; a straight digestive tract with terminal mouth and anus (Vintaned Gamez et al 2011). The early panarthropods quickly evolved through a series of stages of progressive arthropodisation, such as are shown in this diagram, based on the work of formost specialist and theorist in proto-arthropd evolution, Professor Graham Budd.. The actual sequence is probably not as clear cut and linear as is shown here, because of mosaic evolution and the fact that many traits would have evolved differently and in parallel, e.g. the otherwise primitive lobopodian *Diania* evolved a sclerotised exoskeleton before seqmentation, compound eyes, biramous limbs and so on. In this context, Cope and Osborne's idea of orthogenesis seems to have some merit, albeit more as parallel adaptive trends of mosaic evolution, as the arthropod potential would already be there in the lobopodians. The degree of homoplasy and parallelism is probably the reason why it is hard to get a consistent phylogeny; every worker in the feld seems to arrive at a different toplogy. In more recent trees for example, *Pambdelurion* is consistently less derived, rather than more derived, than *Opabinia* (e.g. Edgecombe 2009, Daley et al 2009, Liu et al 2011)

Vintaned Gamez et al 2011 and Zhuravlev et al 2011 suggest that morphologically diverse xenusians (basal lobopodia) could have given rise to four different ecomorphic lineages: to cephalorhynchian or cycloneurian worms by adaptation for burrowing



Generalised reconstructions of early Cambrian xenusian (a), cephalorhynchian worm (b), anomalocaridid (c), tardigrade (d), and extant terrestrial onychophoran (e), according to the phylogeny proposed by Vintaned Gamez et al 2011. Artwork by Anastasia Besedina. See also Zhuravlev et al 2011 fig 5 for a more detailed version of this scenario.

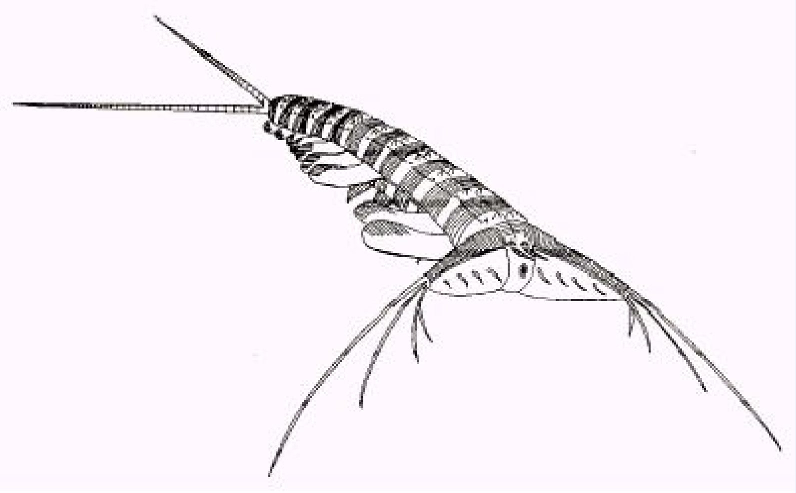
with retractable proboscis, via forms such as *Facivermis* and *Mureropodia*; to tardigrades by adaptation for interstitial habitat (via *Hadranax*-like forms); to euarthropods by adaptation to walking on joint appendages (via *Jianshanopodia* like forms); and to anomalocaridids by adaptation to swimming with lateral flaps (via *Kerygmachela* and similar types). This scneario is shown in the diagram at the left. We believe however that it is more likely that priapulozoan worms came first, as per Dzik and Krumbiegel 1989, Budd 2001, Conway Morris & Peel 2010, etc, and that early lobopodians were transitional forms between these and tardigrades, onychophores, and protoarthropods (anomalocaridids etc) MAK120422

Descriptions

Panarthropoda Nielsen, 1995 = Haemopoda Cavalier-Smith 1998 = Aiolopoda Hou and Bergström, 2006 (lobopodians (note) + arthropods)

Range: Fr ECambrian

Phylogeny: Ecdysozoa **:** Scalidophora + (Nematoida + (Cricocosmiidae + * **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + (Xenusiidae + *Orstenotubulus* + *Microdictyon* + Onychophora + (*Paucipodia* + Archonychophora + *Diania* + (paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))))))))

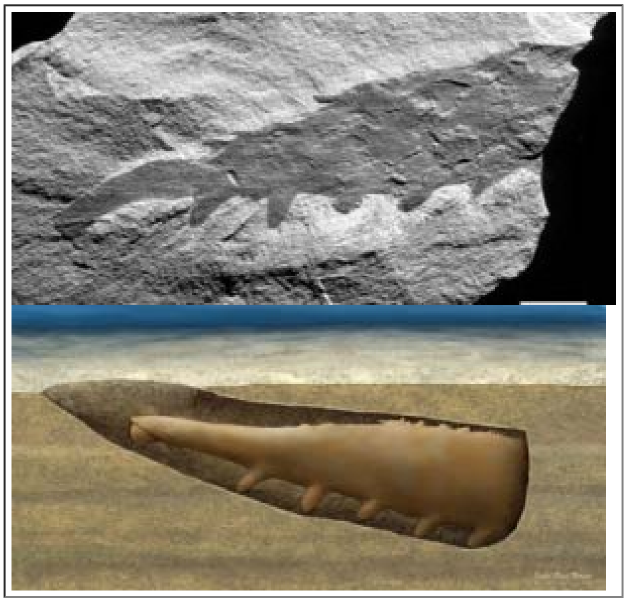


Characters: body segmented, with limbs on several segments; adult body cavity a haemocoel that extends into the limbs Cavalier-Smith (1998), "cuticle of a-chitin which is molted regularly, appendages with chitinous claws, and mixocoel with metanephridia and ostiate heart (absent in tardigrades); several characters, such as the structure of the brain, indicate that arthropods and tardigrades are sister groups." Nielsen, 1998, paired segmental ventrolateral appendages, 2 paired leg nerves, *Engrailed* gene expressed in posterior ectoderm of each segment (Gabriel and Goldstein 2007, cited in Edgecombe 2009). Primitively possess a terminal mouth, a non-retractable proboscis, and a thick integument of diverse plates. Zhuravlev et al 2011, A single differentiated cephalic appendage appears to be a synapomorphy of onychophorans and euarthropods Budd 2001

Comments: **[1]** Panarthropods include true arthropods and their soft-bodied relatives, the tardigrades and onychophorans. They are generally considered a monophyletic taxon, although there is still some uncertainty regarding the phylogenetic status of the tardigrades, this is more likely to be an artifact of molecular analysis rather than reflecting actual phylogeny (Rota-Stabelli et al 2010), an alternative position that cycloneuralian worms are derived (i.e., evolved from) lobopodians has minority support (Vintaned Gamez et al 2011, Zhuravlev et al 2011) but is not widely held.

[2] The Lobopodia constitute a paraphyletic assemblage that includes all non-euarthropodous panarthropods. It is considered a phylum (with alternate spelling, no "i") by Cavalier-Smith (1998). MAK120425

Image: The proto-arthropod *Kerygmachela kierkegaardi* Buen Formation, Cambrian Epoch 2, North Greenland. From the *Transactions of the Royal Society of Edinburgh*: Earth Sciences, volume 89 (1999 for 1998), pp. 249290.



Mureropodia apae Vintaned Gamez et al 2011

Horizon: Murero Lagerstätte, bBase of Level RV 1/5 (Protolenus jiliocanus zone, upper Bilbilian, Latest Early Cambrian) in the Cadenas Ibéricas, NE Spain

Phylogeny: Panarthropoda **:** (*Aysheaia* + (Tardigrada + (various lobopodia + Onychophora + (Archonychophora + (paraphyletic Siberiidae + (*Kerygmachela* + (Dinocaridida + (*Schinderhannes* + Arthropoda)))))))) + *

Comments: *Mureropodia apae* may well represent a non-missing link between priapozoa and lobodous panarthropods, in which case the dendrograms on these pages need to be revised accordingly. The skin has a fine regular reticulated pattern and is covered by tiny wart-like protuberances and plates, and may have had hair-like sensorial organs as tactile and chemoreceptors. It had at least five pairs of short legs equiped with claws, that may have been used to burrow in the seabed. The length/body width ratio reveals that this animal hardly was able to walk on the bottom surface, and more likely used the limbs for anchoring the body to the substrate. There was a well-developed muscular system and a long retractile proboscis for catching prey. The exceptional fossil preservation has enabled researchers describe interwoven muscle fibres distributed throughout the body, and a dermomuscular sac. Although *Mureropodia* may have been able to crawl along the surface, it was better adapted to an infaunal, endobenthic lifestyle, burrowing by peristaltic movements.

Reference Vintaned Gamez et al 2011

Links Descubierto un enigmático fósil ancestro de los artrópodos Investigadores valencianos descubren un fósil de hace 520 millones de años (Spanish), Mureropodia, worm-arthropod link? (brief English comment on previous), Proyecto Murero MAK120422

Images: from first two links above

Lobopodia: *Hallucigenia*

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
         `--+--Xenusiidae
            |--ONYCHOPHORA
            `--+--Diania
               |--+--Cardiodictyon
               |  `--+--Hallucigenia
               |     |  |--Hallucigenia sparsa
               |     |  `--+--Hallucigenia
fortis
               |     |     `--Hallucigenia
hongmeia
               |     `--+--Onychodictyon
               |        `--Luolishaniidae
               `--+==Siberiidae
                  `--+==DINOCARIDIDA
                     `--ARTHROPODA
```

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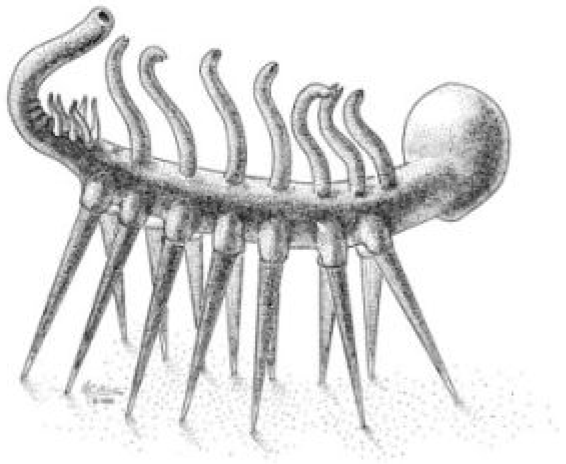
2. *Hallucigenia sparsa* X
3. *Hallucigenia fortis* X
4. *Hallucigenia hongmeia* X

Salvador Dalí. *The Temptation of St. Anthony*, 1946 (image copie dfrom Art Contrarian). Elephamts on stilts, and other weird stuff

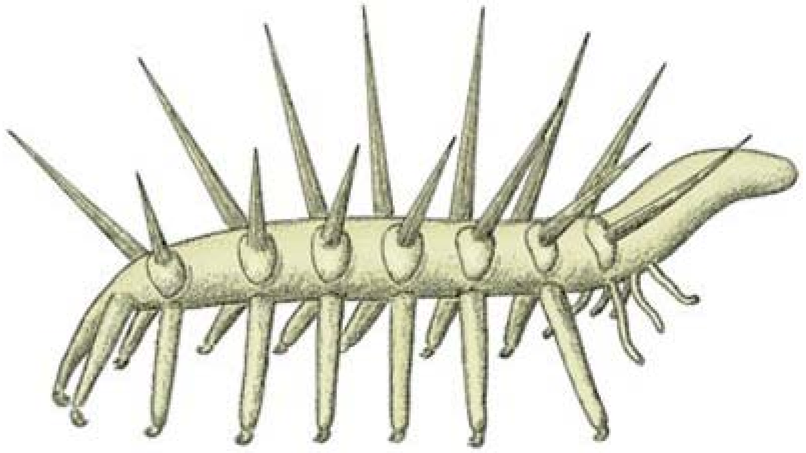
The ballard of *Hallucinogenia* (or elephants on stilts)



Lobopodian on stilts. Classic reconstruction of *Hallucigenia sparsa* by Marianne Collins that appeared in *Wonderful Life*. Illustration © Marianne Collins from The Burgess Shale. This impossible animal never existed, it is the result of incorrect interpretation of the original fossils.

Along with *Anomalocaris*, *Hallucigenia sparsa* is probably one of the best known Cambrian animals. Originally believed to be an annelid worm, it was famously misinterpreted by Simon Conway Morris, who named the genus *Hallucigenia sparsa* because of its "bizarre and dream-like quality". Stephen Jay Gould and later commentators followed him in believing on this an upside-down and back-to-front animal, a creatuire that made no sense, walking on stilts like one of Salvadore Dali's elephants. Inspired by this and other strange Cambrian forms, Gould wroite *Wonderful Life*, a very readable popular science book on the Cambrian explosion, the premise of which is that Cambrian was full of bizarre short-lived phyla, of which only a tiny perceptage survived, and those only by pure chance or luck, not because any were less well adapted. Gould argued that if the tape of evolution was replayed thousands of times, different phyla would arise each time. Therefore, Gould argued, because it is only by random fluke that vertebrates became ascendent on earth, intelligence is very rare in the universe. Of course this anthropocentrically assumes that only humanoid vertebrates can be intelligent, a premise any good hard science fiction writer would laugh at.

In 1991, Lars Ramskold and Hou Xianguang, working with additional specimens of a



Lobopodian on rubbery stilts. Hallucinogenia the right way up. The tentacles of the earlier reconstruction are actually lobopods, and the spines grew out of plates and probably protected the animal from preditors. Even so, the posture here is unrealistic, because long-leged lobopodians could not have stood erect on such narrow lobopods (unless they had neutral buoyancy); ironically, stilt-waking would be more biomechanically realistic. In lfe the lobopods were held horizontally. Illustration from Harold L. Levin, *The Earth through Time*, 8th edition, chapter 12.

"hallucigenid," *Microdictyon*, from the lower Cambrian Maotianshan shales of China, reinterpreted Hallucigenia as an Onychophore (velvet worm). They inverted it, interpreting the tentacles, which they believe to be paired, as walking structures and the spines as protective. Interestingly, none of the 30 or so known Burgess Shale specimens shows any sign of pairing in the large tentacles; nor do their Chinese counterparts. The pairing is based on a dissection of the actual fossil, which revealed what is probably a second tentacle structure. Ramskold and Hou also believe that the blob-like 'head' is actually a stain that appears in many specimens, not a preserved portion of the anatomy (Ramskold 1992) - Wikipedia

In the end Conway Morris and Gould came up with opposite evolutionary phylogenies. Gould had a model of evolution as a totally random bush, with absolutely no direction, Conway Morris not only placed many of the exotic Cambrian problematica as stem groups to current phyla (Conway Morris 1998), but even saw evolution and intelligence as converging on the same (humanoid) form (Conway Morris 2003), an anthropomorphic premise even less imaginative than Gould's, even if would give some scientific credibility to *Star Trek*'s rubber-forehead aliens. One gets the feeling that maybe evolution is sometimes bush-like (Gould) and sometimes linear (Conway Morris) but more often it is oi somewhere in between, tending to emergent complexity as systems theory reveals.

Ironically, modern ideas of *Hallucinogenia* were almost as wrong as the original. Whilst the animal was no longer back to front and upside down, it was still walking on stilts, only now they were soft rubbery ones. The mechanics of this has of course never been questioned, until Maas et al 2007 discvered and described a long-legged lobopodian that had been preserved in three dimensions. It was realised that, unlike modern onychophores, the legs were held out horizontally; the animal may have crawled through the mud, but probably preferred clinging to the epibenthos. Add retractable spines (assuming this feature is shared with *Orstenotubulus* and modern tardigrades), and it turns out that *Hallucinogenia* really was a pretty weird critter after all MAK120426

Descriptions

Hallucigenia (= monotypal Family Hallucigeniidae Conway Morris, 1977

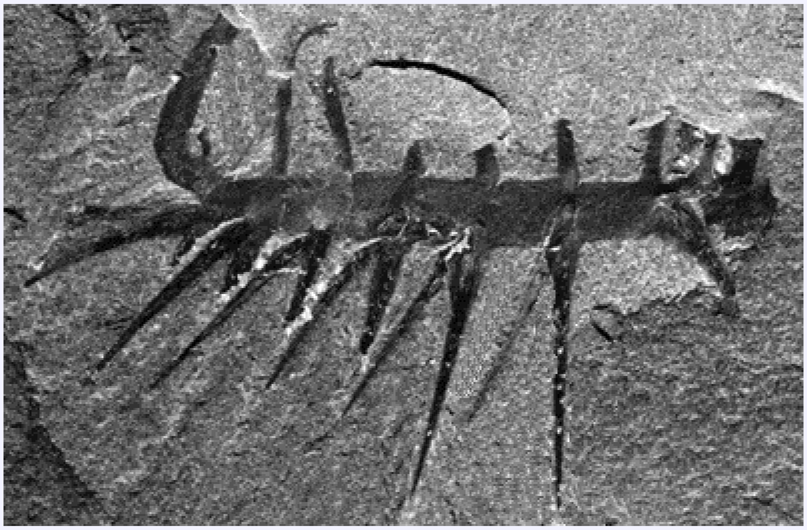
Range: Known from Early to Mid Cambrian of China & Nth Am; but doubtless would have had a wider distribution)

Phylogeny: Archonychophora **:** *Cardiodictyon* + ((*Onychodictyon* + Luolishaniidae) + * **:** *Hallucigenia sparsa* + (*Hallucigenia fortis* + *Hallucigenia hongmeia*))

Comments A small, long-legged lobopodian. There are seven pairs of legs, each with a corresponding pair of sclerites or spines, plus two pairs of longer but slighter anterior appendages two pairs in the head region in front of the most anterior pair of sclerites, and a further pair at the rear. The three known species, one trom the Burgess Shale and two from Chengjiang, hint at what must have been a much greater diversity. They differ in the shape of the sclerites (which only appear as long spines in the type species, *H. sparsa*, length of claws (long and curved in *H. hongmeia*, doubtless for clinging to epibenthos) and other minor features.. On the basis of general morphology, Ramsköld & Chen 1998 argue *Hallucigenia* is related to *Microdictyon*. Statistical-computational cladistic studies however place it near *Cardiodictyon* and *Onychodictyon* instead. Of course it may be that both these interpretations are valid.

Although in Liu et al 2011's analysis, *Hallucigenia* and the more derived forms share the synapomorphies of "elongate spine with plate-like armour on the trunk and the shape and size of spines variable", *Orstenotubulus* also possesses elongate spine with plate-like armour on the trunk but is given a more basal position, which illustrates that spines are more likely a primitive rather than a derived feature of Cambrain lobopodians, with non-spiny forms being secondarily unarmoured. MAK120501

Hallucigenia sparsa (Walcott, 1911)



Horizon: Burgess Shale of British Columbia (Middle Cambrian - Cambrian V / Drumian)

Phylogeny: *Hallucigenia*: (*Hallucigenia fortis* + *Hallucigenia hongmeia*) + *

Comments famously reconstructed as a back to front upside down stilt walker, this small animal, only a few centimerers in length, is now known to be a fairly representative Cambrian lobopodian. it is distinguished by long paired dorsal spines along the back and three pairs of appendages at the anterior end of the trunk. Although in many ways a typical lobopodian, it is exceptional in the length of its spines. It is not known what the spines were made of and how much protection' they offered, if any. They do not seem to be preserved independent of the soft-shelled animals as carbonate or chitinous shells would probably be. The absense of such structures (or their presence as much shorter retractable spines, cones etc) in other lobopodian species implies that the purpose of these spines may not actually have been for defensive purposes (however most lobopodians do have spines of some sort). It is also not easy to explain why 30 or more specimens — each hypothesized to have seven pairs of rather long, flexible legs — do not show even one example of paired legs. MAK120427 (incorporating also content from Wikipedia)

Image: *Hallucigenia sparsa*, image © the Smithsonian Institute

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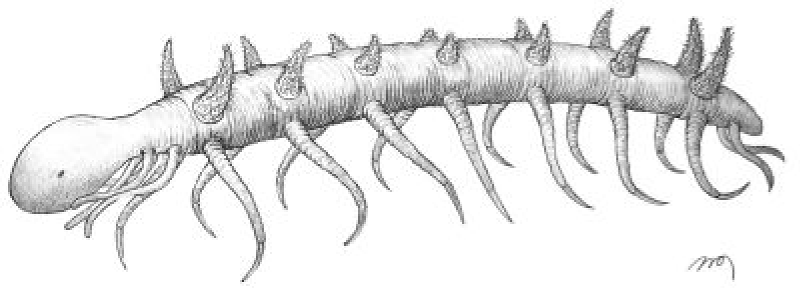
Hallucigenia fortis

Horizon: Chengjiang and Guanshan Lagerstätten, Yunnan, China, (Atdabanian to Toyonian - Early Cambrian)

Phylogeny: *Hallucigenia*: *Hallucigenia sparsa* + (*Hallucigenia hongmeia* + *)

Comments a wide ranging species, spanning much of the second half of the Early Cambrian (eight or ten million years), *H. sparsa* is currently reconstructed with a long slender head, whereas H. fortis still displays the expanded and rounded head of the stilt walking *H. sparsa*, implying it is simarily reconstructed back to front (if at least not upside down) Steiner et al 2012. The mouth is an antero-ventrally located Liu et al 2008, an "advanced" condition relative to most lobopodians, which was achieved a number of times. MAK120426

Hallucigenia hongmeia Steiner et al 2012



Horizon: Guanshan Lagerstätte (lower Wulongqing Formation, Yunnan, South China, (Early Toyonian age - Early Cambrian)

Phylogeny: *Hallucigenia*: *Hallucigenia sparsa* + (*Hallucigenia fortis* + *)

Comments Described as a "slender lobopodian with an annulated trunk with seven pairs of sclerites, eight pairs of legs, and a short tail. The sclerites are slightly sclerotized and show an antero-posterior differentiation with small, cone-shaped sclerites in the middle part and the largest spinose sclerites at the posterior end. A similar structure of sclerites can be seen in *Onychodictyon ferox* from the slightly older Yuanshan Formation (Chengjiang). Claws of the legs are long, curved, and also sclerotized." Steiner et al 2012. This newly discovered species of *Hallucigenia* is equipped with blunt cone-shaped sclerites, which, unlike the homologous very large, closely arranged and sharp sclerites of *Hallucigenia sparsa* , would not seem to serve any defensive purpose . The prominent claws in *Hallucigenia hongmeia*, similar to but larger than those Onychodictyon posesses, point to adaption for a specific habitat. The animal would seem to be less adapted for walking pr crawling on a muddy substrate and more to a climbing mode of life, perhaps on other benthic organisms or larger algae. Steiner et al 2012 p.120. Compare here the association of *Aysheaia* wirth sponges. Many lobopodians doubtless had a specialised lifestyle and commensual or mutualist interaction with specific plants and animals in their enviornment MAK120426

Image: *Hallucigenia hongmeia*, life reconstruction from Steiner et al 2012. Although the bulbous head indicates that this species is reconstructed back to front (compare the more recent reconstruction of *Hallucigenia sparsa*) the two pairs of small limbs not paired with sclerites show that this is indeed the correct orientation. MAK120427

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PANARTHROPODA
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Lobopodia: Luolishaniidae

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Archonychophora
                |  |--Hallucigenia
                |  `--Luolishaniidae
                |     |--Luolishania
                |     `--Facivermis
                `--+==Siberiidae
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

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2. *Luolishania* X
3. Luolishaniidae X

Descriptions

Luolishaniidae Hou & Bergström, 1995

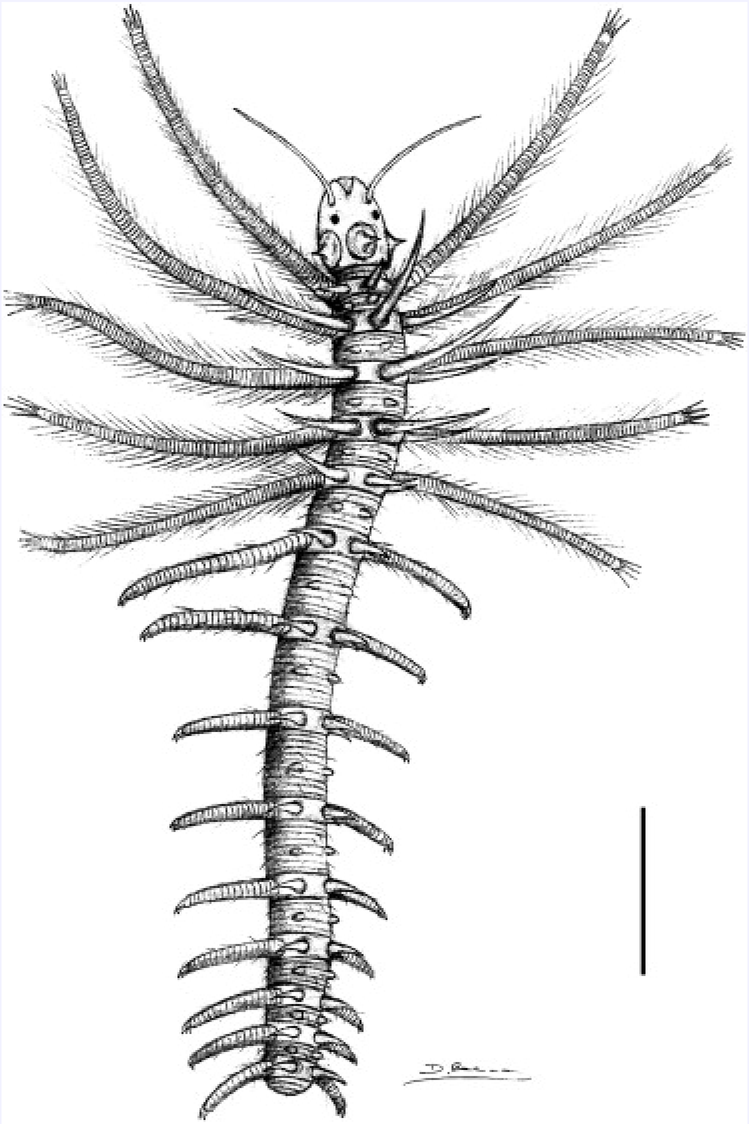
Range: Early to Mid Cambrian of China & Nth Am.

Phylogeny: Archonychophora : *Cardiodictyon* + (*Hallucigenia* + (*Onychodictyon* + * : *Luolishania* +

Facivermis))

Comments: Filter feeders close to the protoarthopods. Here used to include *Luolishania* (*Miraluolishania* is probably a synonym) and the unnamed Burgess Shale lobopodian called Collins' monster (perhaps another species of *Luolishania*?), which appear together on several phylogenetic analyses (Ma et al 2009, Liu et al 2011) and the bizarre *Facivermis*, here interpreted as a highly specialised secondarilty partly limbless lobopodian (Dzik 2011) rather than a transitional priapulozoan-panarthropod. According to Ma et al 2009 the Luolishaniids are specialised (crown group using the term in a non-neontological sense) Archonychophora, although *Luolishania* displays arthropod-like antennae and compound eyes which imply the group may be more derived (closer to true arthropods) than related taxa such as *Hallucigenia*. MAK120430

Illustration: *Luolishania longicruris* (= *Miraluolishania haikouensis*), life recosntruction from Ma et al 2009



Luolishania longicruris Hou & Chen 1989

Synonym: *Miraluolishania haikouensis* Liu et al., 2004

Horizon: Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Luolishaniidae **:** *Facivermis* + *

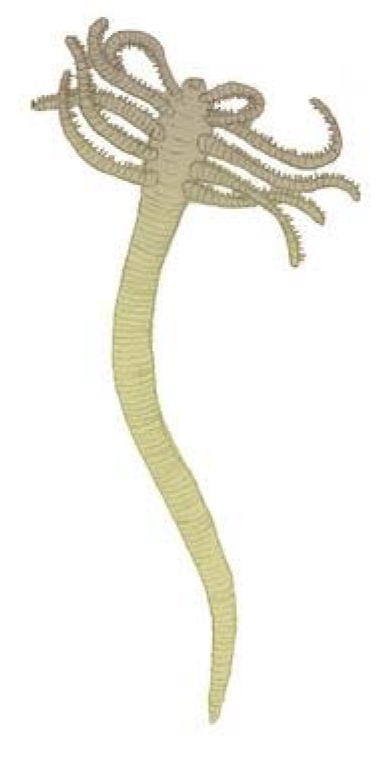
Comments: Previously considered a standard long-limbed lobopodian, this taxon has jumped around the phylogenetic tree quite markedly, as a glance at the cladograms reveals. Hou & Bergström 1995 considered that *Luoishania* is the sister taxon to all other fossil and recent onychophorans. Ramsköld & Chen 1998 in the first cladistic analysis of the group placed it next to *Xenusion*. Eriksson et al 2003 considered Luolishania to occupy an inrtermediate position above extant onychophores but below all other fossil forms other than the basal taxon *Aysheaia*. Liu et al 2008 p.280 *Luolishania* as a generalised form, without specialized head structures, whereas Miraluolishania is much more derived, with pairs of eyes and antennae on the head and the trunk showing primitive tagmosis. But a study by Ma et al 2009 using newly discovered *Luolishania* material, shows the same advanced arthropod like features, and show *Miraluolishania* to be a junior synonym. They place *Luolishania* in the newly defined clade Archonychophora as sister taxon to protoarthropods and arthropods.. Liu et al 2011 reject this interpretation and restore *Miraluolishania*, which now becomes the sister taxon to the Crown group Onychophora. But in view of the reported arthropod-like features of *(Mira)Luolishania* we have chosen to place the We have followe Ma et al (2009)'s interpretation here.

Luolishania (= *Miraluolishania*) is thus a transitional form, possessing a mosaic of both lobopodian and arthropod characters. Its lobopodian features are worm-like body design, dorsal spines, differentiated sclerites, lobopod interspaces and non-segmented limbs or lobe-like legs with standard lobopod claws. Arthropod features include primary cephalization with paired eyes, paired antennae (or antenniform-like outgrowths), setae and other cuticular projections, and incipient tagmosis and head shield. (Cambrian lobopods, Ma et al 2009). Although the holotype of *Luolishania* seems to show three or more claws per limbs, all specimens identified as *Miraluolishania* unquestionably show two claws terminally per limb (Liu et al 2011). As with the related Collins' monster, and *Diania* (which may or may not belong in this clade) the trunk divided into two sections (bipartite) (Ma et al 2009, Liu et al 2011).

Evidence from gut filling and specialized morphological characters indicates that *Luoishania* may have been a filter feeder (Ma et al 2009).

More: *Luolishania longicruris*, Virtual Fossil Museum

Facivermis yunnanicus Hou & Chen, 1989



Horizon: Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Luolishaniidae **:** *Luolishania* + *

Comments: For a long time a problematic form, due to poorly preserved specimens, appearing to be a worm-like fossil with five pairs of tentacles and a perceived shrunken end. *Facivermis* has been variously been regarded as related to polychaete annelids, lobopodians, pentastoma and lophophorates. Newly discovered complete specimens show that the apparent tentacles are in fact five pairs of standard lobopods, most resembling the appendages of the fore-trunk of lobopodian *Miraluolishania* (= *Luolishania*). The rest of the body is divided into a slender region devoid of appendages and a pear-shaped posterior bearing two or three circles of hooks. As with *Hallucinogenia*, *Facivermis* is another Cambrain species that turns out to be more understandable on further examination. Which is not to say that all the problems have been cleared up. Although clearly a transitional form of some sort, the question remains whether *Facivermis* is a priapulozoan worm becoming a lobopodian, or a lobopodian secondarily becoming a worm (Zhuravlev et al 2011), or for that matter a pentastomatid. On the one hand, *Facivermis* shows features consistent with the transition from priapulid-style burrowing and lobopodian-style creeping on the seafloor (Liu et al 2006, 2008 also cited in Edgecombe 2009). Studies of molecular and development biology indicate that the first five to seven segments seem to be important in development of the arthropod condition, with appendages begining in the cephalon area, and trunk appendages controlled by the budding zone. The Late Cambrian Orsten (3-dimensionally preserved microfossil) crustaceans suggest that the anterior five to seven limbs- bearing segments develope into the cephalon of the euarthropods Liu et al 2006

Yet *Facivermis* does not resemble a primitive lobopodian like *Aysheaia*, but a more highly derived one like *Luolishania*. Add to the fact that *Luolishania* seems to have been a sedentary filter feeder Ma et al 2009 it is quite likely that *Facivermis* was a simialr but even more specialised form (Dzik 2011),, in which case the original annelid and lophorphorate filter feeding hypotheses may not have been that far fetched after all. Rather than beinga trabnsitional priapulozoan (whether worm to lobopodian or lobopodian to worm) *Facivermis* seems to have represnted a unique development in Cambrian evolution, illustrating again the great ecological and morphological diversity of the ecdysozoa during this time MAK120424

Reference Liu et al 2006

Illustration: Life reconstruction of *Facivermis yunnanicus*, artwork by Ghedoghedo Wikipedia, Creative Commons Attribution-Share Alike/GNU Free Documentation License.

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Luolishania longicruris, Rarest of the Chengjiang Lobopodians
Cambrian Explosion Lobopodian

Name: Luolishania longicruris

Phylum Lobopodia

Early Cambrian (~525 million years ago)

Size: 13 mm long

Fossil Site: Chengjiang Maotianshan Shale - Quiongzhusi Section, Yu’anshan Member, Heilinpu Formation, Maotianshan, Yuxi, Yunnan Province, China

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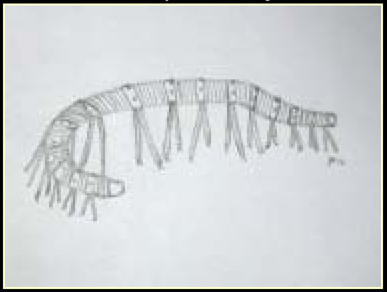
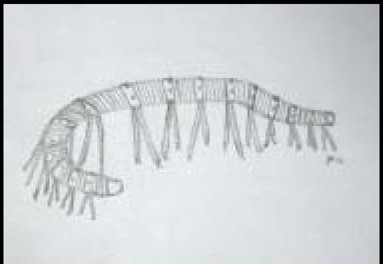
The Lobopodians are small marine and terrestrial animals termed colloquially “velvet worms” or “worms with legs”. While all Recent forms are terrestrial, most fossil Lobopodians are marine, and are known primarily from the Cambrian. Six named genera, each with a single species, are known from the Chengjiang Biota, making it the richest source of fossils of the type on Earth.



This Lobopod comes from Maotianshan (Mao Tian Hill), site of the original discovery of the Chengjiang Biota by Hou Xian-guang in 1984. The specimen is most striking, and concomitantly rare; as of 2004, only but six examples were known. A complete Luolishania is thought to be some 15 mm long, making this specimen typical. Each leg bears curved claws that are thought to have served the creature as an adaptation to crawling on other organisms. Luolishania has been found in association with Proferans. Some authors suggest that Luolishania is most closely related to Xenusion from the Early Cambrian of Germany. The genus is unknown outside of Yunnan Province. This fine example has incredible detail, with its long legs clearly evident.

click to enlarge



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Unit Back: Nematoida	Clade Down: Dinocaridida / Arthropoda	Ecdysozoa Dendrogram	Ecdysozoa References	Unit Next: Tardigrada

Ecdysozoa: Panarthropoda: Siberiidae

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Luolishaniidae
                `--+--Siberion
                    |--Jianshanopodia
                    `--+--Megadictyon
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

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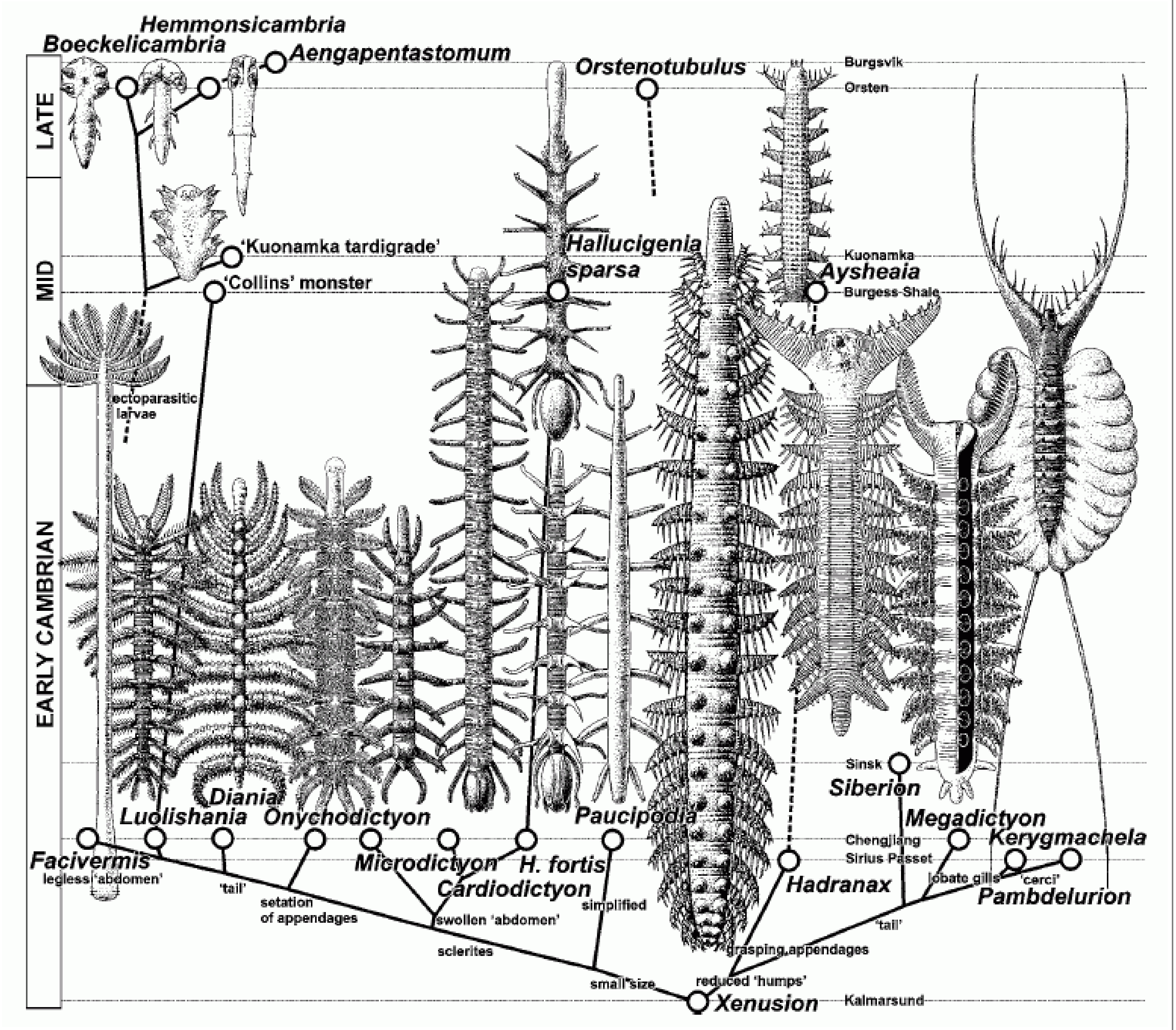
1. *Siberion* X
2. *Jianshanopodia* X
3. *Megadictyon* X



Not a forest of Christmas trees, but a selection of Cambrian lobopodians (paraphyletic class Xenusia), from Dzik 2011 fig 3. Compare this stylised mode of illustration (a bit like Greg Paul's dinosaur silouhettes) with Monge-Nájera & Hou's "photorealistic" illustrations of many of the same taxa. Dzik's stratigraphic-evolutionary phylogeny is based strongly on the presence or absense of large grasping appendages, which results in two main evolutionary lines, lobopodian and proto-arthropod. *Siberion* and *Megadictyon*, decsribed on this page, are on the right of the diagram, and one can see the obvious similarity (at least in these reconstructions) with *Kerygmachela*. *Xenusion* here becomes a "metataxon" at the base of the panarthrpod tree, both because of its generalised morphology and its early stratigraphic record. This phylogeny differs from many of the cladograms shown earlier, although the division into lobopodians (shown on the left) and protoarthropods and arthropods (shown on the right) is in keeping with Liu et al 2011, and even with Ma et al 2009's "Archonychophora" clade

Paleontological research over the last six years has recovered several extraordinary Early Cambrian lobopodians, specifically *Jianshanopodia* and *Megadictyon* from the Chengjiang Fauna of China, and *Siberion* from the Lena River of Siberia. Their compelling status as candidates for stem-group arthropods (we have used the informal term "protoarthropod" to rever to this grade) derives from characters shared with anomalocaridids or proto-anomalocaridids. These include generally large size, robust, annulated frontal grasping appendages with a row of strong spines along the inner margin, and segmentally repeated midgut glands (caecae-like structures). (Edgecombe 2009, Dzik 2011)

The same kind of segmentally repeated midgut glands is also found in both advanced arthropods, primitive true arthropods such as *Leanchoilia*, and protoarthropods such as *Kerygmachela* and *Pambdelurion*, as well as Jianshanopodia, Megadicyton, and Siberion. The detailed structure of these glands, consisting of an internal structure of lamellae on a submillimetric scale, illustrates the arthropod affinities of these advanced lobopodians (Edgecombe

2009).

Although the grasping arms of *Jianshanopodia, Megadictyon*, and *Siberion* differ from the anomalocaridid frontal appendages that first appear in *Kerygmachela* and *Pambdelurion*, in that the latter are more sclerotized (stiffened) and arthropodized, (having pivot joints and membrane between the stiffened regions), their equivalent position and general structural similarity strongly support their homologous nature (i.e. they are the same type of structure, with the same evolutionary origin, although found in different species)

There is however some variation among these early forms in that *Jianshanopodia* has complex branched appendages and a sucking pharyngeal mechanism, whereas *Megadictyon* possesses anomalocaridid-like 'Peytoia' or pineapple-ring-shaped slicing mouthparts (Liu et al 2008 p.280), and a ventrally (downward-facing) positioned mouth. The ventral mouth is an advanced feature that is shared with arthropods and, although already acquired in the basal proto-arthropod *Pambdelurion* is absent in the very similar and contemporary *Kerygmachela*. Here, as with the arthropodised but otherwise unexceptional lobopodian *Diania* we have another instance of mosaic evolution among parallel and related but distinct evolutionary lines, with the more primitive *Megadictyon* being more advanced in this regard than the ortherwise more specialised *Kerygmachela*. (Edgecombe 2009)

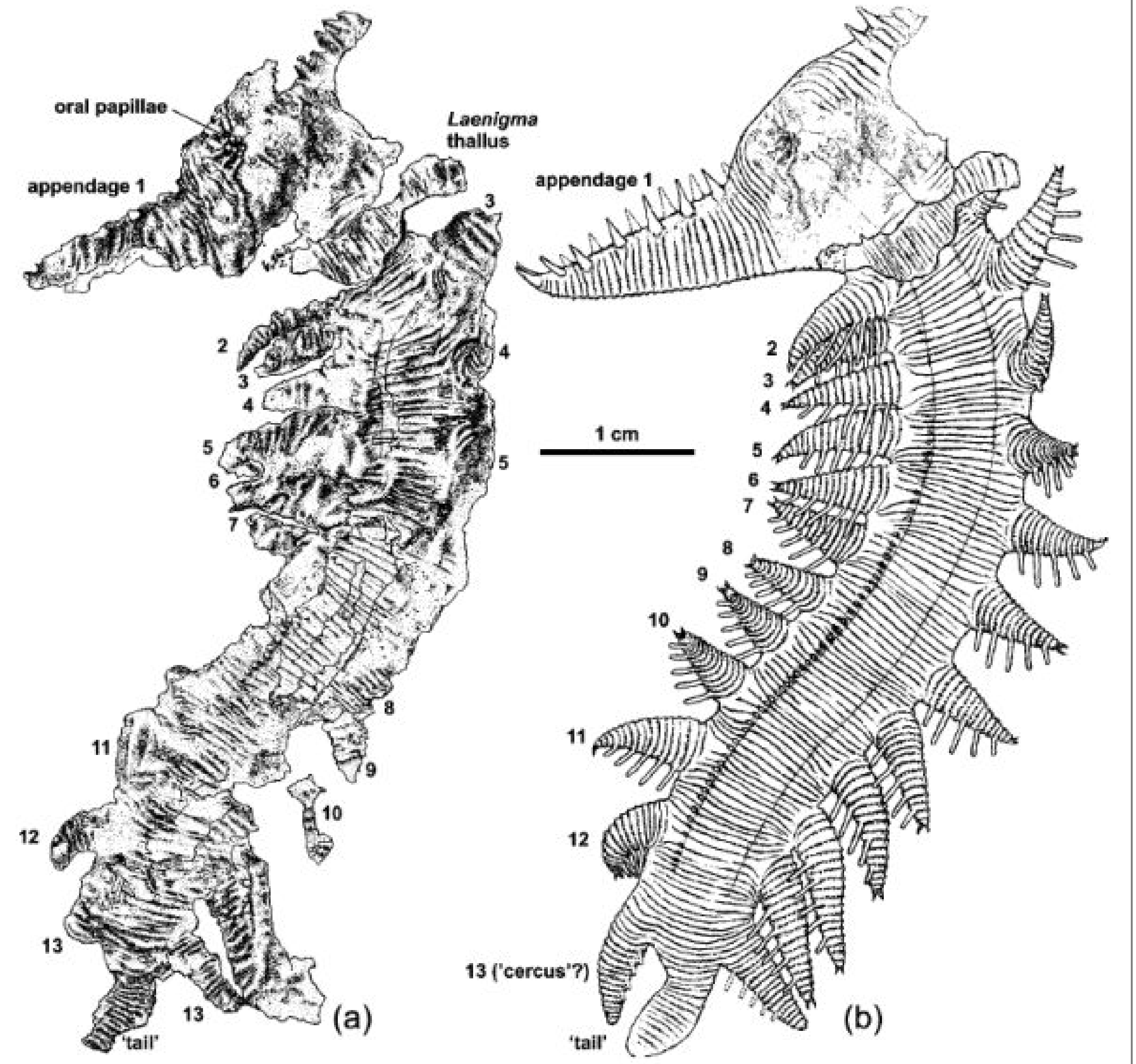
In this way, both prey capture (grasping arms), oral processing (pineapple ring mouthparts) and digetsion (specialised gut morphology) are advanced over the earky lobopodian condition, and would clearly have provided a great adptive advantage to these precursors of the arthropods. Yet by the Atdabanian and Botomian ages, these innovative panarthropods had already been morphologically surpassed by their euarthropod descendents. Proto-lobopodians (*Mureropodia*), several grades of lobopodians (*Aysheaia*, Xenusiids, *Hallucigenia*, Luolishaniids, *Diania*, etc), Siberiids, both basal (*Kerygmachela*) and advanced (*Opabinia*, *Anomalocaris*) dinocaridids, stem arthropods, great appendage arthropods, early trilobites, and proto-chelicerates and proto-crustaceans all co-existed in a highly diverse ecological setting, in which panarthropods were represented by a great-chain-of-being-like unbroken continuum from unarmoureed and armoured scalidophoran worm through a great morphological and evolutionary diversity of lobopodians to an even greater diversity of arthropods. It was a world very different from our own, but just as rich and unique MAK120501

Descriptions

Siberion lenaicus Dzik 2011

Horizon: Sinsk Formation of Lena River, Siberia, Botomian, *Bergereniellus gurarii* or early *B. asiaticus* trilobite Zone. Early Cambrian,

Phylogeny: Panarthropoda : *Aysheaia* + (Tardigrada + (various lobopodia + Onychophora + (more lobopodia + (*Jianshanopodia* + (*Megadictyon* + paraphyletic Dinocaridida + (*Schinderhannes* + Arthropoda)) + *))))



Siberion lenaicus **A** Camera lucida drawing of the holotype ZPAL V37/1. **B**. Interpretation of the holotype specimen with tentative restoration of appendages. Illustration and caption from Dzik 2011 fig 2.

Characters: 'Tail' with annulation, a row of minute tubercles on sides of the body with about 9 annuli per appendage pair; all 12 postoral appendage pairs of similar size and shape bear probably tubular extensions, serially emerging from annuli; the cylindrical gut probably lacks caeca. ILike *Jianshanopodia*, and *Megadictyon*, *Siberion* is a large lobopodian with These ae a prominent grasping first pair of appendages, reduced proboscis in relation to *Aysheaia*, tail-like terminal extension of the body; and appendages with weakly sclerotised serial gill-like structures extending dorsally from some annuli.

Comments: Dzik 2011 coined the monotypal Order Siberiida and family Siberiidae for the three genera *Siberion*, *Jianshanopodia*, and *Megadictyon*. This is a paraphyletic or evolutionary grade, of transitional forms intermediate between lobopodians and protoarthropods, not a monophyletic clade. The large grasping appendages are very similar to those of the anomalocaridids and indicate predatory habits. Unlike the anomalocaridids there are no flaps or arthropodial appendages. So far, *Siberion* has not been ranked cladistically. As *Jianshanopodia* and *Megadictyon* have been variously considered lobopodians (Ma et al 2010) and protoarthropods (Liu et al 2011), *Siberion* can be placed there as well. This specimen is rather smaller than its Chengjiang equivalents, about 5 1/2 rather than 20 cm in length. MAK120501

On a depressing note, Dzik reports that there is little chance of additional specimens being found at this fossil locality as it was recently destroyed by commercial fossil collectors (Dzik 2011). While we support responsible fossil collecting, it is essential for science that those rare and special regions where important fossils occur are safeguarded from abuse and destruction

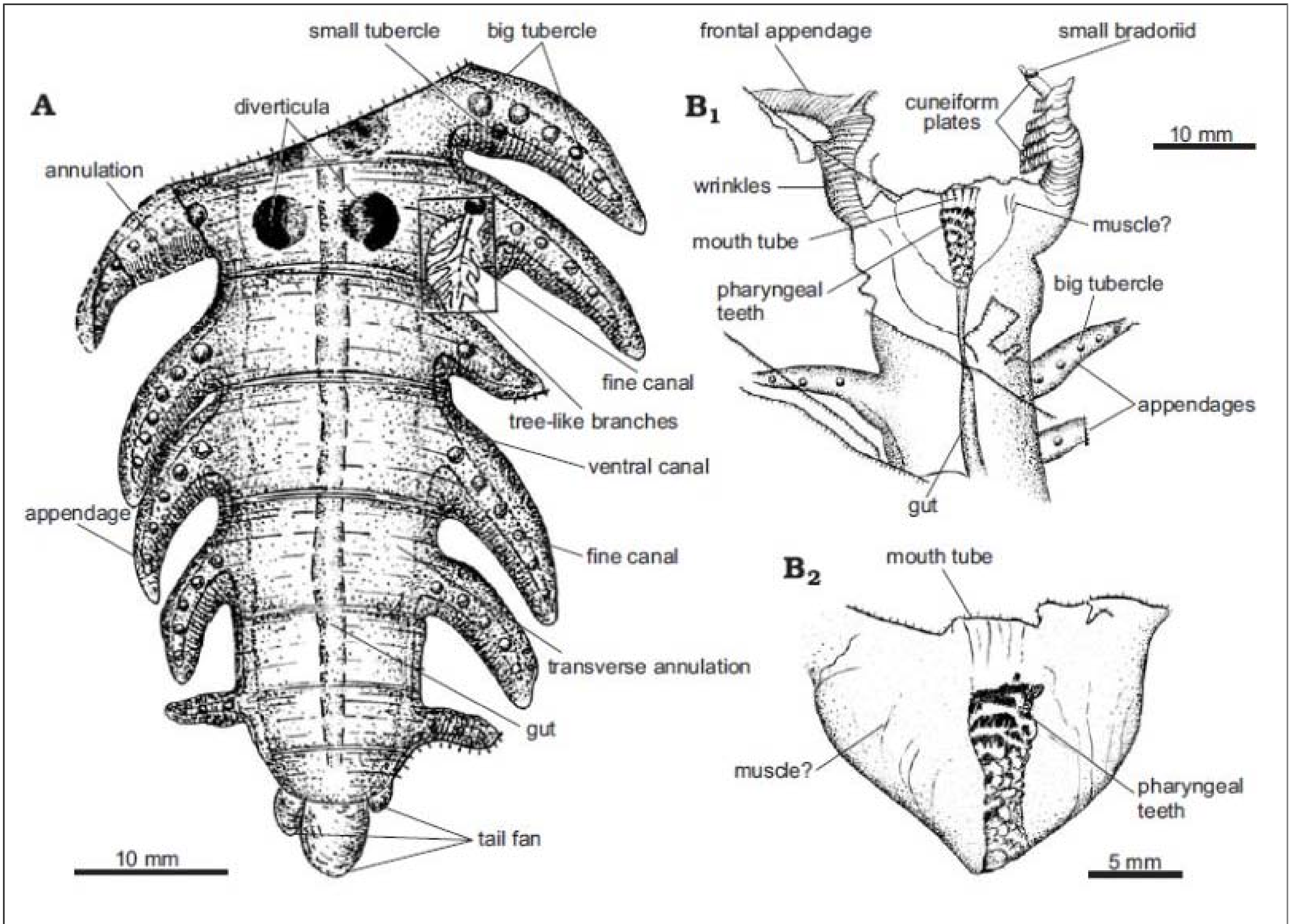
Reference: Dzik 2011

Jianshanopodia decora Liu et al., 2006

Horizon: Helinpu (Chiungchussu) Formation, Yu'an-shan Member (Eoredlichia Zone), Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Panarthropoda **:** *Aysheaia* + (Tardigrada + (various lobopodia + Onychophora + (more lobopodia + (*Siberion* + (*Megadictyon* + paraphyletic Dinocaridida + (*Schinderhannes* + Arthropoda)) + *))))

Characters body length (excluding appendages) ~22cm, centrally situated mouth; pair of strong frontal appendages equipped with a series of cuneiform plates. trunk region with at least nine segments, each bearing a pair of complex appendages with two rows of tubercles on their dorsal side, with tree-like or lamellate branches protruding from the tubercles. Three small lobes seem to be arranged into a tail fan . (Liu et al 2006b).



Janshanopodia decora, camera lucida drawings, showing morphology evident from the Chengjiang fossils. **A**. A sketch drawing of the specimen ELI-J0005A, demonstrating all available features. **B**. specimen ELI-J0001. B1, the anterior part of *Jianshanopodia* , showing the strongly wrinkled frontal appendages, mouth tube and funnel-like pharynx structures; B2, enlargement of the funnel-like pharynx structures of the same specimen. Illustration and caption from Liu et al 2006b fig.2.

Comments: As a rare truly transitional form, *Jianshanopodia* combines characteristics both of primitive xenusian lobopodians such as *Aysheaia* and *Xenusion* with the most primitive protoarthropods like *Kerygmachela* and *Pambdelurion*. Liu et al 2006b placed it in the family Xenusiidae, and more recently Dzik (2011) transferred it to his new ordinal rank taxon Siberiida. But the features *Jianshanopodia* shares with *Xenusion* - large cylindrical body with annulations and stout and strong lobopods each bearing bases of serial tubercles - would simply be primitive (plesiomorphic) for large lobopodians as a whole, and most cladograms are unanimous in placing it above a paraphyletic lobopodia. The features shared with protoarthropods are more evolutionarily significant. *Jianshanopodia* is the most basal taxon to show specialization and differentiation of limbs, such as frontal appendages or trunk limbs. (Liu et al 2011 fig. S1). It shares with Early Cambrian protoarthropods*Pambdelurion* and *Kerygmachela* pairs of mid-gut diverticula, a tail fan, a mouth cone, frontal pharyngeal structures and a pharynax are surrounded by the bases of large grasping frontal appendages. But unlike the segmentally arranged, paddle-like, movable side flaps of

Pambdelurion and *Kerygmachela*, *Jianshanopodia* possesses distinct complex appendages with tree-like or lamellate branches, and may throw new light on the origin of biramous limbs. (Liu et al 2006b) In other respects though, *Jianshanopodia* seems to be too primitive to serve as a biramous arthropod ancestor, and as with the arthropodisation of *Diania* may serve as a "prophetic" form, and an example of mosaic evolution. there is also an ecomorphic distinction, in that the presence pof strong complex limbs imples a walking or crawling rather than a swimming lifestyle. In any case. with its fascinating combination of primitive and advanced characteristics, *Jianshanopodia* represents a non-missing link between loboipods and arthropods, just as loboipods are a link between worms and arthropods. MAK120501

Megadictyon haikouensis Luo & Hu, 1999

Horizon: Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Panarthropoda **:** *Aysheaia* + (Tardigrada + (various lobopodia + Onychophora + (more lobopodia + (*Siberion* + *Jianshanopodia* + (paraphyletic Dinocaridida + (*Schinderhannes* + Arthropoda) + *)))))

Characters: *Megadictyon* alone: Heteronomous annulation (Daley et al 2009 cladogram, supplement fig S3). In common with more derived taxa: paired, segmentally arranged midgut glands; - *Megadictyon* Edgecombe 2009) fig 3; Circumoral structure plate-like with teeth at inner margins of plates. (Daley et al 2009 cladogram, supplement fig S3); Lobe-like trunk limbs without spines or tubercles Liuetal2011 fig. S1, ventrally positioned mouth (Edgecombe 2009)

Comments: *Megadictyon* cf. *haikouensis* had a head bearing caecae-like structures resembling those of the proto-trilobite *Naraoia* and some chelicerates, and possesses anomalocaridid-like 'Peytoia' mouthparts and grasping frontal appendages. These latter two features are shared with the AOPK (Anomalocaris-Opabinia-Pambdelurion-Kerygmachela) grade of protoarthropods (ref Cambrian lobopods) showing the advanced and transitional nature of this taxon. MAK120501

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Panarthropoda Classification

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Luolishaniidae
                `--+==Siberiidae
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

Contents

The following classification is from Cavalier-Smith (1998), Dzik&Krumbiegel1989 and Hou and Bergström. The following incorporates the list from the Wikipedia page Xenusiid and includes a number of monotypal taxa. The Onychophora is here made a paraphyletic taxon to avoid innumerable unplaced taxa that don't firt in the crown group. In addition, Cambrian lobopodians were at least morphologically closer to recent onychophores as shown by the fact that they would frequently cluster in cladistic analyses (e.g. Ramsköld & Chen (1998) Liu et al 2011) which at least indicates a phenetic similarity. Even so, this risks making the Onychoiphora into a watsebasket taxon. In any case, since the precise evolutionary relationships of these animals is still so uncertain, it should not be taken too seriously MAK120424

Superphylum Ecdysozoa Aguinaldo et al. 1997 (cont.)

Phylum Lobopodia Snodgrass, 1938 (= Protarthropoda Lankester, 1904 = Lobopoda Cavalier-Smith 1998 ; soft cuticle; unjointed limbs with terminal claws ; both muscles and hydraulic pressure involved in locomotion; evolutionary grade, Camb-Rec).

Subphylum Onychophora Grube 1853

Class Xenusia Dzik & Krumbiegel, 1989(Paleozoic Lobopodians, traditionally included under Onychophora - paraphyletic/ancestral panarthropod grade - Cambr - Sil)

Order unspecified

Mureropodia (intermediate between priapozoa and lobopodia)

Order Protonychophora Hutchinson 1930 (ancestral to other lobopodians)

Family Aysheaiidae Walcott, 1911 (monotypal, includes only Genus *Aysheaia*)

Order Xenusiida Dzik & Krumbiegel, 1989(paraphyletic taxon for Cambrian lobopodians; includes the Orders Scleronychophora Hou & Bergström 1995, Paronychophora Hou & Bergstrom, 1995, and Archonychophora Hou & Bergstrom, 1995)

Family Cardiodictyidae Hou & Bergstrom, 1995 (monotypal taxon - should probably be synonymised with anther family)

Family Eoconchariidae Hou & Shu, 1987 (= Microdictyonidae) (monogeneric taxon)
Family Hallucigeniidae Conway Morris, 1977
Family Luolishaniidae Hou & Bergstrom, 1995 (filter feeders, reduced limbs, sedentary?)
Family Onychodictyidae Hou & Bergstrom, 1995 (monogeneric taxon - - should probably be synonymised with anther family)
Family Paucipodiidae Hou et al., 2004 (monotypal taxon)
Family Xenusiidae Dzik & Krumbiegel, 1989 (large early lobopodians)
Order Siberiida Dzik 2011 (large advanced forms with grasping appendages)
Family Siberiidae Dzik 2011
Class Euonychophora Hutchinson, 1930 (terrestrial onychophora, velvet worms, e.g. *Peripatus*, Cambrian? or Carb to Rec)
Subphylum Tardigrada Doyère 1840 (water bears, e.g. *Echiniscus*. Microscopic.Camb-Rec).
Subphylum Protarthropoda Lankester, 1904 (used here as paraphyletic bridging taxon between lobopodians and arthropods, and could be eqially placed in either phylum)
ClassDinocaridida Collins, 1996 (paraphyletic grade of swimming and gilled lobopodians, include Anomalocaridid superpredators Camb to Dev)
Order Radiodonta Collins 1996
Phylum Arthropoda von Siebold and Stannius 1848 (jointed exoskelton Camb-Rec).

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Panarthropoda: Dendrogram

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Luolishaniidae
                `--+==Siberiidae
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

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Panarthropod phylogeny.

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
  PANARTHROPODA
  |--Mureropodia
  `--+--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |  |--Xenusion
             |  `--Hadranax
             |--Orstenotubulus
             |--ONYCHOPHORA
             `--+--Paucipodia
                |--Microdictyon
                |--Archonychophora
                |  |--Cardiodictyon
                |  `--+--Hallucigenia
                |     |  |--Hallucigenia sparsa
                |     |  `--+--Hallucigenia fortis
                |     |     `--Hallucigenia hongmeia
                |     `--+--Onychodictyon
                |        `--Luolishaniidae
                |           |--Luolishania
                |           `--Facivermis
                |--Diania
                `--+--Siberion
                    |--Jianshanopodia
                    `--+--Megadictyon
                       `--+==DINOCARIDIDA
```

```
                                         `--ARTHROPODA
```

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Panarthropoda: References

Abbreviated Dendrogram

```
ECDYSOZOA
|==SCALIDOPHORA
`--+--NEMATOIDA
   |
   `--PANARTHROPODA
      |--Aysheaia
      `--+--TARDIGRADA
          `--+--Xenusiidae
             |--ONYCHOPHORA
             `--+--Luolishaniidae
                `--+==Siberiidae
                   `--+==DINOCARIDIDA
                      `--ARTHROPODA
```

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Facivermis

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Dinocaridida

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

Contents

The Cambrian apex preditor *Anomalocaris canadensis* (Dinocaridida - Anomalocarididae). This animal had unparalled vision by Cambrian, or even contemporary, standards. Note the stiff (not cuttlefish-like) swimming lobes.
Artwork by Katrina Kenny, commissioned by the University of Adelaide. (see also Everything Dinosaur
Picture Credit: Katrina Kenny/South Australian Museum/University of Adelaide.

Anomalocaris

Cambrian superpredator

early Cambrian to Early Ordovician
nektonic apex predator
length: half a meter or more

Anomalocaris canadensis was about 60 cm long, which may not seem much in today's terms, but was huge relative to anything else around during the Cambrian and Early Ordovician (some specimens seem to have been even larger, a meter in the case of one early Ordivician giant). For tens of millions of years this slow-moving swimmer dominated Cambrian seas. It had a pineapple-ring mouth and a pair of long spiky grasping appendages. It was originally believed to be three separate animals (the pineapple ring mouth was thought to be a jellyfish (*Peytoia*) - the large lobed body a sponge, the grasping appendages the body of a crustacean - that was the original "Anomalocaris"). Swimming was accomplished by means of undulations of fin-like appendages along the side of the body (and as shown in the above illustration, these would have been stiff, like blades of fan, not soft like those of a cuttlefish or sea slug.

Anomalocaris early on acquired something of a mystique rare among prehistoric invertebrates. Because of its relative size and carnivorous habits (for a number of reasons we do not consider the hypothesis that it was a suction feeder of plankton or worms persuasive), it has become a kind of *T. rex* of the Cambrian, a reputation that was probably well deserved.

Other Cambrian creatures like *Opabina* (itself a close cousin, unexpectedly) and *Sanctocaris* (a stem Chelicerate) were also probably predators, but at 7 to 10 cm are much smaller.

We now know of more than a dozen different species of Anomalocaridids, which would only be a fraction of their original diversity. They have been given their own class , Dinocaridida, the "terrible shrimps" , although calling these creatures shrimps is about as appropriate as calling dinosaurs lizards (*sauros*); such are the limitations of Greek and Latin suffixes. MAK990601, revised and updated MAK120507,

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notes:

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Dinocaridida: Dinocaridida

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

Contents

Taxa on This Page

1. Dinocaridida

Class Dinocaridida

Introduction

(The first few paragraphs are adapted and modified from Wikipedia - MAK120507):

The Dinocaridida (sometimes spelled Dinocarida, but the second 'id' is linguistically correct Hou et al 2006) is a linnaean-evolutionary taxon (paraphyletic, not cladistic) of early Paleozoic arthropod-like marine animals that are best known (whether actual abundance or taphonomic bias) from the early and middle Cambrian, but continue dthrough to at least the Devonian, and very likely later. IThe name comes from Greek, "deinos" and "caris," meaning "terror shrimp" or "terror crab," due to their crustacean-like appearance and the hypotheses suggesting that members of this class were the apex predators of their time.

Dinocaridids are bilaterally symmetrical, with a non-mineralized cuticle and a body divided into two major tagmata, or body-sections. The frontal section should have one or more claws found just in front of the mouth, which is located on these creatures' underside. The body will possess thirteen or more segments, each with its own gill branch and swimming lobe. It is thought that these lobes moved in an up-and-down motion to propel the animal forward (Usami 2006); although commonly imagined as similar to the fins of a cuttlefish, the lobes were rigid and would have been more like blades of a fan or paddles.

After original uncertainty, it is now agreed that Dinocaridids are a stem group to arthropods, intermediate between Lobopodia and true arthropods.

(Most of the rest of the page is taken more or less verbatum from Chris Clowes Peripatus website, and quotes mostly from a now dated overview essay by Jeffrey Minicucci, which is for now quoted here verbatum. This material no doubt needs to be modified or added to in the light of newer discoveries and research. Additional comments by yours truely are dated accordingly. MAK120512)

> "Anomalocarid arthropods have been reported from Cambrian fossil lagerstätten localities around the world. While exceptional fossil preservation, skilful preparators, and comprehensive studies have revealed much about the palaeobiology of some of these formerly enigmatic metazoans, much work still needs to be done in order properly to address the more detailed aspects of anomalocarid anatomy and the interrelationships among the genera and species placed within the family.
>
> "The studies of the mid to late 1990s have presented us with intriguing revelations, and the most complete fossils of these animals. The level of current research and discovery is at its most promising since Whittington and Briggs (1982) pieced together the first reasonable reconstruction of *Anomalocaris*. Collins (1996) has provided a complete account of the history of *Anomalocaris* reconstructions.
>
> "While the studies of the previous decade tended to be dominated by the publications of Whittington, Briggs, and Conway-Morris, attention in the mid to late 1990s has shifted towards three investigative ‘blocs’ represented by Hou, and Bergström; Chen, Zhou, and Ramsköld; and Collins. The studies of these competing researchers are characterized by descriptions of complete anomalocarids, identifications of new anomalocarid genera, and/or more aggressive attempts to define the family systematically (*e.g*. Chen *et al.* 1994; Collins 1996; Hou *et al.* 1995; Ramsköld 1995). Despite the thoroughness of the above studies, questions still remain unanswered.
>
> "Briggs (1994) and Ramsköld (1995) are correct in demanding a phylogenetic analysis of the Anomalocaridae. Since the anomalocarid bauplan appears to be more variable than previously assumed, efforts should be directed towards compiling a new, complete list of diagnostic characters for the family. A revised list of diagnostic characters could ultimately affect the relationship between the Anomalocaridae and other possible families within Collins (1996) proposed Order Radiodonta and Class Dinocarida (although the corrected spelling is Dinocaridida). Both of these taxa are important in the effort to place anomalocarids and other similar problematic metazoans (*e.g*. *Opabinia regalis*, *Kerygmachela kierkegaardi*) into an eventually coherent phylogenetic context" - Minicucci 1999.

Morphology

Mouthparts

> "Using deductive logic, Rudkin (1979) postulated the existence of a large Cambrian predator responsible for inflicting wounds on individuals of the

trilobite *Ogygopsis klotzi*. The association of this trilobite with *A. canadensis* grasping appendages from the Middle Cambrian Stephen Formation (*Bathyuriscus-Elrathia* Zone, *O. klotzi* faunule) prompted him to consider the enigmatic *A. canadensis* as the culprit. Other authors have since envisioned *Anomalocaris* a trilobite terror (*e.g*., Briggs and Mount 1982; Babcock and Robison 1989; Babcock 1993).

Trilobite's eye view of *Laggania cambria*. Life size model (about 60 cm) created by Espen Horn. This model presents a very plausible reconstruction of interior and exterior teeth. However Daley et al. 2009 pp.S3-4 argue strongly that only *Hurdia* has mouthparts with extra rows of teeth within the central opening. *Anomalocaris* may have used a different feeding strategy, such as using its arms to break open trilobites. (the appendages of *Laggania* are not well known).

Image from Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

"In direct opposition to such studies, Hou, Bergström and Ahlberg (1995) suggest that anomalocarid mouthparts could not 'bite off pieces of trilobites and other arthropods with a hard exoskeleton' (p.181) and further allege that the mouthparts of previously reported anomalocarids were 'not directed ventrally as in previous reconstructions' (p.163). Alleged backward-facing mouthparts present in their *Parapeytoia yunnanensis* specimen are introduced as evidence. A major flaw in their argument is that the evidence derives from an unrepresentative sample. There are assorted complete specimens of other genera confirming the presence of mouthparts in the familiar, ventral position (see Chen *et al.* 1994; Collins 1996). Further, both the illustration (Hou *et al.* 1995, p.173, Fig. 10) and description suggest that the mouthparts of *P. yunnanensis* are, perhaps, different from the typical '*Peytoia*' jaws of other anomalocarids.

"Both in appearance, and in proposed function, typical anomalocarid mouthparts must have been deadly weapons possessed of substantial cutting and crushing power. Certainly, the fact that mouthparts are more readily preserved attests to their durability. The recommendation of ... Chen and Zhou (1997) that anomalocarids should be sorted among different Dinocaridid orders because of alleged differences in mouthpart morphology is probably not warranted.

"The anomalocarid referred to as *Hurdia* by Collins (1992) is described as having mouthparts with an extra set of teeth that would have lined the interior of the buccal cavity (Whittington and Briggs 1985). This configuration, suggestive of a 'pharyngeal mill', could have been even more effective at processing hard-bodied prey" - Minicucci 1999.

"The aperture itself [of *Anomalocaris*] was rectangular, not circular. It could not be closed; the teeth did not meet in the middle. The jaw could be opened, however, to admit prey, and the plates could then be pulled together to draw the prey into the mouth. This would have had the effect of cracking or breaking the exoskeleton of an arthropod. Indeed, trilobites are known with healed bites in the edge of the exoskeleton that may have been made by the jaw of *Anomalocaris*. Some specimens of the jaw preserve additional teeth inside ..., which lined the wall of the mouth and further processed the food" (Briggs et al. 1994, pp. 201-202). According to Daley et al. 2009 p.S5, these would be *Hurdia victoria*, originally referred to as *Anomalocaris nathorsti* MAK120511

Lateral Lobes

"Linear striations present on the surface of the lateral lobes of anomalocarids have been reported in several genera. Chen *et al.* (1994) have interpreted these features as a vein network. Hou *et al.* (1995) simply note them as 'lines'. Collins (1996) suggests that *A. canadensis* and *L. cambria* possess gills on the lateral lobes, but no identifiable gill-like structures appear on the lateral lobes of his photographed specimens. Collins' complete specimens of *A. canadensis* indicate a virtually 'naked' animal, without any surface ornamentation or raised features of any kind on the integument (pers. obs.). Examinations of *L. cambria* material by Whittington and Briggs (1985) suggest the equivocal presence of linear markings on the lateral lobes. Both *A. saron* and *A. symbrachiata* in Chen *et al.* (1994) seem to preserve traces of setae / gill-like structures (in addition to the vein network) on several of the lateral lobes. In these specimens, the alleged setae appear to lie on the ventral surface of each lateral lobe. Setae performing an alleged respiratory / gill function are usually attached to the distal edge of either a thin or paddle-shaped exopod in Cambrian arthropods and trilobites, but seeing the setae originate from the exopod surface is more complicated to explain (a similar situation exists in *Opabinia regalis*). In order to address the inconsistencies, we must formulate a diagnosis for correctly identifying what constitutes an anomalocarid gill. Hou and Bergström (1997) have wisely and justifiably identified problems with the fundamentally colloquial use of the term 'gill' in relation to descriptions of other Burgess Shale-type arthropods. If neither *A. canadensis* nor *L. cambria* possessed external gills, other locations for organs of gas exchange must be found. Further preparation of existing specimens or discoveries of new material should help to settle the issue";

"Chen *et al.* (1994) reported the existence of 'two exsaggital rows of segmentally repeated ventral or internal structures of unknown function, preserved as black or light-reflective patches' (p. 1308) in the specimens Hou *et al.* (1995) would later identify as *A. saron* and *A. symbrachiata*. They further allege that these nodular structures are 'composed of bunches of fine, curved threads' (Chen *et al.* 1994, p. 1305) and describe them as 'equalling the nodular mineralized areas' described in *Anomalocaris nathorsti* (p.1306). Collins (1996) mentions the same structures in his discussion of the transverse mineralized strips (lateral lobe supports) on the ventral surface of *L. cambria*. I believe that any attempts to draw a connection between the nodular structures identified by Chen *et al.* with the club-shaped structures found on the ventral surface of *L. cambria* are premature. Such structures appear on the lateral lobes as the terminal ends of the lateral lobe support rods. The nodular structures discussed by Chen *et al.* (1994) are present only on the trunk region, and are isolated from each other, not being transversely connected by mineralized strips. The possibility could exist that the nodular structures represent caeca. In Ramsköld *et al.* (1997), the Lower Cambrian petalopleuran xandarellid *Cindarella eucalla* shows evidence of caeca preserved as serially-repeated, dark stains with an 'internal system of approximately transverse or slightly splayed tubules' (p.29). It is tempting to compare the thread-like structures observed by Chen *et al.* (1994) with these" - Minicucci 1999.

Cuticle

"Collins' complete specimens of *A. canadensis* confirm that there was no evidence of trunk annulation or external segmentation in this genus. The trunk region of *A. saron* in Chen *et al.* (1994) is described as having transverse lines, but the 'irregularity and wrinkling of the lines' (p.1305) suggests that these are most probably preservational folds caused during diagenensis and compaction of the carcass. Ramsköld (1997) has successfully demonstrated the existence of such misleading folds in naraoiid and tegopeltid arthropods. He has, however, hinted at the existence of certain undescribed genera with higher degrees of tagmosis possessing intersegmental trunk bars (Ramsköld 1995). A fact not discussed by researchers is the significant disparity between the virtually 'naked' soft-cuticle condition of *A. canadensis* and the high degree of tagmosis and sclerotization of *P. yunanensis*. According to the fossil evidence, while the most complete specimen of *P. yunanensis* (NIGPAS 115334) represents a substantial body moult (Hou *et al.* 1995), ecdysis in *A. canadensis* would seem to have been limited to moulting of the grasping appendages and mouthparts (Collins 1996). Persistent collecting seems to show that Royal Ontario Museum specimens of *A. canadensis* remains tend to consist of either a complete carcass or isolated mouthparts and grasping appendages (as seen in Collins 1996). Anything in between consists of a smeared blob (pers. obs.). As a consequence, it can be inferred that *P. yunnanensis* had a more significantly sclerotized cuticle. An increase in the degree of cuticle sclerotization may be correlated with an increased complexity of tagmosis in each genus"

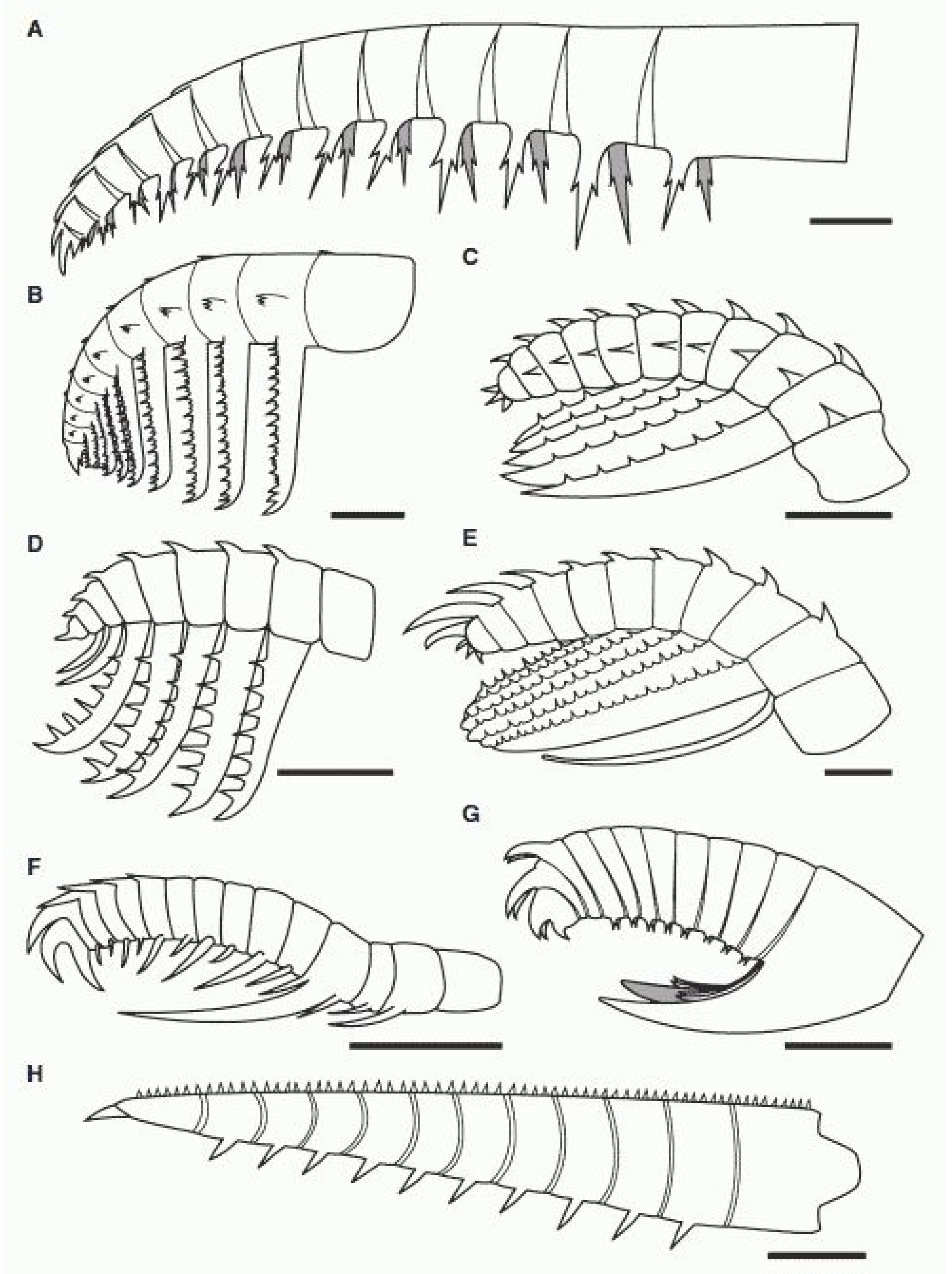
"The high degree of anatomical detail preserved in specimens of Chengjiang anomalocarids attests to the quality of Chengjiang fossils. If the criticisms of Hou and Bergström (1997) are accepted at face value, it is arguable that the apparently smooth, featureless surface of the soft-cuticle of Collins' Burgess Shale *A. canadensis* is an artefact resulting from comparably inferior preservation associated with fossils from the Burgess Shale biota. The small size of reported Chengjiang anomalocarids correlates with the assumption that their remains represent juveniles, while Collins' described *A. canadensis* specimens represent adult organisms. Whether the preservational environments or different ontogenetic stages account for the differences in visible anatomical details is unclear" - Minicucci 1999.

Tail

"The 'fantail' reported in *A. canadensis* (Collins 1996), *A. saron*, and *A. symbrachiata* (Chen *et al.* 1994) presents a comparative problem. Phylogenetically, it is certainly not homologous with a telson, and no other arthropod has a similar posterodorsally placed structure. The presence of caudal furcae in the Chengjiang material is certainly an arthropodan character, but the 'fantail' complex is a uniquely derived feature. Part of the problem in adequately classifying the anomalocarids is that they developed a significant amount of derived features masking their ancestry after diverging from basal arthropods. Unclear is whether the 'fantail' elements were rigidly fixed in position, or moveable, like the pliable lateral lobes. If the animals could adjust their orientation with respect to the flow of water, they may have stabilized the anomalocarid body in a manner comparable to the way in which rudders stabilize ... aircraft in the air" - Minicucci 1999.

Grasping Appendages

"Recent studies dramatically emphasize the variations found in frontal grasping appendages among anomalocarid genera. Described examples are the relatively stout crushing claws of *A. canadensis* (Collins 1996); the wicked impaling claws of *A. symbrachiata*; and the long, slender claws of *A. saron* (Chen *et al.* 1994; Hou *et al.* 1995). The morphology of the grasping appendages of *L. cambria*, *Cassubia infercambriensis* and the unknown 'appendage F' anomalocarid (Briggs 1979) may militate against the view that all anomalocarids were active hunters



Comparative sketches of anomalocaridid frontal appendages from the Burgess Shale and the Chengjiang Fauna, showing the morphological diversity of this group . A, *Anomalocaris canadensis*, (modified from Briggs 1979). B, 'Appendage F' of Briggs 1979. C, *Hurdia victoria* appendage morph A (drawn from Daley et al. 2009). D, *Hurdia victoria* appendage morph B (drawn from Daley et al. 2009). E, ?*Laggania* F. *Amplectobelua symbrachiata* (modified from Hou et al. 1997). G, *Amplectobelua stephenensis*. H, *Caryosyntrips serratus*. All scale bars represent 10 mm. Clearly, anomalocaridids occupied different ecological niches and specialise din different prey types and feeding strategies. Drawing from Daley & Budd 2010 fig.1. Also at Amplectobelua stephenensis. Burgess Shale Fossil Gallery. Virtual Museum of Canada.;

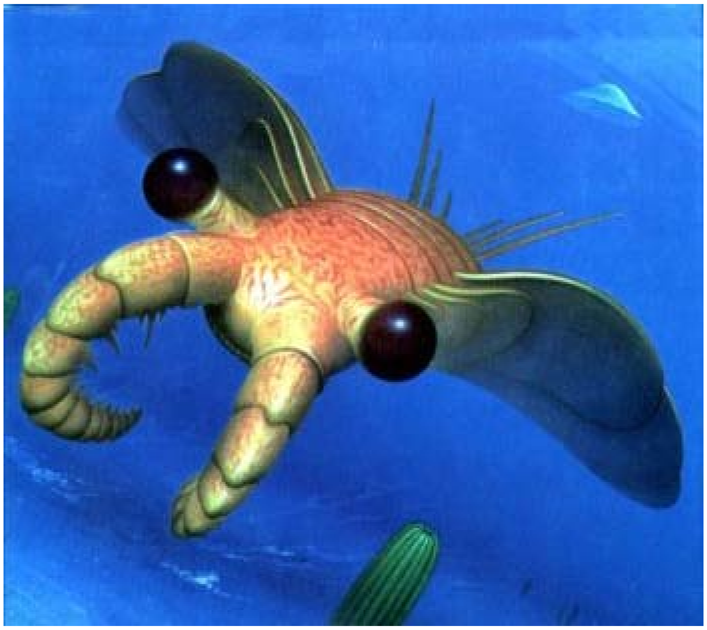
(Whittington and Briggs 1985) because such appendages could be interpreted as the instruments of sweep-feeders (see discussion by Dzik and Lendzion 1988, and Nedin 1995). The Emu Bay Shale anomalocarid *Anomalocaris briggsi*, known only from grasping appendages with extensive comb rows on all but the first podomere endites, also seems to be a confirmed sweep-feeder (Nedin 1995). Nedin alleges that the serrated endites on the first podomere were capable of impaling prey caught within the flexed appendage. In sharp contrast to the morphology of the fourth podomere endite on the grasping appendage of the confirmed impaler *Amplectobelua symbrachiata* (Chen *et al.* 1994), these particular endites show no appreciable increase in length relative to the lengths of the other podomere endites, casting some doubt on their effectiveness as impaling organs. The morphological differences between the grasping appendages of *A. briggsi* and those of other species of *Anomalocaris* are probably both sufficient and necessary to warrant assigning this species to a new genus. The grasping appendages of *P. yunnanensis* are worth mentioning because these differ significantly from those of other described anomalocarids. According to Hou *et al.* (1995), a complete appendage consists of five segments the lowest number yet reported in any genus. Rather than being composed of several podomeres, the proximal half of the grasping appendage

> consists of a long, stout podomere, and the arrangement of endites on each subsequent podomere gives the distal half of the appendage an almost chelate appearance. An approximately chelate grasping appendage has not been reported in any other anomalocarid"
>
> "Superficially comparable are the frontal grasping appendages of the megacheiran fortiforcipid *Fortiforceps foliosa* (Hou and Bergström 1997; p.36, Fig. C). The functional morphology and development of the above type of appendage in anomalocarids merits further investigation. The endites are long, but the fact that there are only four probably indicates that they did not form a comb filter-feeding mechanism. Flexing the four distal podomeres would bring them into contact, making the appendages seem better suited for picking and manipulating, as opposed to squeezing and crushing using a deadly 'bear-hug' embrace, as suggested by the morphology of 'typical' predatory anomalocarid appendages." - Minicucci 1999.

Here *Parapeytoia* represents the possibility of an intriguing transitional form, assuming that the great appendages of dinocaridids and megacheirians are homologous MAK120511

Eyes

Primitive dinocaridids such as *Kerygmachela* and *Pambdelurion* were either blind or - perhaps more likely - had small simple eyes that did not easily appear in fossils, More advanced forms such as *Opabinia* and Anomalocaridids are extraordinary in possessing very large, compound eyes. This has been shown by recently discovered specimens of *Anomalocaris* from the Emu Bay Shale, South Australia. These fossils exhibit well-preserved bulbous stalked compound eyes, 2-3-cm in diameter, very like the eyes of modern insects. The paleontologists were able to count the density of lenses and estimate how many would have been present in the living animal. From the abstract (Paterson et al 2011) (photos here):



Life reconstruction of *Anomalocaris canadensis* by Yukio Sato, showing the huge eyes, in a large animal a sign of a strongly visual preditor. This beautiful artwork appeared on the cover of Simon Conway Morris' *The Crucible of Creation*,

> "(The) preserved visual surfaces are composed of at least 16,000 hexagonally packed ommatidial lenses (in a single eye), [note: *Drosophila*, the common fruit fly, has about 800] rivalling the most acute compound eyes in modern arthropods [Larger specimens with correspondingly larger eyes would have had even more lenses]. The specimens show two distinct taphonomic modes, preserved as iron oxide (after pyrite) and calcium phosphate, demonstrating that disparate styles of early diagenetic mineralization can replicate the same type of extracellular tissue (that is, cuticle) within a single Burgess-Shale-type deposit. These fossils also provide compelling evidence for the arthropod affinities of anomalocaridids, push the origin of compound eyes deeper down the arthropod stem lineage, and indicate that the compound eye evolved before such features as a hardened exoskeleton. The inferred acuity of the anomalocaridid eye is consistent with other evidence that these animals were highly mobile visual predators in the water column. The existence of large, macrophagous nektonic predators possessing sharp vision—such as Anomalocaris—within the early Cambrian ecosystem probably helped to accelerate the escalatory 'arms race' that began over half a billion years ago" - Paterson et al 2011

It's worth comparing and contrasting the gigantic eyes of the proto-arthropod anomalocaridid with the equally huge - comparatively speaking - eyes of the advanced cephalopodian giant squid and the large (9 meter) ichthyosaur *Temnodontosaurus*. While each of these three animals were or are actively swimming giant preditors in their respective environments, anomalocaridids with their insect-like compound eyes hunted in the bright midwater photoic zone, whereas the other two with their large single lense camera eyes emphasise deep water and very little light. MAK120512

Carnivore, not Planktivore

It has long been suggested that *Anomalocaris* fed on hard-bodied animals, including trilobites.

There is a *Scientific American* article (and also I think a more in-depth article in *Paleobiology*) that mentions predation on trilobites, and has a photo of a trilobite with a big bite taken out of the side. Interestingly, trilobite eyes were apparently designed to give optimal upward facing vision - so as to detect something swimming at them from above. They would not have evolved such organs were there not a pressing biological need for them.

"The Emergence of Animals" by Mark A. S. McMenamin - which features Anomalocaris on p.91 (the trilobite photo - an *Olenellus robsonensis*, is on the facing page). Unfortunately I did not record the issue when I photocopied the article - it is most probably late 80s, maybe 1987." MAK990601

Some Cambrian trilobites have been found with round or W-shaped "bite" marks, which were identified in shape with the mouthparts of Anomalocaris. Stronger evidence that Anomalocaris ate trilobites comes from fossilised faecal pellets, which contain trilobite parts and are so large that the anomalocarids are the only organisms large enough to have produced them.] However, since Anomalocaris lacks any mineralised tissue, it seemed unlikely that it would be able to penetrate the hard, calcified shell of trilobites. (Nedin, 1999) - Wikipedia

It has been argued that lack of wear on anomalocarid mouthparts suggests they did not come into regular contact with mineralised trilobite shells. Computer modeling of the Anomalocaris mouthparts suggests they were in fact better suited to sucking up smaller, soft-bodied organisms (and could not have been responsible for many trilobite deformations). (Hagadorn, 2009) - Wikipedia. Yet The premise that anomalocarids had external teeth only and so were only inoffensive munchers of organic detritus or plankton makes as much sense to the present author as the theory that *T. rex* was a wussy scavenger.

The role of anomalocaridids as superpreditors is inferred by a number of mutually reinforcing factors such as large body size, robust spinose frontal appendages, mouth with a dentate or tooth-like margin (of no use to a filter- or succtionfeeder), size and form of the mid-gut glands, large coprolites containing trilobite remains (anomalocaridids being the only known anoimals large enough to have made them), streamlined body, lateral swimming flaps and tail fan that all imply strong swimming capabilities (again, unnesscery in a filter feeder, unless it had to escape predators, a Cambrian animal of anomalocarid size was too large tpo have had preditors), and large stalked eyes located at the side of the head (Just as the tyrannosaur as slow-moving scavenger hypothesis is refuted by that animal's binocular vision (evident from the position of the eyes as indicated by the shape of the skull), something a scavenger wouldn't requireas t has is no need to judge precise distance, so a giant plankton feeder or mud grubber with no obvious predators wouldn't have any use for the sharpest eyes in the Cambrian seas. All of which adds up to a highly visual apex predator), all provide mutually reinforcing evidence for a large animal adapted to tracking and capture of smaller animals (Paterson et al 2011), the Cambrian equivalent of a shark, a pliosaur, or a killer whale for example. Such an animal would have placed considerable selective pressures on prey that would have resulted in or contributed to an evolutionary arms race between the hunter and prey. MAK120511

Phylogeny and Evolution

Affinities

> "The majority of conclusions on anomalocarid functional morphology and anatomy in Hou *et al.* (1995) tend to be based on evidence from an unrepresentative sample. The described material of *P. yunnanensis* is hardly complete. Contrary to what Hou *et al.* (1995) clearly state in their paper, their best-preserved specimen of a single genus cannot reasonably serve as a template for redefining or dismissing the reconstructions of other anomalocarids. The

> ventral reconstruction (p. 180, Fig. 19) is problematical because there is no direct, conclusive evidence confirming the form of the anterior tagmata, and backward-facing position of the mouthparts and grasping appendages. It is ironic that Hou *et al.* choose 'the radial arrangement of circum-oral sclerites' (p. 163) as an homologous feature uniting aschelminthes and anomalocarids, while dismissing a virtual mountain of arthropod characters as irrelevant convergent features. Also problematical is their assertion that anomalocarids were dorsally covered in lanceolate scales. Such structures are allegedly identified in their specimens of *P. yunnanensis*, [they are not visible in the the photographs published in Hou *et al*. 1999 (figs. 77-78) - CC] *Anomalocaris saron*, and *Cucumericrus decoratus*. The scales are almost impossible to identify from the published photographs, casting doubt on the accuracy of the camera lucida drawings. The fact that Chen *et al.* (1994) did not observe the same markings in more complete specimens of the same genera casts even further doubt on the observations of Hou *et al.* (1995). The interpretation by the latter authors of '*Peytoia nathorsti*' (= *Laggania cambria* of Collins 1996) assumes that USNM 274142 represents a dorsal view of the animal showing 'transverse sets of lanceolate scales' (Hou *et al.* 1995, p.179, Fig. 17A). Collins (1996) has successfully proven that this particular fossil represents a ventral view, and that the so-called 'scales' are better interpreted as 'flexible rod supports of the lateral lobes' (p. 290). Thus one key piece of evidence for the existence of dorsal lanceolate scales evaporates. Rather than being scales, the markings observed (if they truly exist) in the other above genera could be artefacts of preservation / effects of Neogene weathering, wrinkling caused by decay of the carcass, or a surface wrinkling of the integument actually present in life" - Minicucci 1999

Cladograms

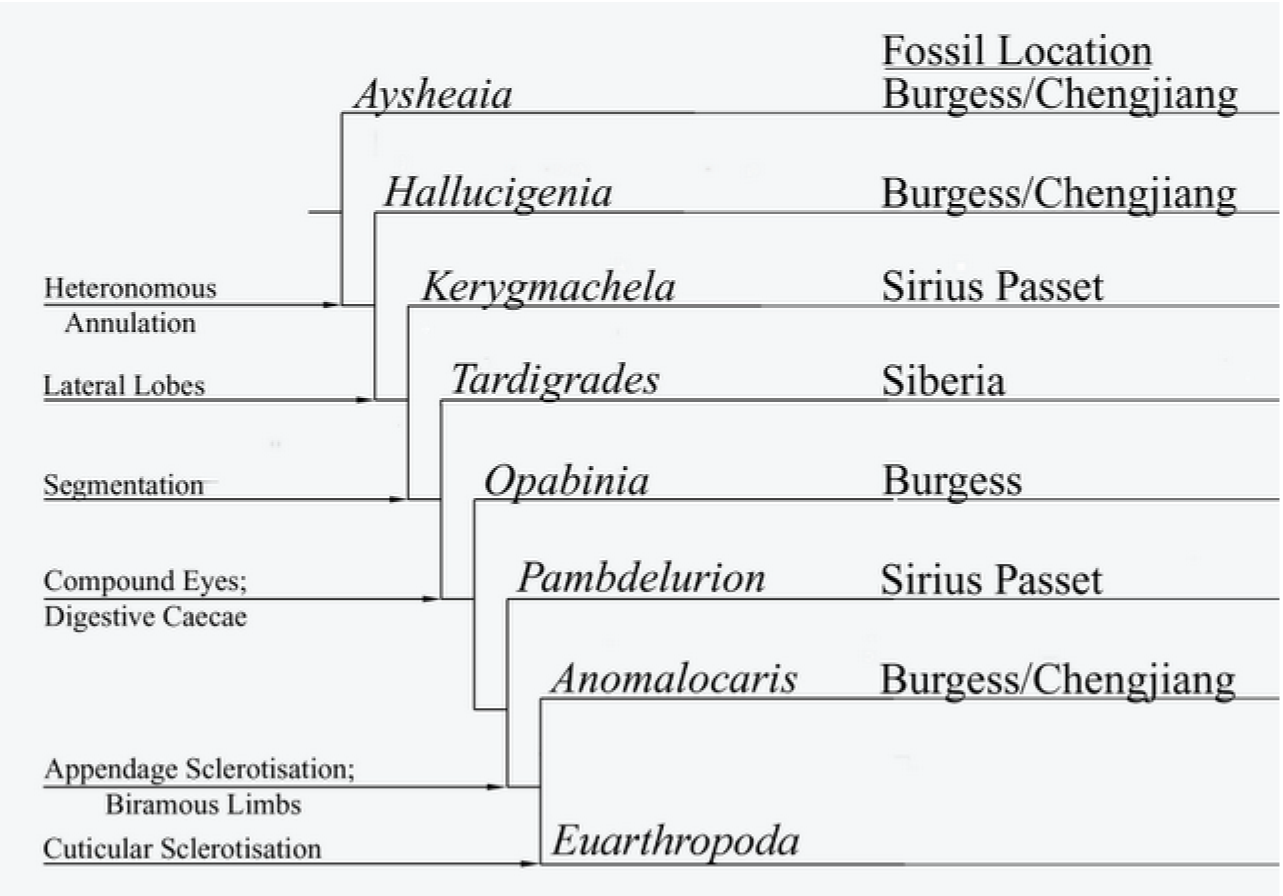
The following was written in 1999:

> "Of course it remains to be seen whether Collins' conclusions can be supported by a comprehensive cladistic analysis. Chen and Zhou (1997) do not even believe that anomalocarids comprise a family level taxon. Curiously, they place anomalocarids at the phylum level, but without providing a formal, comprehensive diagnosis, or cladistic analysis. Of prime importance is the need to identify and trace morphological trends relating to the acquisition and loss of characters. For example, at some point in their evolution, certain groups of anomalocarids ceased developing biramous trunk appendages in favour of retaining only the lateral lobes. Interpreted in an arthropod context, this change translates into the loss of the endopod and the retention of the exopod. The assumption that the anomalocarid lateral lobe may be a true exopod is partly based on the presence of reported ventral, limb-like appendages being consistent with the gross morphology of the arthropod endopod. Some morphotypes also show an increase in their degrees of tagmosis and sclerotization, while others show the opposite" - Minicucci 1999.

In subsequent years (and even before, with the work of Graham Budd) a great deal of confusion has bene cleared up, although some questions still remain. With the exception of Hou & Bergström (2006 and other papers), all workers in this field agree that Collin's class Dinocaridida are not a distinct monophyletic clade by a paraphyletic grade leading up to a monophyletic Euarthropoda (true arthropods). As such they constitute a series of progressive stem forms (although the Linnaean rank remains unaffected; in this context the Dinocaridida are equivalent to the cynodonts betwene reptiles and mammals, or the theropod dinosaurs between reptiles and birds. Some of the following cladograms have already been discussed under the heading of lobopodia but will here be considered in the context of Dinocaridida. MAK120512

Budd 1996, 1999:

Graham Budd's scenario of



panarthropod evolution, showing successive morphological innovations. This diagram, modified from Budd, 1996, 1999), is copied from Species splitting). The most basal taxa here are lobopods such as *Aysheaia* and *Hallucinogenia*, followed by a succession of dinocaridids. The very basal placement of *Kerygmachela*, beneath tardigrades, is due to the former's primitive features, such as a centrally located mouth (shared with most Cambrian lobopods). The current consenus is that tardigrades are a more basal panarthropod group which aquired arthropod-like characteristics by convergence. However Budd's phylogenetic position, according to which both Lobopodia and Dinocaridida constituite a single gradational series, is confirmed in all cladistic analyses

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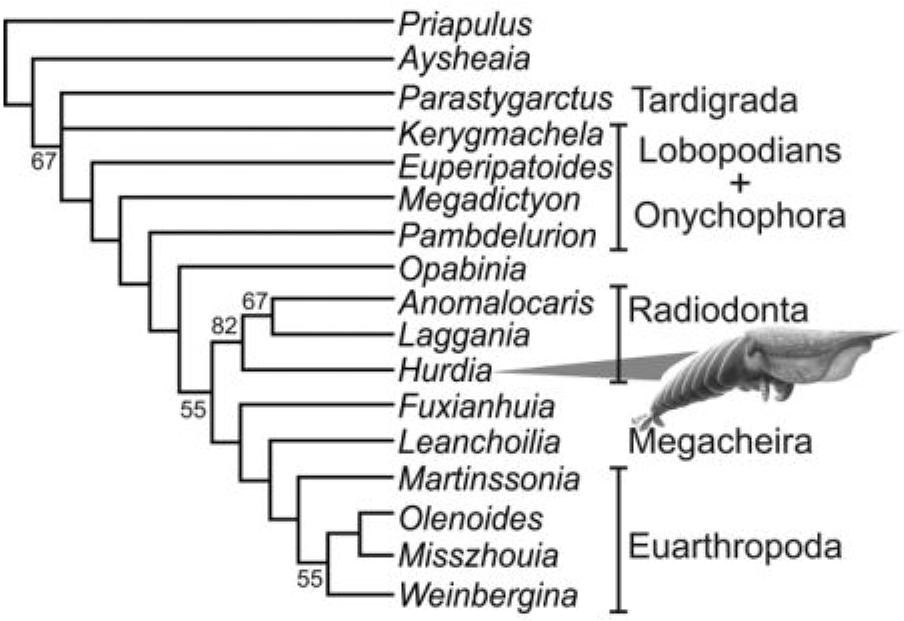
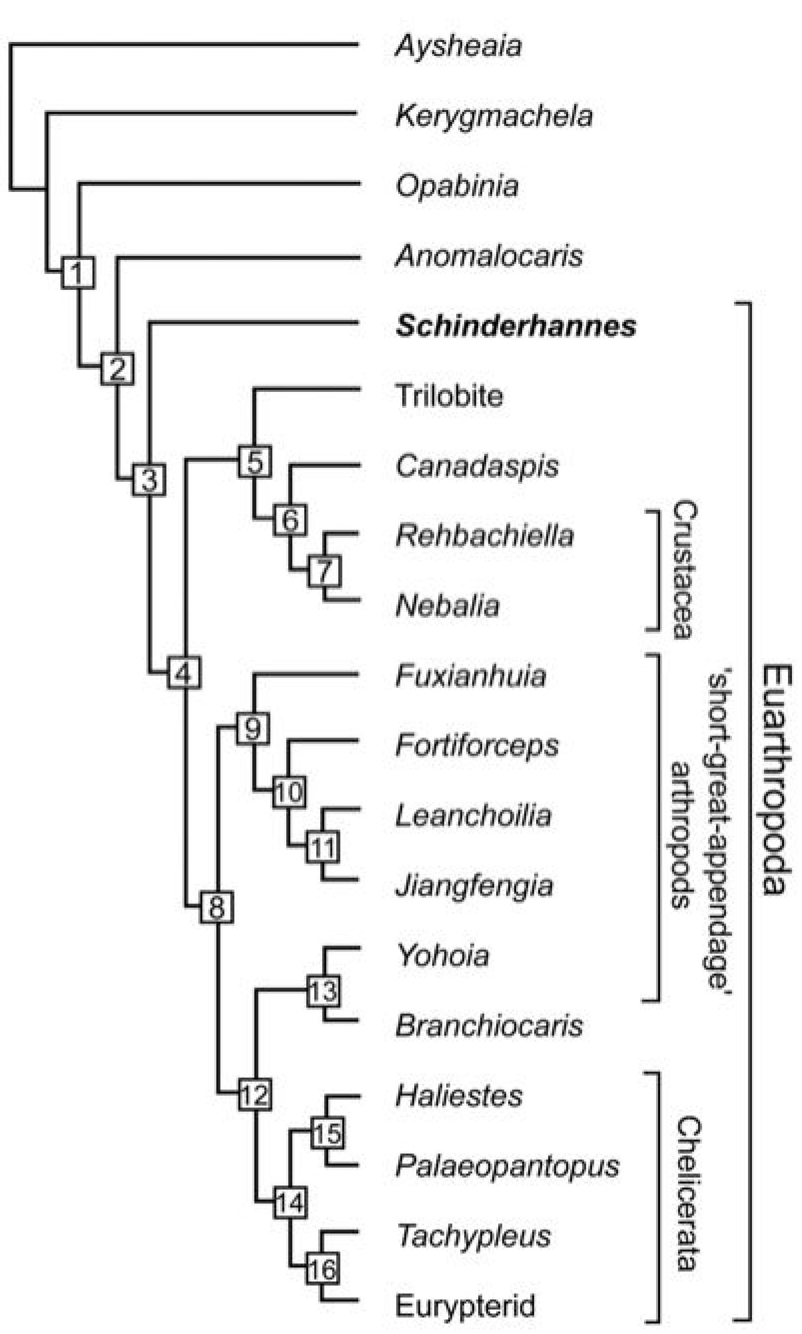
Daley et al 2009:



Cladistic analysis of selected stem and crown group (pan)arthropods, strict consensus of three trees, from Daley et al 2009's study of the Burgess Shale Anomalocaridid *Hurdia victoria* (illustrated). Although basically in agreement with Budd's earlier phylogeny, the position of *Opabinia* and *Pambdelurion* are here reversed. *Hurdia*, *Anomalocaris*, and *Laggania* here form a specialised side-branch and sister taxon to true arthropods beginning with *Fuxianhuia*. *Kerygmachela* is here placed even stemward of (beneath) the onychophora, based on the premise that the ventrally placed mouth (an advanced feature) only evolved once. But in view of the otherwise more advanced features of *Kerygmachela*, it is more parsimonious to assume that this at least happened twice, once with onychophores (perhaps an adaptation or preadaptation to terrestrial lifestyle) and once with the dinocaridid protoarthropods. Liu et al (2011)'s analysis for example place *Kerygmachela* above the siberiid (raptorial appendage) lobopods but beneath *Pambdelurion*, and we have tentatively followed that phylogeny here.

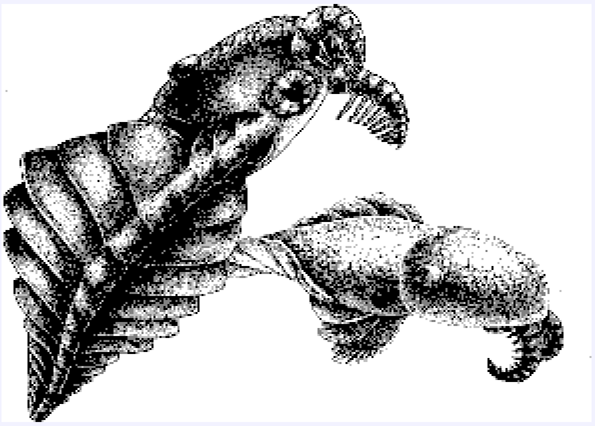
Kühl et al 2009:



The discovery of the Devonian anomalocaridid *Schinderhannes bartelsi* was important not only in illustrating that the dinocaridids continued well into the Mid Palaeozoic at least, but also in the case of this advanced form provoiding a further non- ,missing link between lobopods and arthropods. The cladogram here emphasises arthropods rather than panarthropods. Cladogram; tree length, 87. Consistency index, 0.5402; retention index, 0.6552. (1) Peytoia-like mouth sclerites, terminal mouth position, lateral lobes, loss of lobopod limbs, and stalked eyes. (2) Great appendages. (3) Sclerotized tergites, head shield, loss of lateral lobes, and biramous trunk appendages. (4) Stalked eyes in front and loss of radial mouth. (5) Post-antennal head appendages biramous and antenna in first head position. (6) Free cephalic carapace, carapace bivalved, and two pairs of antennae. (7) Maxilla I and II. (8) Exopods simple oval flap. (9) Two pre-oral appendages and a multisegmented trunk endopod. (10) Post-antennal head appendages biramous and tail appendages fringed with setae. (11) Long flagellae on great appendage and exopods fringed with filaments. (12) Trunk appendages uniramous and eyes not stalked. (13) No posterior tergites. (14) Tail spines and chelicere/chelifore on first head position. (15) Proboscis. (16) Six post-antennal head appendages. - from Kühl et al 2009, via PZ Myers' Pharyngula. Note that Great appendages (synapomorphy 2) are already knoown from siberiid lobopodians, and Hou & Bergström (2006) argue that anomalocaridids did have limbs (contra the claimed reversal at 1), but that these were not sclerotonised and hence not preserved.

One taxon not considered in any of the above analyses is *Parapeytoia*, which has characteristics both of dinocaridoid protoarthropods and megacheirian "great appendage") arthropods. This ambiguity may be due to poor or partial preservation, or it may be the that *Parapeytoia* is a truly transitional form. If the latter, it may be either more primitive than, or more advanced than, *Schinderhannes*. We have tentatively placed it as more advanced, on the basis of what seems to be similarities to the great appendage arthropods. MAK120507

Descriptions



Dinocaridida Collins 1996

Range: As an evolutionary taxon Early Cambrian to Mid Devonian. As monophyletic stem + crown Arthropoda ("Paneuarthropoda" (Lieberman, 2003) or "Total Group Arthropoda" (Paterson et al 2011) from E Camb.

Phylogeny: Panarthropoda ::: Paraphyletic Siberiidae + * : *Kerygmachela* + (*Pambdelurion* + (*Opabinia* + (Anomalocarididae + (*Schinderhannes* + (*Parapeytoia* + Arthropoda)))))

Characters: As a paraphyletic assemblage or evolutionary grade, therefore no synapomorphies. Dinocaridid apomorphies that were previously considered unique (pineapple ring circumoral mouth plates; arthropodized frontal grasping appendages, were already acquired by the Siberiid lobopods. If used as basal taxon: **$** Trunk appendage flaps in the form of lateral lobes (Edgecombe 2009) fig 3 ; Liuetal2011 fig. S1.) (this synapomorphy is lost in True Arthropods) MAK120507

Comments: As defined by Collins, Dinocaridids are bilaterally symmetrical arthropods with a body divided into two principal tagmata, recalling the prosoma and opisthosoma of chelicerates, and a non-mineralised cuticle. The front part shows no external segmentation, bears one or more pre-oral claws, one or more pairs of prominent eyes, and a ventral mouth; differing from other arthropod classes in possessing no antennae and only one appendage or pair of pre-oral appendages on the prosoma, and in bearing gilled lateral lobes on the metameric trunk. The jaws vary from none to forms with both radiating teeth and teeth in rows.

Collins included within the group the Anomalocaride (*Anomalocaris* and *Laggania*), Opabiniidae (*Opabinia*), *Hurdia*, *Proboscicaris*, *Cassubia*, and "three, possibly five, unnamed genera from China" within the Dinocarida, but was unconvinced of any close relationship between *Anomalocaris* and *Kerygmachela*. However, it is retained here for the present on account of the gill-bearing lateral lobes of the trunk. - Chris Clowes., although the central-placed mouth is a persitantly primitiv feauture already absent even in Siberiid lobopods MAK120507.

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Image: *Laggania* (previously classified as a species of *Anomalocaris*), from *Wonderful Life*, by Steven J Gould, artwork © Marianne Collins.

Links: Anomalocaris Homepage by Dr S.M. Gon III **Best on the Web**; Art Evolved - Anomalocarids; Anomalocaridid - Wikipedia MAK120507

Dinocaridida: Dinocaridida (2)

Kerygmachela and *Pambdelurion*

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

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2. *Pambdelurion* X

The protarthropods of the Sirius Passet

Note: unless otherwise indicated, the following is from Chris Clowes Peripatus website

Introduction

The Sirius Passet fauna (named after the Sirius sledge

patrol that operates in North Greenland) derives from the Buen Formation, exposed on the eastern shore of J.P. Koch Fjord in the far north of Greenland.

The fauna is inevitably compared to that of the Burgess Shale, although it is probably ten to fifteen million years older – 518 vs. 505 Ma (Martin et. al. 2000) – and more closely contemporaneous with that from Chengjiang.

Stratigraphy

The Sirius Passet soft-body fossils are found in rocks of the Lower Cambrian Buen Formation, in mud shales, representing a rather deeper water facies than the Burgess Shale, formed on the outer continental shelf, off-shore from a carbonate escarpment. "Large chunks from the edge of the carbonate platform occasionally fell or slid into the adjacent basin, where the Sirius Passet fauna lived" (Conway Morris 1998, p. 117).

Preservation

In general, preservation of the Sirius Passet fossils is not spectacular.

Systematics

Discussion of early metazoan evolution has for many years been dominated by fossil evidence from the Middle Cambrian Burgess Shale and, in particular, by its famous problematic arthropods – *Anomalocaris*, *Leancoila*, *Opabinia*, and so on. "No one would dispute that these fossils are problematic, in the sense that they are difficult to understand. However, that methodological difficulty should not be confused with the possibility that these fossils have only remote affinities with all living groups" (Budd 1997, p.125).

The Sirius Passet fossils are approximately ten to fifteen Ma older than those of the Burgess Shale, presenting us

with an even earlier window upon metazoan evolution; a glimpse of forms which, if anything, are even more challenging to interpret.

As in the Burgess Shale, arthropods are the most abundant component of the Sirius Passet fauna although there is only one or two species of trilobite whereas, in the Burgess Shale, there are twelve or so. In fact there are generally few taxa having shelly skeletons; the trilobites, "rare hyoliths, a number of sponges with prominent spicules, a few small brachiopods, and no echinoderms or molluscs" (Conway Morris 1998, pp. 120-121). Of the arthropods lacking calcified exoskeletons, some are somewhat – but not markedly – similar to Burgess Shale species. Many are large, reaching 50 cm or more in length. In addition there are a number of polychaete annelids and large priapulids (*ibid.*) - Chris Clowes 2002

The two species of so-called "gilled lobopods" from the Sirius Passett Lagerstätte - *Kerygmachela* and *Pambdelurion* - both combine anomalocaridid-like imbricated lateral body flaps with lobopodian trunk limbs. Their mouthparts however are quite distinct; *Kerygmachela* retains the ancetsral terminal mouth cone as in cycloneuralian worms and Cambrian xenusian lobopods, whereas *Pambdelurion* posesses an anomocaridid-like ventral mouth consisting of a circlet of overlapping plates with denticles along their inner margin (Edgecombe 2009). In comtrats to the unambigiously radiodontan and dinocaridid *Pambdelurion*, *Kerygmachela* posesses a typical mosaic mix of primitive and advanced features, showing it

to be a true transitional form. MAK120507

Descriptions

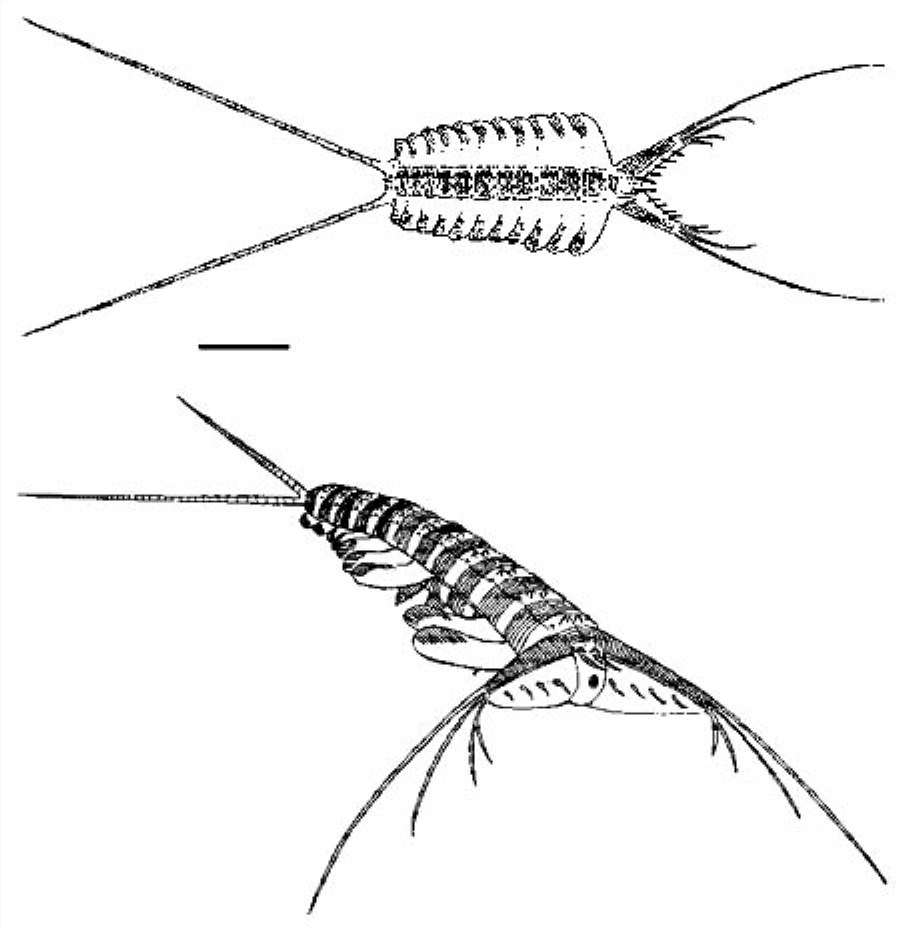
Kerygmachela kierkegaardi Budd 1998

Horizon: Buen Formation, Sirius Passett Lagerstätte of Greenland. Early Cambrian (Atdabanian age)

Phylogeny: Dinocaridida **:** (*Pambdelurion* + (*Opabinia* + (Anomalocarididae + (*Schinderhannes* + (*Parapeytoia* + Arthropoda))))) + *

Characters: Trunk exites as lateral lobes; heteronomous annulation. (Daley et al 2009 cladogram, supplement fig S3)

Description: The cephalic region is characterised by a pair of stout unsegmented appendages each bearing long spinose processes, and an anterior mouth. The trunk shows alternating rows of tubercles and transverse annulations along the axis, to which are attached 11 pairs of gill-bearing lateral lobes and lobopodous limbs. The caudal region is small, and bears two long tail spines. There is some evidence for circular musculature arranged around the trunk and a dorsal, longitudinal sinus, and several details of the muscular pharynx have been preserved. - Chris Clowes 2002



Comments: The combination of characters found in *Kerygmachela* allows it to be allied with the lobopods, represented in the extant fauna by the onychophorans, tardigrades, and possibly the pentastomids, and in the Cambrian fossil record by a morphologically diverse set of taxa, some of which are not assignable to the extant groupings. It also shares important characters with the problematic Burgess Shale forms *Opabinia regalis* Walcott and *Anomalocaris* Whiteaves, and another Sirius Passet form, *Pambdelurion* Budd. These taxa together form a paraphyletic group at the base of the clade of biramous arthropods.

"In the Sirius Passet, the putative lobopod *Kerygmachela* shows marked similarities to Burgess Shale *Leanchoilia*, suggesting an alternative interpretation for its axial structure. I argue here that most three-dimensionally preserved axial structures in Burgess Shale-type arthropods can be interpreted as well developed midgut diverticula. Such a condition is characteristic of living carnivorous arthropods and provides a key to interpreting the ecology of ancient forms" (Butterfield 1999). Chris Clowes 2002

Kerygmachela lacks almost all of derived arthropod features apart from lateral flaps (a precursor to biramous limbs (Budd 1996) and heteronomous annulation. The terminal mouth (a primitive/ancetsral ecdysozoan feature) shows that the ventral mouth in both onychophorans and arthropods can be seen to be a convergence Budd 2001

Image: Reconstructions of *Kerygmachela kierkegaardi* from Budd 1998.

Pambdelurion whittingtoni Budd 1997

Horizon: Buen Formation, Sirius Passett Lagerstätte of Greenland. Early Cambrian (Atdabanian age)

Phylogeny: Dinocaridida : *Kerygmachela* + ((*Opabinia* + (Anomalocarididae + (*Schinderhannes* + (*Parapeytoia* + Arthropoda)))) + *)

Characters: a representative ancestral form, important synapomorphies are shared with other protoarthropods. These include: ventral Peytoia-like mouth (circumoral plates; also shared with Megadictyon), trunk appendage flaps in the form of lateral lobes (shared with *Kerygmachela*, *Opabinia*, and Anomalocaridids); cuticularized, sclerotized, or arthropodized frontal appendage (shared with Opabinia, Kerygmachela, Jianshanopodia, Megadictyon, and anomalocaridids). MAK120507

Description: "almost 30 cm length, its ventral mouth being armed with cuneiform plates, 11 pairs of flaps along the body, and possibly two or three additional flaps in the head region (Budd 1997). Limbs bearing about fifty annuli were present in conjunction with lateral flaps. In these respects it occupies, together with anatomically more advanced coeval Kerygmachela, an intermediate position between xenusians with grasping anterior appendages and the more typical anomalocaridids." - Dzik 2011

Artwork: Graphic from by Senzakitatsuya's Cambrian Cafe (in Japanese)

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Dinocaridida: Anomalocarididae

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |?--Amplectobelua
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

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5. *Laggania* X

Laggania cambria, life size model (about 60 cm) created by Espen Horn, København, Danmark, based on fossils from Burgess Shale (middle Cambrian), Canada; Staatliches Museum für Naturkunde Karlsruhe, Germany. Photo: H. Zell.
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The largest and most impressive animals of the Cambrian and Early Ordovician periods, the Anomalocaridids represent the culmination of dinocaridid evolution (although not the msot lasting legacy; that honour would go to their somewhat smaller descendants the early arthropods).

The earliest known Anomalocaridid to date is *Cassubia infercambriensis*, from the earliest Cambrian of Poland, predating the first trilobites (Dzik & Lendzion 1988). Anomalocaridids, like Dinocaridids in general, are best known from the mid Early Cambrian through to the mid Middle Cambrian. Their rarity as fossils thereafter is due to their non-mineralised (soft-bodied) cuticle and the the scarcity of post- Midlde Cambrian lagerstatten. It is now known that large bodied anomalocaridids continued well into the early Ordovcian at least (Van Roy & Briggs 2011).

In life anomalocaridids would have been easily recognisable (see image above) as large segmented, swimming arthropod-like animals with a distinctive pair of raptorial appendages under the head, huge compound eyes (*Anomalocaris* had extremely acute vision even by contemporary standards (Paterson et al 2011)), and pairs of swimming lobes along the trunk. The mouth is a circular or rectangular structure resembling a pineapple slice, consisting of a ring of hard sharp teeth in the central orifice. The teeth did not meet in the middle, which led to the hypothesis, which we reject, that anomalocaridids were harmless plankton feeders (Hagadorn, 2009) . In *Hurdia* at least, there were further rows of teeth behind the first (a bit like the creature from *Alien* perhaps), while *Anomalocaris* itself would have used a different killing stratergy, using its powerful arms to grab and shake a trilobite to pieces (Nedin, 1999).

Being soft bodied (they did not have a heavy exoskeleton like trilobites), they would have quickly disintegrate after death. The hard parts most easily preserved are the pineapple-ring mouth and the grasping arms. Not surprisingly, when the fossils were originally discovered, in the first decades of thr 20th century, each part of the animal was found in isolation and thought to belong a different phylum. The arms were considered an arthropod, (*Anomalocaris*), the mouth interpreted as a jellyfish (*Peytoia*), and the body, which appeared as a mostly shapeless blob, was interpreted as a sponge (*Laggania*) or an echinoderm (*Hurdia*). It was only in trhe 1980s (Whittington & Briggs 1985) that it was realised that all these different elements were part of a single animal, larger than any other Cambrian animal. This was named *Anomalocaris* because these were the first of the various part-names rto be coined (in the case of plant fossils there is a simliar problem, when the seeds, bark, leaves., stem, roots, etc are each given different names)

When Stephen Jay Gould first popularised this creature in his book *Wonderful Life*, and for some years afterwards, it was not known what phylum of organisms *Anomalocaris* belonged to. It was frequently lumped with arthropods on the basis of its jointed body; however, other creatures like annelids have also evolved a segmented body). An alternative explanation was that it was a kind of aschelminth (pseudocoelomate worm), as indicated for example by its asymmetrical mouth. Without doubt it is among the "molting animals" (a group that includes many segmented animals). Its difference from modern organisms was considered a reminder, as are all the problematica, of the diversity of life, and the fact that the type of creatures around at present are only a fraction of the number and diversity that have ever lived.

Thanks to cladistic analysis and new fossil discoveries we know a lot more about *Anomalocaris* than we did in the 1980s. We know now for example that it is a transitional form between lobopods and true arthropods, although whether it is classed as a lobopod or an arthropod depends on where you draw the line. Despite arguments by Hou & Bergstrom (e.g. 2006) it is no longer considered a giant aschelminth worm, or anything as alien as Gould imagined. In fact the aschelminth attributes are simply inherited primitive features (plesiomorphies) possessed by ancestral ecdysozoa. The current consensus is that *Anomalocaris* is an arthropod whereas its more primitive cousin *Kerygmachela* is a lobopod. This despite there probably more similarities between *Anomalocaris* and *Kerygmachela* than between *Kerygmachela* and typical lobopods, or between *Anomalocaris* and true arthropods.

Today, at least four genera of anomalocarids are known: *Anomalocaris*, *Hurdia*, *Laggania*, and *Amplectobelua*. Similar and clearly related animals include *Kerygmachela*,, *Parapeytoia*, *Pambdelurion* and *Schinderhannes*. These probably belong to different families, although they would all seem to be part of the same evolutionary gradation. MAK990601, Wikipedia, MAK120511

Descriptions

The first complete Anomalocaris fossil found, Royal Ontario Museum, Toronto.
Photo by Keith Schengili-Roberts, via Wikipedia, GNU Free Documentation/Creative Commons Attribution Share Alike

Anomalocarididae Raymond 1935

Range: Early Cambr- early Ord, Cosm.

Phylogeny: Dinocaridida : *Kerygmachela* + (*Pambdelurion* + (*Opabinia* + ((*Schinderhannes* + (*Parapeytoia* + Arthropoda)) + * : + *Amplectobelua* + *Hurdia* + (*Anomalocaris* + *Laggania*))))

Characters: Trunk walking legs either absent or if present not sclerotised (Hou & Bergström (2006)); large size (20 to 100 cm) . *With Arthropoda*: Hypostome; arthropodization of appendages (Daley et al. 2009) ; very large (~16,000 lenses) compound eyes consistent with a lifestyle of midwater predators in the photic zone (Paterson et al 2011)6.

Comments: The following is from Minicucci (1999), via the Peripatus website, and is included because it gives a comprehensive tabulation of anomalocarid species. As this material was written more than a dozen years ago it is obvious in need of revision and updating MAK120509

"In accordance with the criteria established by Collins (1996), all anomalocarids may be diagnosed as being bilaterally symmetrical, with two distinct tagmata, but other features, such as lateral lobes, grasping appendages, biramous appendages, form of the trunk, and anterior tagmata vary between types of genera.

"Based only on the current descriptions of anomalocarids, and a casual observation of the available evidence, I have listed several groups possibly comprising distinct grades of anomalocarid body organization. The inadequately described Chen and Zhou arthropod (1997), if it is truly an anomalocarid, could very well represent an ancestral grade of anomalocarid body organization unknown in other described forms. Groups 1, 2 and 3 comprise a grade of genera possessing a soft cuticle, simple body organization, and uniramous trunk appendages. Group 4 contains the grade of genera with complex degrees of tagmosis and sclerotization, and biramous trunk appendages, while group 5 represents the grade of genera that have made a radical departure from the body designs of the other grades. A thorough cladistic analysis incorporating all described and undescribed taxa will ultimately determine the viability of this concept" .

Character	Group 1	Group 2	Group 3	Group 4	Group 5
Mouthparts & grasping appendages	sclerotised	sclerotised	sclerotised	sclerotised; mouthparts facing backwards	anterior tagmata formed of several carapace-like components bearing two sheathed claws on stalks. Below the carapaces, the jaws have an inner set of teeth, and are surrounded by pair of claws
Sclerotisation of body	‘naked’	‘naked’		significantly sclerotized body including median sternites	
Body ornament	smooth-surfaced; no ornamentation or raised features of any kind	smooth-surfaced; equivocal evidence of striations on the entire ventral surface of lateral lobes	diagonal striations on the lateral lobes (interpreted as veins by some authors); two exasaggital ventral rows of serially-repeated, nodular structures	?dorsal lanceolate scales; diagonal striations are present on lateral lobes	
Trunk annulation/external segmentation	no visible annulation or segmentation	no visible annulation or segmentation	no confirmed trunk annulation or external segmentation		trunk has 11 segments and a tail
External gill-like structures	none apparent	none apparent			

Lateral lobes	13 pairs	14 pairs, with support ‘rods’ present	setae-like structures present on lateral lobes		
Jointed trunk appendages	none	none	none	gnathobasic biramous trunk appendages, grasping appendages	gnathobasic, biramous trunk appendages
‘Tail’	posterodorsal finlets arranged en echelon	tapers to blunt extremity	tail furcae present; posterodorsal ‘tail’ finlets arranged en echelon		
Example(s)	*Anomalocaris canadensis*	*Laggania cambria*	*Anomalocaris saron*, *Amplectobelua symbrachiata*	*Parapeytoia yunnanensis*, *Cucumericrus decoratus*	*Hurdia* sp., (jnr syn: *Proboscicaris* sp.)
References	Collins 1996	Collins 1996	Chen *et al.* 1994; Hou *et al.* 1995	Hou *et al.* 1995; other forms awaiting description by Ramsköld (1995) could fall into this group	Collins 1992, 1996

Table 1: Minicucci’s (1999) five ‘grades’ of anomalocarid organisation.

> "The reported morphological variations present in assorted anomalocarid genera emphatically illustrate the former diversity of these animals. Indeed, preliminary descriptions of very unusual genera with several frontal carapace-like components forming the anterior tagmata (Collins 1992, 1996), and reports of more genera with gnathobasic, biramous appendages (Ramsköld 1995) indicate that anomalocarids evolved an assortment of specialized forms, and varying degrees of tagmosis and sclerotization, perhaps enabling them to occupy different feeding guilds. At this juncture, virtually no substantive information has been published on such forms. It appears that all described and even undescribed genera may be sorted according to several distinct grades of anomalocarid body organization. Superficially identifiable are the genera with a soft-cuticle or minimal sclerotization, possessing uniramous trunk appendages (lateral lobes only); the genera with complex degrees of tagmosis and sclerotization, possessing biramous trunk appendages; and the *Hurdia*-type genera, which radically depart from the two former body designs (see Collins 1992). Assigning the different grades taxonomic rankings, either by assigning each to sub-familial status within the Anomalocaridae, or by erecting family level taxa for each within an Order, depends on how each grade could be proven to be distinct cladistically. More grades of body organization must surely have existed, and are as yet unrepresented or unrecognized in fossil collections. It is, of course, possible that the same type of body organization expressed among similar genera could merely reflect homoplasy in anomalocarids not closely related" (Minicucci 1999). - url.)

Recent cladistic analysis by Daley et al. 2009 has *Hurdia* as a more distinct taxon (no doyubt due to its unusual characteristics such as the larger head shield and multiple tooth rows), with *Anomalocaris* + *Laggania* as the crown group. *Anomalocaris* is also considered the most advanced (derived) taxon. *Amplectobelua* and *Parapeytoia* were not included so their position in the Anomalocaridid family tree remains unknown. We tentatively consider *Parapeytoia* a transitional anomalocarid-arthropod on the basis of its equally being able to be included with either group. It may be however that *Parapeytoia* may turn out to be a more convemntional "great appendage" arthropod. From the above table, perhaps *Anomalocaris saron* is better placed under the genus *Amplectobelua*. For now however we have retained it under *Anomalocaris*. MAK120512

Amplectobelua Hou, Bergström & Ahlberg, 1995 **:** *A. symbrachiata* Hou, Bergström & Ahlberg, 1995 *A. stephenensis* Daley & Budd, 2010

Range: Early to Middle Cambrian (Chengjiang and Burgess Shale)

Phylogeny: Anomalocarididae **:** *Hurdia* + (*Anomalocaris* + *Laggania*) + *

Comments: known from two species, *Amplectobelua* was smaller and more compact, with wider body, than other anomalocarids. Large eyes positioned laterally (to the side of) of the mouth. The grasping appendages have pairs of spine-like endites generally devoid of 'auxiliary' spines, and several extended lobes on both sides, the endite near proximal end stout and exceptionally long, one-third to nearly half as long as the length of the appendage.. It had a pair long, feeler-like cerci that extended from the posterior end of the body. Daley & Budd 2010, Wikipedia. MAK120507

Links: *Amplectobelua symbrachiata* by Sam Gon III

Anomalocaris Whiteaves 1892 **:** *A. canadensis* Whiteaves 1892 (Burgess Shale, type species) ; *A. saron* Hou, Bergström & Ahlberg 1995 (Chengjiang); *A. briggsi* Nedin 1995 (Emu Bay Shale, South Australia, photo)

Range: Early to Middle Cambrian, Chengjiang, Burgess Shale, and Emu Bay Shale Lagerstätten, Greenland (Briggs et al. 1994, pp. 201-202. and Nevada (Lieberman, 2003))

Phylogeny: Anomalocarididae **:** *Amplectobelua* + *Hurdia* + (*Laggania* + *)

Characters: Spinose robust great appendage with 15 articles and a double row of spines; posterior tagma composed of three paired tail flaps; with *Laggania*: Posterior tapering of lateral lobes. Daley et al. 2009)

Comments: The archetypal dinocaridid, first discovered by Joseph Frederick Whiteaves, who described *Anomalocaris canadensis* from the *Ogygopsis* Shale on Mount Stephen (actually the grasping forelimbs); Walcott found similar limbs in the Burgess Shale, together with those of *A. nathorsti* (= *Laggania cambria*). Walcott also discovered the circlets of plates, that he named *Peytoia* and interpreted as a medusoid, which are now known to be anomalocaridid mouthparts (however as the mouthparts of *Anomalocaris* itself are in not tetraradial like 'Peytoia', but have three major axes and a small central opening). The name *Anomalocaris* (meaning "strange shrimp") originally referred to the detached arms; these were believed to the be the body of a Crustacean-like animal for which always seemed to be found minus the head. (*left*)

Harry Whittington and Derek Briggs recognised that these were different parts of the same animal, which they described in 1985 (Whittington & Briggs 1985). Gould's *Wonderful Life, published only a couple of years later, brought the animal to the public eye, but also confused several species. It is now known that these various* *anomalacarii belong to at least four related genera, although all can be included in the same family. Simon Conway's The Crucible of Creation* written about a decade after Gould's work, also features *Anomalocaris*, and it has featured in popular science documentaries in the following years and decade (*Walking with Monsters* (2005), David Attenborough's *First Life* (2010), and *Australia: The Time Traveller's Guide* (2012) - see still at right. It is unfortunate (if understandable given the need to impress a non-technical audience) that such useful eduactional series, with their impressive special effects, should give in to a tendency to exagerration, with the 50 to 60 cm original animal now uniformly reaching 2 meters in length [1], a three to four-fold increase in linear dimensions (a better known instance of this is the 25 meter *Liopleurodon* of *Walking with Dinosaurs*; however the case for a two meter anomalocaridid is a lot stronger than for a 25 meter pliosaur)

Anomalocaris had very developed vision and it and its close relatives were among the most primitive animals to evolve compound eyes. The exceptionally large eyes indicate that anomalocaridids were visually-based midwater predators in the photic zone (Paterson et al 2011)

Since *Anomalocaris* lacks any mineralised tissue, it seemed unlikely that it would be able to penetrate the hard, calcified shell of trilobites. One possibility is that anomalocarids fed by grabbing one end of their prey in their jaws while using their appendages to quickly rock the other end of the animal back and forth. This produced stresses that exploited the weaknesses of arthropod cuticle, causing the prey's exoskeleton to rupture and allowing the predator to access its innards. This behaviour is thought to have provided an evolutionary pressure for trilobites to roll up, to avoid being flexed until they snapped (Nedin, 1999) - Wikipedia. Although *Anomalocaris* did not seem to have the inner tooth rows of *Hurdia* Daley et al. 2009 and hence was unable to close its mouth, it would certainly have used its circular outer teeth for other purposes, perhaps to break open the weakened trilobite carapace.<./p>

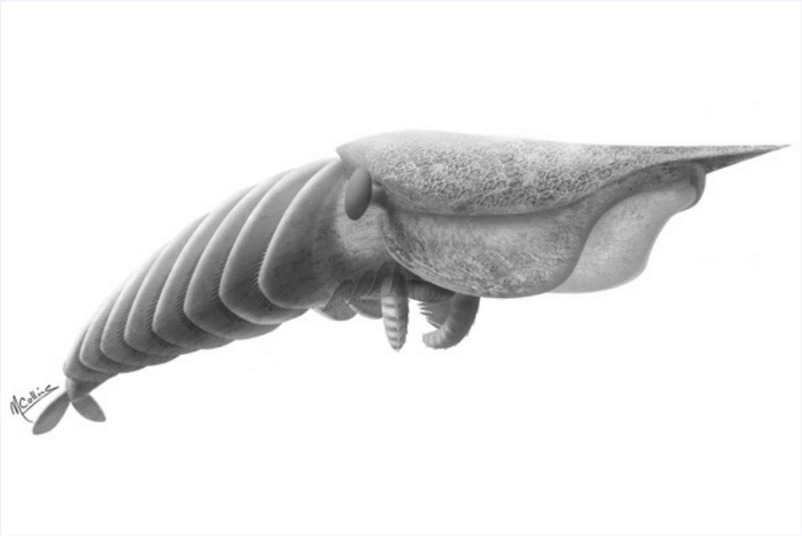
A number of species of this cosmopolitan animal are now known. The best known are the original *A. canadensis* from the Middle Cambrian Burgess Shale, and *A. saron*, a somewhat earluier form from the Earky Cambrian of Chengjiang, China. *Anomalocaris briggsi* is a very large Gondwanan species, also Early Cambrian, from South Australia. Two additional species have been reported from the Early-Middle Cambrian boundary in the Comet Shale Member of the Pioche Formation in Nevada (Lieberman, 2003). *Anomalocaris briggsi*, *Anomalocaris pennsylvanica* (incl. cf. *pennsylvanica*), *Anomalocaris* sp. and the ‘appendage F’ anomalocarid are indeterminate forms based on grasping appendages only (Minicucci 1999). The largest known Anomalocarid, either a genus of *Anomalocaris* itself or a related form, is a meter long giant from the Early Ordovican Fezouata Biota of southeastern Morocco (Van Roy & Briggs 2011) MAK120509

Notes: [1] The two meter claim derives from extrapolation based on remains of peyotia mouthparts from the early Cambrian Chengjiang biota of China, but these estimates are uncertain Hou et al 2006, cited in Van Roy & Briggs 2011)

Links: *Anomalocaris canadensis* and *Anomalocaris saron* by Sam Gon III; Smithsonian; Wikipedia, Art Evolved (Anomalocaridids) MAK120509

Images: Upper right, *Anomalocaris* model at Dinosaur Museum, Canberra, Australia. Photo by Photnart, Public Domain; Above left, *Anomalocaris* grasping limb from the Mt. Stephen Trilobite Beds, Middle Cambrian, near Field, British Columbia, Canada. Photograph by Mark A. Wilson, Department of Geology, The College of Wooster, Public domain, via Wikipedia; Above right *Anomalocaris hunting*, a still from *Australia: The Time Traveller's Guide*, © ABC

Hurdia *Hurdia victoria* Walcott 1912, and *Hurdia* spp.



Synonyms: *Amiella ornata*/*Sidneyia ornata*, *Anomalocaris nathorsti*, *Liantuoia inflata*, *Huangshandongia yichangensis*, *Proboscicaris* spp. Some specimens attributed to *Emeraldella brocki*. and *Sidneyia inexpectans* are actually *Hurdia victoria*. (Daley et al. 2009)

Range: Early to Middle Cambrian; known from six Burgess Shale localities in the Canadian Rockies (mid Middle Cambrian), as well as in the Marjum Formation of Utah (slightly later Middle Cambrian), also the Middle Cambroian of Bohemia (*Proboscicaris hospes*), and possibly Nevada, and China (*Liantuoia inflata* and *Huangshandongia yichangensis* from the Early Cambrian Shuijingtuo Formation in Huangshandong, Yichang, West Hubei; originally considered Crustacean carapaces) .

Phylogeny: Anomalocarididae **:** *Amplectobelua* + (*Anomalocaris* + *Laggania*) + *

Characters: Extra teeth rows within central mouth part opening; poorly defined, non-tapering lateral lobes - Daley et al. 2009

Comments: First described from fragmentary fossils by American paleontologist Charles Walcott in 1909, (Probably named for Mount Hurd nearby, itself commemorating Major Hurd, a Canadian Pacific Railway engineer and explorer.) while cataloging the Burgess Shale. However he mistakenly thought that the various body parts belonged to different creatures, which led to them being misclassified variously as a species of jellyfish, sea cucumber and its close relative *Anomalocaris*. In the late 1990s, then-curator of the Royal Ontario Museum Desmond H. Collins connected the elements of the Hurdia animal, presenting his ideas in informal articles, (Collins 1992, 1999) but it was not until 2009, after three years of painstaking research, that the complete organism was reconstructed. (Daley et al. 2009)

Hurdia possesses a general body architecture similar to those of *Anomalocaris* and *Laggania*, including the presence of exceptionally well-preserved gills, but differs by possessing a prominent anterior carapace structure. The function of this organ remains mysterious; it cannot have been protective as there appears to have been no underlying soft tissue. As with other dinocaridids, lateral lobes ran along the sides of the organisms, from which large gills were suspended. Daley et al. 2009, Wikipedia)

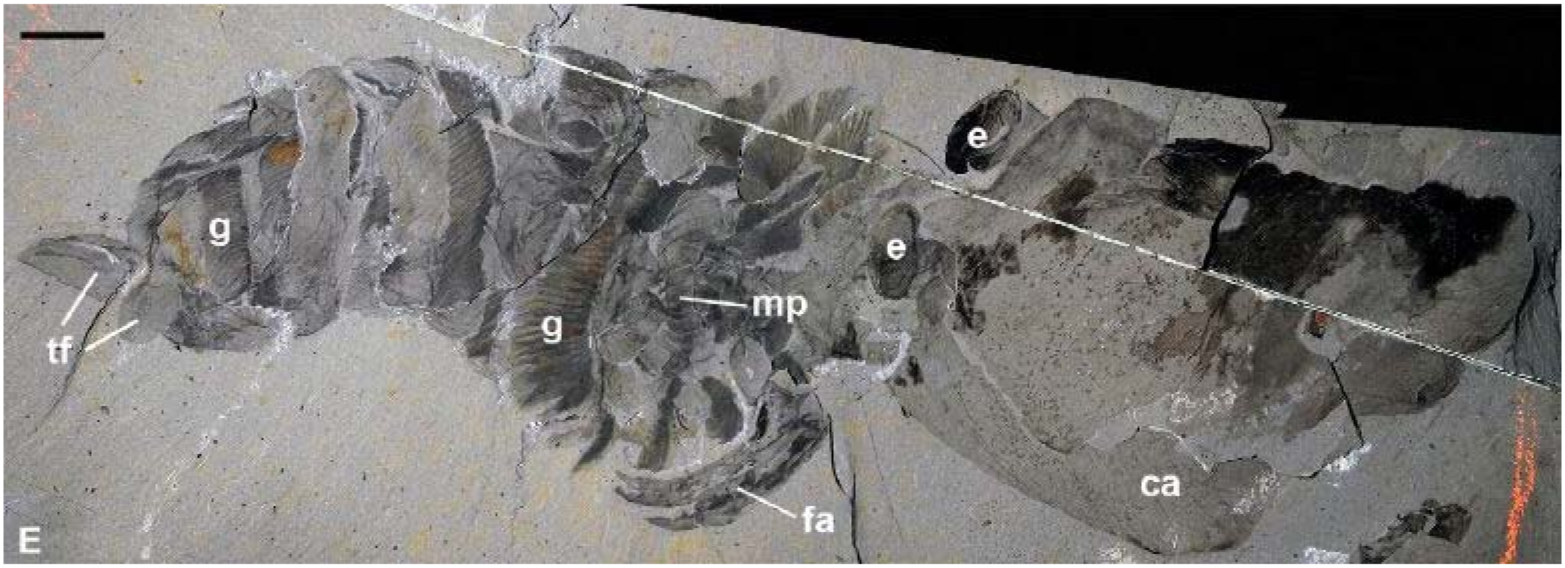
The mouthparts consist of an outer radial arrangement of 32 broadly elliptical plates, as in *Laggania* and *Anomalocaris*, which make up a domed structure. Within the central opening are upto five inner rows of teeth Daley et al. 2009 argue that these are lacking in *Laggania* and *Anomalocaris*. There is an inconsistency here by the fact that *Hurdia* has less robust grasping appendages than *Anomalocaris*, It may be however that *Hurdia* bit down on medium-sized prey, whereas *Anomalocaris* fed on larger and more heavily armoured animals like trilobites but bending and tearing them apart (Nedin, 1999) MAK120511

Hurdia was one of the largest organisms in the Cambrian oceans, reaching approximately 50 cm in length. -Wikipedia It displayed a cosmopolitan distribution; it has been recovered from the Burgess shale as well as sites in the USA, China and Europe. It's wide distribution suggests that Hurdia was a generalist adapted to a range of environmental conditions (Daley et al. 2009)

Regarding the list of synonyms given above, given the temporal and geographic range, and contra Daley et al. 2009 we do not believe ithey all belong tot the same species, although it is quite reasonable to assume they would belong to the same genus. This implies there were a number of distinct parallel evolutionary lineages of anomalocaridids existing side by side during the Cambreian, each specialising in specific lifestyles.. MAK120511

69 specimens of *Hurdia* are known from the Greater Phyllopod bed, where they comprise 0.13% of the community (Caron & Jackson 2006), although some of the specimens identified with other species may belong; according to Daley et al. (2009), *Hurdia* is the most common anomalocaridid in at least the Walcott Quarry.

Image: Life reconstruction by Marianne Collins, from Daley et al. 2009 , © ;Science AAAS



Hurdia victoria from the Burgess Shale, in dorsolateral aspect. The front of the animal (the headshield) is to the right. Abbreviations: ca, carapace; e, eye; fa, frontal appendage; g, gill; hs, head shield; mp, "Peytoia" mouth part; tf, tail fan. Scales 1 cm. Photo and caption from Edgecombe 2010, fig.5

Laggania cambria Walcott 1911

Synonym: *Peytoia nathorsti* Walcott 1911, *Anomalocaris nathorsti*

Horizon: Burgess Shale

Phylogeny: Anomalocarididae : *Amplectobelua* + *Hurdia* + (*Anomalocaris* + *)

Comments: Originally described by Charles Walcott in 1911 as a holothurian echinoderm (Durham 1974). Compared with *Anomalocaris* species, *Laggania* species lacked tail structures and had a considerably larger head with the eyes placed behind instead of in front of the mouth, which would have been disadvantagous for active hunting. Because of these characteristics, some scientists have described *Laggania* as a cruising, plankton feeder (Dzik & Lendzion 1988). Alternatively, it may simply have had a different hunting and feeding strategy. We have already expressed our opinion on the planktonic anomalocarid hypothesis elsewhere. The co-existence of so many types of anomalocarids in the same localities points to a diversity of guilds. 108 specimens of Laggania are known from the Greater Phyllopod bed, where they comprise 0.21% of the community. (Caron & Jackson 2006), Wikipedia, although some of these specimens may belong to *Hurdia* MAK120507

Links: *Laggania cambria* by Sam Gon III; "Laggania cambria". Burgess Shale Fossil Gallery. Virtual Museum of Canada. 2011. **Image:** *Laggania cambria* from the Burgess Shale, fossil in the Royal Ontario Museum, Toronto. Photo by Keith Schengili-Roberts, via Wikimedia, GNU Free Documentation/Creative Commons Attribution Share Alike. See top of page for how this animal would have appeared in life. MAK120509

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page MAK120511;

Dinocaridida: Anomalocarididae (2)

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  |?--Cucumericrus
                  `--+--Parapeytoia
                     `--ARTHROPODA
```

Contents

Taxa on This Page

1. *Cucumericrus* X
2. *Parapeytoia* X
3. *Schinderhannes* X

Descriptions

Cucumericus decoratus Hou, Bergström & Ahlberg 1995

Horizon: Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Dinocaridida **:** *Kerygmachela* + (*Pambdelurion* + (*Opabinia* + (Anomalocarididae + (*Schinderhannes* + (*Parapeytoia* + Arthropoda) + *))))

Comments: *Cucumericrus* is a genus of anomalocaridid known from a few poorly-preserved specimens. Its great appendages are never preserved (Daley & Budd 2010) but it does seem to bear walking legs, which have been interpreted as somewhere between lobopod legs and segmented arthropod legs. (Bergstrom & Hou 2003) - Wikipedia

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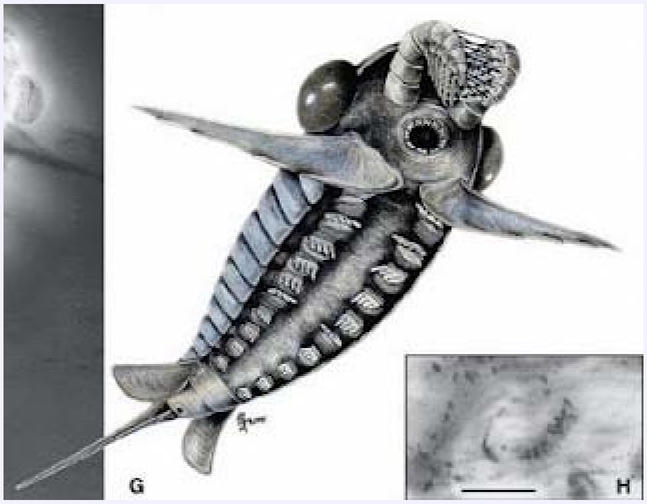
Schinderhannes bartelsi Kühl et al 2009



Horizon: Early Devonian German HunsrÃ¼ck Slate.

Phylogeny: Dinocaridida **:** *Kerygmachela* + (*Pambdelurion* + (*Opabinia* + (Anomalocarididae + (*Cucumericrus* + (*Parapeytoia* + Arthropoda) + *))))

Comments: (modified from Christopher Taylor's posting on this creature MAK120507). *Schinderhannes bartelsi*, and its fossil remains are described in a paper by Kühl et al (2009) (from whence comes the reconstruction at the right). It's apparently named after an 18th century bandit in the area from which it was found. At just under ten centimetres long, it is a smaller cousin of *Anomalocaris* and *Laggania* of the Cambrian Burgess Shale. However, *Schinderhannes* bears a few significant differences from those taxa: (1) it has that bizarre pair of 'wings' attached to the back of the head; (2) certain details of its anatomy suggest that it is more closely related to living arthropods than is *Anomalocaris*, showing that arthropods are descended from an 'anomalocarid' grade; and (3) it doesn't come from the Burgess Shale or Chengjiang, but the German HunsrÃ¼ck Slate, which is from the Earky Devonian, shows that 'anomalocarid'-type animals were around for some 100 million years longer than we previously knew (at the risk of repeating an old clichÃ© about it being like discovering a *Tyrannosaurus* alive today, although the amount of time separating *Tyrannosaurus* from the present is rather *less* than 100 million years.

Schinderhannes resembles anomalocarids in its radial mouth, and the large pair of spiny pre-oral appendages. However, certain of its features are more like true arthropods - it has a dorsum divided into distinct, sclerotised tergite plates, and it has biramous (two-branched) appendages like crustaceans. The combination of the large 'wings' and 'flukes' on either side of the tail spine suggest that it was an active swimmer.

Large raptorial pre-oral appendages (dubbed 'great appendages') have also been found in a number of Cambrian arthropods such as *Leanchoilia* and *Yohoia*. The phylogenetic position of such 'great-appendage' arthropods has been hotly debated. Budd (2002) suggested that they were a stem grade to the arthropod crown clade, but Cotton & Brady (2004) placed them within the crown clade, in the stem group for chelicerates. Researchers have also debated whether the great appendages of these arthropods are homologous to those of anomalocarids, and whether the great appendages are homologous to the chelicerae of modern chelicerates. The (admittedly pretty rudimentary) phylogenetic analysis of *Schinderhannes* by Kühl et al 2009, supports a position of great-appendage arthropods as stem chelicerates (despite the great appendages of these arthropods being *a priori* coded as homologous to those of anomalocarid-grade animals), which supports the comparison between great appendages and chelicerae. It also suggests that trilobites are closer to crustaceans than chelicerates, contrary to the idea of a trilobite + chelicerate "Arachnomorpha" clade. In some regards, this would make sense - trilobites, like crustaceans and insects, have lost the plesiomorphic state of grasping pre-oral appendages as found in chelicerates and have filamentous antennae instead. However, the position of trilobites in the tree above seems to be primarily due to the presence of antennae, so I don't know if it can be considered well-supported. - CKT090206

Parapeytoia yunnanensis Hou, Bergstrom & Ahlberg, 1995

Horizon: Qiongzhusi Formation, Maotianshan Shales, Chengjiang Lagerstätte, Yunnan, South China, (Atdabanian age - Early Cambrian)

Phylogeny: Dinocaridida **:** *Kerygmachela* + (*Pambdelurion* + (*Opabinia* + (Anomalocarididae + (*Schinderhannes* + (Arthropoda + *)))))

Comments: *Parapeytoia* resembles anomalocaridids in having a pair of large grasping appendages, eyes on stalks, and a fleshy-lobed posterior with a fan tail. The other distinguishing feature of the group, the “Peytoia” (pineapple ring) mouth part, is unconvincingly described and illustrated, and so any statement regarding its presence must be taken with caution, at least until better fossil material turns up. In differs in possessing euarthropod-like trunk legs and strongly sclerotized, segmental sternites ((Daley et al. 2009; suppl). The presence of legs may not be so strange as it seems, as Hou & Bergström (2006) argue that anomalocaridids did have legs, but they were not sclerotised (there was no arthropod-type exoskeleton) and hence did not fossilise (or didn't fossilise clearly). This makes more sense than the premise that ancestral protoarthropods had legs, then lost them, then re-acquired them again (or alternatively developed toally new legs). Because it is assumed that anomalocaridids and even dinocaridids in general lacked legs, it is thought that *Parapeytoia* might be more closely related to great appendage stem euarthropods like *Yohoia* or *Haikoucaris*, If Hou & Bergström are correct this need not be the case. The Anomalocaris Homepage - Parapeytoia yunnanensis & Opabinia regalis shows drawings of *Parapeytoia* reconstructed as a megacheiran "great-appendage" arthropod. When compared to other megacheirans,, the similarity reagrding the anterior appendages is quite obvious. Alternatively, *Parapeytoia* could be a transitional form, a non-missing link, and the great anterior appendages of anomalocaridids and megacheirans may be homologous. This also fits with the hypothesis of the megacheirans being stem group arthropods, prior to the division into the various crown taxa.

Parapeytoia has 13 pairs of legs altogether; the first two pairs about half the length of the remaining ones. These may indicate a benthic rather than a nektonic lifestyle (Wikipedia). It may not have even had a pineapple-ring mouth at all, as sclerites interpreted as its mouthparts have since been assigned to a new priapulid worm genus, Omnidens. (Houetal2006) MAK120507

Links *Parapeytoia yunnanensis* by Sam Gon III

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Dinocaridida: *Opabinia*

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

Contents

Life reconstruction of the specialised dinocaridid *Opabinia regalis*, shown here probing a worm burrow. Image from Opabinia (collection of images)

Opabinia regalis Walcott 1912

Horizon: Burgess Shale of British

Columbia (Middle Cambrian)

Phylogeny: Dinocaridida **:** *Kerygmachela* + (*Pambdelurion* + ((Anomalocarididae + (*Schinderhannes* + (*Parapeytoia* + Arthropoda))) + *))

Characters: Opabinia + higher panarthropods: trunk without annulation; (Edgecombe 2009 fig 3); Opabinia only: Loss of plate-like circumoral structure; posterior tagma composed of three paired tail flaps (Daley et al 2009 cladogram, supplement fig S3)

Opabinia regalis from the Burgess shale on display at the Smithsonian in Washington, DC. This appears to be the exact specimen pictured in Fig. 42 of 'The Crucible of Creation: The Burgess Shale and the Rise of Animals', by Simon Conway Morris, Oxford University Press, 1998.
Photograph and caption by Jstuby Wikipedia, , Public domain

Comments: One of the most bizarre animals that ever lived, *Opabinia* has five eyes at the front of the head and a long, flexible proboscis ending in an array of grasping spines. The trunk comprises 15 segments, each bearing a pair of downward-directed lateral lobes, thought to have been used for propulsion, each overlain by a lamallate gill. Three pairs of upward-directed flaps form a tail fan, possibly served a stabilising or steering function during swimming.

The systematic position of *Opabinia* was for some time very unclear. It was originally interpretated as a branchiopod or a trilobitomorph. Whittington thought it might belong to the stem group leading to a annelid+arthropod clade. Gould naturally used it (along with the upside down Hallucinogenia) as an illustration of the bizarre nature of Cambrian life, considering it toally unrelated to any living phylum. As with most of Gould's problematica however, *Opabinia* soon turned out to be a stem form of extant animals. Collins placed it in the Dinocaridida, as did Budd, who placed it between lobopods and arthropods. Recent cladistic analyses support this, and locate *Opabinia* as a Dinocaridid immediately basal to the anomalocaridida (Daley et al 2009; Liu et al 2011.). As such, *Opabinia* is actually a highly specialised anomalocaridid, rather than a unique member of its own phylum.

*Opabinia*l is thought to have lived primarily in the soft sediment of the seabed, but to have been a predator capable of active swimming. The proboscis was presumably used to capture and handle prey, and may possibly have served to extract burrowing organisms from their burrows. (After Briggs *et al*. 1994, p. 210.) Chris Clowes, MAK120511

Links: *Opabinia regalis* by Sam Gon III; Wikipedia

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Dinocaridida: Classification

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

Contents

There does not seem to be a current evolutionary-linnaean taxonomy for the Dinocaridids, and that classification as there is about a decade out of date. The following is offered as a provisopnal arrangement., until something better comes along MAK120507

Superphylum Ecdysozoa Aguinaldo et al. 1997 (cont.)
Phylum Lobopodia Snodgrass, 1938 (cont.) *or* Arthropoda [1]
Subphylum Protarthropoda Lankester, 1904 [2]
Class Dinocaridida Collins 1996 [3] (monotypal - Order Radiodonta)

Orders and families unspecified: the basal dinocaridids (*Kerygmachela* & *Pambdelurion*, probably each deserve a monotypal family, E Cam of Greenland)
Order Opabiniida Størmer 1944 (currently monotypal, *Opabinia regalis* Walcott 1912 only, M Cam of Nth Am)
Family Opabiniidae Walcott 1912
Order Radiodonta Collins 1996 [4]
Family Anomalocarididae Raymond 1935 (nektonic apex preditors; Cam to Dev, Cosm.)
Subfamily Anomalocaridinae [5] (*Anomalocaris* & co; Cam to E Ord, Cosm.)
Subfamilies unspecified (*Schinderhannes*, *Parapeytoia*, and other forms more advanced to the arthropod condition than standard Anomalocarididae, Camb to Dev)

Notes

[1] Such is their status as transitional forms that dinocaridids can equally be conbsidered highly arthropod-like lobopodians or stem arthropods. Although there is a tendency to consider more primitive forms like *Kerygmachela* as lobopod and more derived froms like *Anomalocaris* as arthropods, this creates an artificial distinction between a grade of very similar animals (*Kerygmachela*'s only really distinctive primitive feature here is the centrally located, xenusian-like mouth) MAK120503

[2] Regardless of which phylum they are included in, we believe that Dinocaridids are distinct enough (as transitional forms) to deserve their own subphylum MAK120503

[3] As defined by Collins, Dinocarids are bilaterally symmetrical arthropods with a body divided into two principal tagmata, recalling the prosoma and opisthosoma of chelicerates, and a non-mineralised cuticle. The front part shows no external segmentation, bears one or more pre-oral claws, one or more pairs of prominent eyes, and a ventral mouth; differing from other arthropod classes in possessing no antennae and only one appendage or pair of pre-oral appendages on the prosoma, and in bearing gilled lateral lobes on the metameric trunk. The jaws vary from none to forms with both radiating teeth and teeth in rows. - Chris Clowes..

[4] Collins (1996, p. 291) restricted the Radiodonta to exclude the Opabiniidae and, although these genera were not described at the time, certainly he would have excluded *Kerygmachela* and *Pambdelurion* also. These two taxa are highly problematic, being known from a single locality, the Sirius Passet location in northeastern Greenland, and occupying an uncertain position intermediate between the onychophorans, anomalocaridids, and euarthropods. Graham Budd, who described both taxa, interprets them to imply that at least the biramous arthropods actually arose from within the anomalocaridids, the biramous limb having evolved before full cuticular sclerotisation. - Chris Clowes..

[5] We have here made an arbitrary distinction between mainstream anomalocaridids, which constitute a mostly Cambrian monophyletic clade, and more advanced and derived forms. MAK120503

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Unit Back: Onychophora | **Clade Down: Arthropoda** | **Dendrogram** | **References** | **Unit Next: Arthropoda**

Dinocaridida: Dendrogram

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

Contents

Dinocaridid phylogeny. This phylogeny is based mostly on Daley et al 2009 and Liu et al 2011. *Kerygmachela* is sometimes considered a basal lobopod because of the terminal rather than ventral mouth. But as most of its other characteristics are clearly Dinocarididian we have placed it as a basal member of that evolutionary grade. MAK120423

Abbreviations:

MH = Mikko Haaramo's Phylogeny Archive

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA (= monophyletic Paneuarthropoda)  MH
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Amplectobelua
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  |?--Cucumericrus
                  `--+--Parapeytoia
                     `--ARTHROPODA
```

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Dinocaridida: References

Abbreviated Dendrogram

```
PANARTHROPODA
`==Siberiidae
   |
   `--DINOCARIDIDA
      |--Kerygmachela
      `--+--Pambdelurion
         `--+--Opabinia
            `--+--Anomalocarididae
               |  |--Hurdia
               |  `--+--Anomalocaris
               |     `--Laggania
               `--+--Schinderhannes
                  `--ARTHROPODA
```

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Dinocaridida

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ECDYSOZOA | OVERVIEW

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Ecdysozoa: Tardigrada

Abbreviated Dendrogram

```
PANARTHROPODA
|
`--+--TARDIGRADA
    `--+==Cambrian Lobopods
        |--ONYCHOPHORA
        `--+==DINOCARIDIDA
            `--ARTHROPODA
```

Contents

Pseudobiotus, a tardigrade or water bear
Photo by Antonio Guillén Flickr: EOL Images , Encylclopaedia of Life, Creative Commons Attribution Non-Commercial Share Alike

Tardigrades, or "water bears", are tiny, eight-legged, segmented creatures, accorded subphylum (Cavalier-Smith (1998)) or phylum (Neilsen 2001) rank. They live in water, although the 'water' may be the moisture held between the leaves of a moss, and they are capable of producing a thick-walled, protective resting cyst and surviving long periods of dessication (and, apparently, immersion in alcohol, freezing, boiling, vacuum and irradiation; Tudge 2000, p. 257).

Closely related to onychophores and arthropods (Budd 2001), they would have evolved from a Cambrian abcestor not unlike *Aysheaia*. By the Middle Cambrian they had already acheived microscopic size and other specialised features of the group (Müller et al 2005) - Chris Clowes and MAK120425

Page Back: Panarthropoda	**Unit Up: Ecdysozoa**	**Unit Home** **(you are here)**	**Page Next: Tardigrada**

Tardigrada

Something about "Water Bears"

Abbreviated Dendrogram

```
PANARTHROPODA
|
`--+--TARDIGRADA
    `--+==Cambrian Lobopods
        |--ONYCHOPHORA
        `--+==DINOCARIDIDA
           `--ARTHROPODA
```

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Introduction

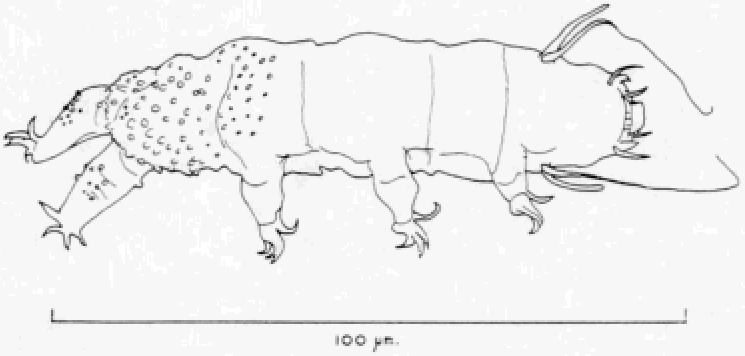


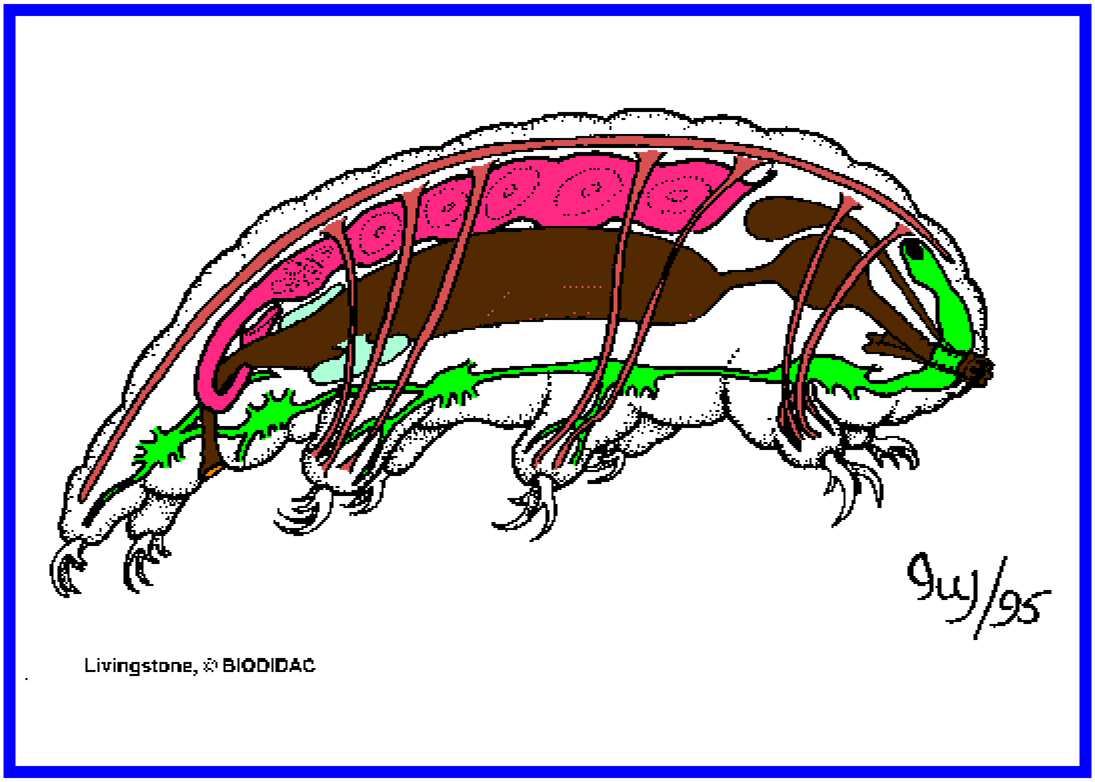
Fig. 1. *Oreella mollis* J. Murr. General body plan.

"Water Bears"!? No one really knows why tardigrades are called "water bears." It's surely a stupid name. There are a number of explanations for the name in circulation, but the explanations tend to conflict and don't make much sense **[1]**. In any case, it's ridiculous to call a 500μ long (1/50th of an inch) primitive arthropod, which doesn't necessarily live in water, a "water bear." Tardigrades do require a thin layer of water to respire, when active, and they do move in a sort of ungainly, rolling fashion, but the resemblence ends there. Ecologically, they're more like aphids or nematodes, anatomically more like insects, morphologically more like pill bugs, and functionally more like vegetarian vampires. Phylogenetically -- well, who knows? They seem to be near the base of the Arthropoda, but could be more closely related to the "acoelomate" worms.

It has recently been learned that tardigrades are very old bugs indeed, with quite distinctive fossils from Siberia dated at about 530 My. Currently there are about 800 known species, although this is undoubtedly a very small fraction of the actual diversity of the Tardigrada. Tardigrades are capable of living in even the most extreme environments due, in part, to an almost unique talent for surviving in a dehydrated, "cryptobiotic" state which they can maintain for years at a time, like instant oatmeal. They are known from every continent, including Antarctica, and every ocean (although the majority of living forms are terrestrial). They normally live in close association with mosses or other vegetation which holds moisture. They have a little straw-like stylet which they stick into plant cells and use to suck out the contents.

Developmentally, they remind one a little of nematodes. That is, the body elements tend to be single, very specialized cells -- lone muscle cells for example. The cells get bigger during growth, but there is little cell division after birth. While tardigrades do have some degree of organ-level development, most of the body plan seems to be nematode-like cell-by-cell differentiation, which may be the original metazoan way.

Anatomy



Tardigrades range in size from 50 (bacteria-sized!) to 1200μ. They have a bilaterally symmetrical, cylindrical body. The head is bluntly rounded, contains the mouth, and may be equipped with sensory (probably tactile) cirri. Some tardigrades have a pair of eyes, consisting of a single pigmented cell each. A feature almost unique (nemertine worms have something similar) in the animal kingdom are the two calcareous stilettos behind the mouth opening. They use it to pierce their food -- usually moss cells, algae, and sometimes other small animals -- before sucking it out.

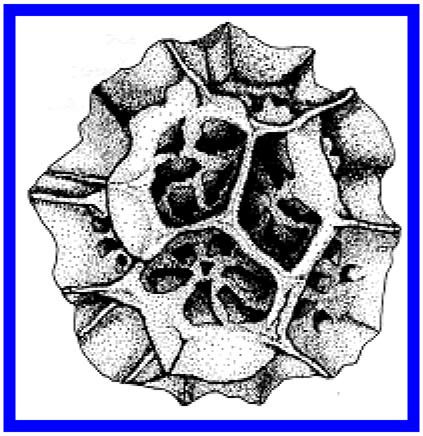
The body is short, plump, cylindrical covered with a rather soft chitinous cuticle. Some tardigrades have hard chitinous body armor. The chitinous cuticle is secreted by the underlying epidermis. The muscular system is composed of numerous muscle bands, each a single muscle cell, extending from one subcuticular point of attachment to another. A single, saccular gonad occupies the coelom. Other internal organs are suspended in a general hemocoel. Tardigrades possess eight legs with ventral orientation. The legs consist of simple extensions of the ventrolateral body wall extending ventrally, ending in four to eight claws each.

The digestive system is composed of an anterior mouth with associated salivary glands and stylet apparatus, a sucking pharynx, an esophagus, a stomach or midgut, and a rectum or hindgut, emptying through the anus or cloaca. The mouth is stiffened by rings of cuticle. The salivary glands, stylets, and sucking pharynx are known as the buccal apparatus. After the stylets are extended to pierce plant or animal cell walls, the sucking pharynx draws the cell fluids into the digestive system. The salivary glands are believed to form new stylets at molt. The esophagus ranges from long to short in length. Secretions in the midgut, where absorbtion occurs, are acidic anteriorly and alkaline posteriorly. The hindgut empties through the anus.

The excretory system is composed of a dorsal excretory gland and a pair of Malpighian tubules. The nervous system is composed of a brain, a pair of longitudinal nerve strands, and four ventral ganglia. The brain is composed of two lateral lobes connected by two circumpharyngeal cords to a subpharyngeal ganglion. The ventral ganglia are united by the longitudinal nerve strands. Paired nerves from the brain and ganglia innervate the body. Long strands may have small terminal ganglia.

The reproductive system is composed of a single saccular gonad in a coelomic pouch lying dorsal to the digestive system. In the Eutardigrada, gonoducts open into the rectum. In Heterotardigrada, gonoducts open to the outside through a preanal gonopore. Males possess two vas deferentia, a swollen portion serving as a seminal vesicle. Females possess a single oviduct which passes to the right of the intestine. In accordance with the small size of tardigrades, there is no respiratory or circulatory system.

Reproduction



Females almost always outnumber males among the tardigrades. This sounds like a good deal for the males, except that some species have learned to do without the males completely and reproduce by parthenogenesis. There is surely a moral lesson in that, but it escapes us at the moment.

Tardigrade eggs are ornamented, and the ornamentation may be unique to the species -- which is helpful in sorting them out. Cleavage is total and apparently equal. Gastrulation occurs by unipolar proliferation. Five pairs of coelomic pouches form. The posterior pair fuse to form the gonad. The others degenerate and form the buccal apparatus and body muscles.

The embryo undergoes direct development. Hatching is accomplished by the piercing of the egg by the stylets and legs. Cell division ceases with birth, and all development thereafter occurs by growth of individual cells.

Ecology and Lifestyle

Tardigrades occur in marine, freshwater, and damp terrestrial habitats. Typically, they are found as part of interstitial communities, on filamentous algae, or inhabiting the surface films of mosses, lichens, and damp forest litter. Tardigrades feed on the fluids of plant and animal cells. A few tardigrades are entirely carnivorous, preying on amoebas, nematodes, and other tardigrades. Most species appear to he eurythermal, tolerating temperatures from near freezing to upwards of 30 degrees C. Food is stored in some epidermal cells. Respiration occurs by diffusion.

Tardigrades frequently display cryptobiosis, a sort of freeeze-dried suspended animation. Anhydrobiosis occurs under conditions of dessication. The animal contracts, loses water, and takes on a shriveled, wrinkled appearance. This "tun" may survive in this state from four to seven years. Animals have been recovered from this state after immersion in liquid helium, absolute alcohol, brine, and ether. Cysts may be formed when the animal undergoes stress in the form of damage, hunger, or abnormal environmental conditions. The animal withdraws into the cuticle and forms a dark, thick-walled cyst. The internal organs undergo some degeneration. The animal reconstitutes in favorable conditions. When deprived of oxygen, tardigrades will enter an anoxybiotic state: the animal swells, the body becomes turgid and movement ceases -- similar to the effect of television on humans.

Phylogeny and Diversity

Eutardigrada: Lack anterior cirri and lateral filaments

Macrobiotidae: Sucking pharynx with macroplacoids

Milnesiidae: Sucking pharynx without macroplacoids, mouth surrounded hy six papillae.

Heterotardigrada: Head with anterior cirri and lateral filaments, four separate but similar claws on each leg.

Echiniscoidea: Stout posterior legs not set off by cuticular folds.

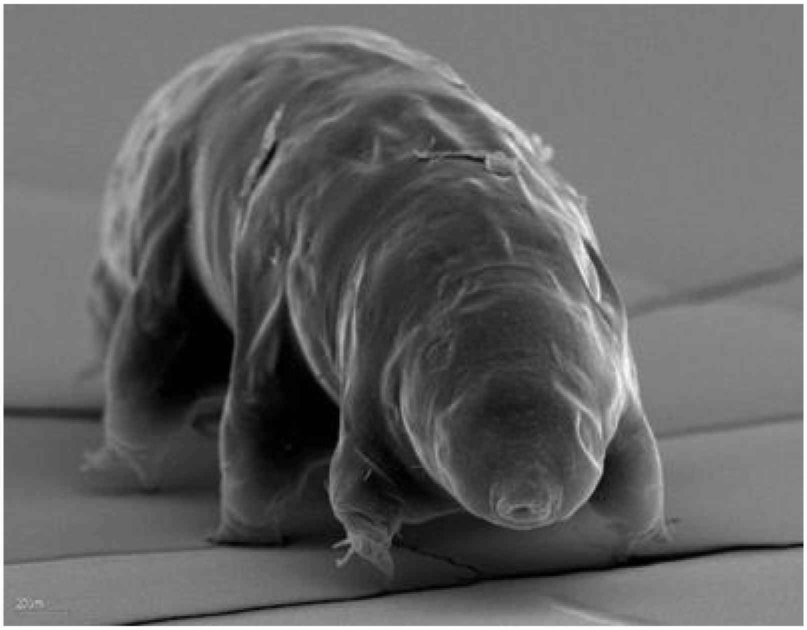
Mesotardigrada: Six similar Long claws on each leg; one species, *Thermozodium esakii* is from Japanese hot springs.

Notes

[1] We are informed by Thorfin Hallas that the name "water bear" name might derive from one of the first tardigrades described, *Acarus ursellus*. This just makes things worse. *Acarus ursellus* means "bear-like mite." Tardigrades are not much more closely related to the mites (Acari) than they are to bears. The mites are probably chelicerates, closely related to spiders.

Descriptions

Tardigrada Doyère 1840 ; Water bears



Range: Fr Cambrian

Phylogeny: Panarthropoda : *Mureropodia* + (*Aysheaia* + ((Euonychophora + (*Kerygmachela* + (Dinocaridida + Arthropoda))))) + *)

Comments: Miniaturized lobopods, convergent on arthropods. Live in moss, leaf litter, damp soil, or freshwater or marine habitats. Capable of astonishing cryptobiosis (dormancy for extended periods) . Fossil tardigrades similar to modern forms, but outside the crown group, are known from the Middle Cambrian Orsten-type lagerstätte of Siberia (Müller et al 2005; CORE - Orsten Research). *Milnesium swolenskyi*, family Milnesiidae, is known from Cretaceous amber from New Jersey and is barely distinguishable from extant forms (Grimaldi & Engel. 2005 p.97) MAK120430

Links: Wikipedia; Encylclopaedia of Life; Tardigrada Tree of Life; Tardigrade Newsletter - current research on tardigrades compiled by two researchers; Tardigrades - Tardigrada - Bärtierchen (in English & German) ; Tardigrades (Water Bears); Tardigrade appreciation headquarters; Tardigrade Facts; ATW040105, revised MAK120424

Image, from lecture notes by Tom Holtz - Invertebrate Paleontology, Ecdysozoa, Panarthropoda

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page uploaded ATW030110, checked ATW040105. Last modified MAK12030

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|
`--+--TARDIGRADA
    `--+==Cambrian Lobopods
        |--ONYCHOPHORA
        `--+==DINOCARIDIDA
           `--ARTHROPODA
```

Budd, G. E. (2001). Tardigrades as "stem-group arthropods": the evidence from the Cambrian fauna. *Zoologischer Anzeiger*, 240, 265–279. **pdf**
Overview.

Cavalier-Smith T (August 1998). "A revised six-kingdom system of life". *Biol Rev Camb Philos Soc* 73 (3): 203–66. doi:10.1111/j.1469-185X.1998.tb00030.x. PMID 9809012.
Overview.

Grimaldi & Engel. 2005 , *Evolution of the Insects*
Tardigrada

Mulleretal2005Müller, K. J., Walossek, D. & Zakharov, A. (1995): ‘Orsten’ type phosphatized soft-integument preservation and a new record from the Middle Cambrian Kuonamka Formation in Siberia. *Neues Jb. Geol. Paläont., Abh*. 197: 107–118.**pdf**
Overview, Tardigrada

Nielsen, Claus 2001: *Animal Evolution*. Second Edition. 563 pp. Oxford University Press.
Overview.

Andreas Schmidt-Rhaesa 2001 Tardigrades – Are They Really Miniaturized Dwarfs? *Zool. Anz*. 240 (2001): 549–555 **pdf**

Tudge, Colin 2000: *The Variety of Life*. Oxford.
Overview.

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Ecdysozoa: Onychophora

Abbreviated Dendrogram

```
PANARTHROPODA
|--Aysheaia
`--+--TARDIGRADA
   |
   `--+--ONYCHOPHORA
      |  |--Antennacanthopodia
      |  `--Euonychophora
      |     |--Helenodora
      |     `--+--Peripatopsidae
      |        `--Peripatidae
      `==DINOCARIDIDA
         `--ARTHROPODA
```

Contents

Velvet Worm (Euonychophora - Peripatidae) from the Amazon Rain Forest in Peru. Photograph taken by Thomas Stromberg, July 2002. Public domain, via Wikipedia

The Onychophora (literally "claw bearers", after the tiny claws at the tips of their stubby limbs) or velvet worms are what seem to be an ancient group, as apparently very similar forms were common and diverse during the Cambrian. This led to the idea that they are "living fossils" prehistoric relics from the time when animals were just evolving legs. But as with other such prehistoric survivors, appearances can be deceiving. Modern or crown group onychophora are highly specialised animals with unique slime glands for prey capture that are not found even in many Tertiary forms, while their stumpy-legged gait is quite different from that of the horizontal-legged crawlers that were their Cambrian forebears. While not very dicverse or abundant in relation to the more successful phyla such as the arthropods, molluscs, and vertebrates, they are clearly survivors, a unique evolutionary lineage successfully continuing alonmgside the big boys. MAK120426

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Ecdysozoa: Onychophora

Abbreviated Dendrogram

```
PANARTHROPODA
|--Aysheaia
`--+--TARDIGRADA
   |
   `--+--ONYCHOPHORA
      |  |--Antennacanthopodia
      |  `--Euonychophora
      |     |--Helenodora
      |     `--+--Peripatopsidae
      |        `--Peripatidae
      `==DINOCARIDIDA
            `--ARTHROPODA
```

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Onychophora

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1. *Antennacanthopodia* X
2. Onychophora

Introduction

Onychophorans, the group that includes the extant velvet worms and their immediate fossil relatives, are a group of shy and retiring invertebrates that frequent the wet tropics and rather resemble elongate caterpillars. They possess a soft chitinous exoskeleton, and share a number of characteristics with both annelids (segmented worms), and arthropods (unbranched limb and insect-like tracheae). Variously included with annelid worms under the Articulata, and with myriapods and inscets under the Uniramia, The embryonic development of is identical to that of annelids and uniramious arthropods, so and it was for a long time thought that these creatures seem to represent a missing link between the two groups. It has even been suggested Ballard et al 1992 that the Onychophora are actually modified arthropods, rather than the other way around. However, modern molecular phylogeny has shown that annelids and arthropods are not at all closely related, and the consensus now is that they belong to the clade of moulting animals (Ecdysozoa). They share a common ancestry to arthropods, but are neither ancestral to nor descended from them; or to put it differently, tardigrades and onychophores are stem-groups (early side branches) on the main arthropod line (Budd 2001, Edgecombe 2009). Similarities with both annelids, myriapods, and insects are therefore the result of evolutionarty convergance. They are variously given class (if included under Arthropoda), subphylum (Cavalier-Smith (1998)) or phylum (Neilsen 2001) rank. MAK120426

Fossil History

A number of Cambrian fossils have been described which look more or less like onychophorans. Some, such as the Middle Cambrian form *Aysheaia* are rather similar to living forms and have been traditionally included in the Onychophora. Others were armored with various plates and spines which, disarticulated, contribute substantially to the "small shelly fauna." The majority opinion now is that Cambrian lobopods represent a paraphyletic assemblage of early panarthropods, many of which were not even on the ancestral line to onychophores, although some may be (see phylogenetic review). All of these Cambrian forms differed from living onychophorans in being marine.

The earliest fossil terrestrial onychophoran was found in the Pennsylvanian deposits of Mazon Creek, near Chicago, a locality that has yielded a great many fossils of soft-bodied organisms. The fossil is not very different from living onychophorans (Thompson and Jones 1980).. Several Cretaceous and Teriary species hacve also been found preserved in amber - Chris Clowes - Peripatatus. upodated MAK120426

Loss of exoskeleton

Euonychophorans differ from Early Paleozoic lobopods in lacking the spines and armour plates of their ancient marine ancestors. This can be related to changes in one of the Hox genes called *engrailed*. To quote (Jacobs *et al*. 2000,

> "Onychophorans are thought to be the sister taxon of arthropods and are segmented. However, onychophorans lack *engrailed* expression in their dermis. Instead, expression is observed in the posterior half of the developing limb and in a segmental pattern in the lateral mesoderm. The limb staining suggests shared ancestry of the onychophoran and arthropod limbs. However, given the close relationship of Arthropoda and Onychophora, and their segmented body plans, the lack of segmental ectodermal expression in Onychophora suggests that the ancestral role of *engrailed* was not segmentation; this absence may be a consequence of evolutionary loss of skeletons. Onychophoran dermis lacks a chitinous cuticle; thus Onychophora lack an exoskeleton. Furthermore, Cambrian fossils thought to be stem group onychophorans, such as *Microdictyon*, *Hallucinogenia*, and *Xenusion*, bear skeletal elements above the limb on each segment. Therefore, the absence of *engrailed* transcription in the ectoderm of modern Onychophora could well be a consequence of evolutionary loss of exoskeletal elements..." (Jacobs *et al*. 2000, pp. 343-345; full text). - via Chris Clowes - Peripatatus

Descriptions

Onychophora **Phylogenetic definition:** here defined as all species closer to .*Peripatus* (Euonychophora) than to *Echiniscus* (Tardigrades) or *Drosopholia* (Arthropoda)

Range: Cambrian? or Carboniferous to Recent

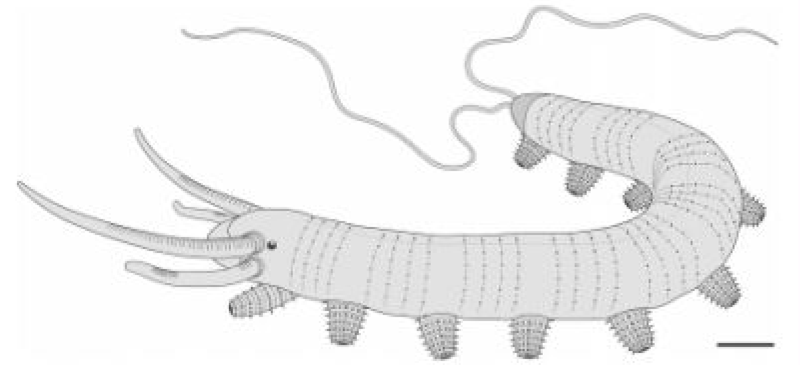
Phylogeny: Panarthropoda **:** *Mureropodia* + (*Aysheaia* + (Tardigrada + ((*Kerygmachela* + (Dinocaridida + Arthropoda)))) + * **:** *Antennacanthopodia* + Eunychophora))

Characters: "Primitively, homonomous annulation (present in crown-node; one pair of differentiated frontal appendages (present in crown and widespread in outgroups); a terminal mouth; and none of the specialist features of the extant Onychophora such as slime papillae; feet and jaws (none of these structures are known from any immediate outgroups)". Budd 2001

Comments: "The class Onychophora was used by Hou & Bergström 1995 to include the terrestrial forms: the modern onychophorans and the single known fossil terrestrial species, Helenodora. These authors also noted their belief that the fossil marine form, *Onychodictyon*, "is closer to modern onychophorans than any of the other Cambrian lobopodians" (p. 11). Their cladogram (Hou & Bergström 1995, fig. 7) depicts *Onychodictyon*, *Helenodora*, and modern onychophorans together comprising a well-formed clade. Yet in their systematic section (p. 17) *Onychodictyon* is left outside Onychophora, in the class Xenusia, on morphologic grounds. In the spirit of a more cladistic taxonomy, the class Onychophora is here broadened to include the marine Onychodictyidae (Onychodictyon)." - Chris Clowes - Peripatatus However cladistic analysis generally presents *Onychodictyon* in a more derived position (see link for references). Other canditates for sister taxon of extant onychophora are *Orstenotubulus* (Edgecombe 2010 fig.1) and *Antennacanthopodia* (Ou et al 2011) MAK120426

Links: UC Berkeley; Wikipedia

Antennacanthopodia gracilis Ou et al 2011



Horizon: Chengjiang Lagerstätte, Yunnan, southwestern China., (Early Cambrian)

Phylogeny: Onychophora **:** Eunychophora + *

Characters: two muscular and slender appendage pairs (prominent frontal and second antenna), simple lateral eyes situated basal of frontal antennae; trunk devoid of obvious annuli and sclerotized plates; a straight, voluminous midgut, diminutive spines arrayed on the leg and the trunk, stout euonychophore-like lobopods with well-developed legs armed with annuli of thorn-shaped spines, highly sclerotized disc-shaped terminal leg pads, pair of putative cirriform appendicules attached to terminal projection of trunk (Ouetal2011)

Comments: an unarmoured form that seems to be intermediate between Cambrian lobopodians and extant Onychophora. (Ou et al 2011) We have tentatively included it here as a stem-group onychophore. MAK120426

Illustration: Life reconstruction of *Antennacanthopodia gracilis* from (Ou et al 2011. The anetnnae in teh name are the frontal and second antennae at the left; what look like long wavy arthropod antennae at the rear are actually a pair of cirriform structures. Scale bar: 1 mm.

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Ecdysozoa: Euonychophora

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|--Aysheaia
`--+--TARDIGRADA
   |
   `--+--ONYCHOPHORA
      |  |--Antennacanthopodia
      |  `--Euonychophora
      |     |--Helenodora
      |     |--Succinipatopsis
      |     |--Tertiapatus
      |     `--+--Peripatopsidae
      |        `--Peripatidae
      |           |--Cretoperipatus
      |           `-- Peripatus
      `==DINOCARIDIDA
         `--ARTHROPODA
```

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Cretoperipatus + *Peripatus*

1. Euonychophora
2. *Helenodora* X
3. Peripatidae
4. Peripatopsidae

Peripatus

5. *Succinipatopsis* X
6. *Tertiapatus* X

Peripatoides sp., (family Peripatopsidae).
photo by Bruno Vellutini, via Wikipedia. Creative Commons Attribution-Share Alike

The Euonychophora

Introduction

The Onychophora include around 110 described species (and likely a similar number undescribed) of caterpillar-like relatives of arthropods. The first description of a living onychophoran was in 1826 (misinterpreted as a leg-bearing "slug", a mollusc). All living species are terrestrial. They are found in humid habitats, stashing themselves away in burrows or other retreats and becoming inactive during dry periods. During wet periods, they can be found sifting through leaf litter. One particularly unusual aspect of onychophoran behavior is their method of prey capture, which involves shooting twin streams of a rapidly hardening adhesive slime up to 30 cm to entangle their prey. With the exception of just a few species, onychophorans have not been well studied and the New World fauna is especially poorly known. text © Leo Shapiro Creative Commons Attribution Non-Commercial Share Alike

Morphology

The body itself is not segmented except for the head, which is divided into three segments. The first contains the two large antennae with an eye at the base (Jamaica and South Africa have cave dwelling species which do not have eyes). Some males also have other appendages believed to be involved in sperm transfer. The second segment contains the jaw like mouth which is used for rasping into prey and then sucking out the nutrients. The third segment holds the first pair of parapodia-like legs.

Contemporary onycophorans are ceolomates and have hemocoel, which means they have a lined body cavity filled with blood, rather than a vascular system. They have a muscular tubular heart which pumps the colorless blood around the body cavity. Locomotion is essentially annelid-like, with the body cavity functioning as a hydrostatic skeleton. The parapodia-like legs are also filled with blood and a valve at the base keeps them firm and muscular coordination can extend them or retract them and make them move forward or make them move backward.

On the end of their legs they bear chitinous claws for gripping, although on smooth substrate they walk on walking pads. Onycophorans have a cuticle with a-chitin but lacking collagen, which is periodically shed to permit growth (ecdysis). New cuticle is secreted underneath the old one by the ectodermal cells which develop microvilli that are subsequently withdrawn. Ecdysteroids have been found in various tissues but their function remains unknown

(Hoffmann 1997; Nielsen 2001, p. 198). Unlike insect dermis, their cuticle is non-articulated, thin and soft and covered in hundreds of papillae and sensory hairs giving them a velvety texture, hence the common name 'velvet worm.'

Like insects the Onycophora breathe through spiracles. Spiracles open out to the environment and oxygen enters through a system of tubules (tracheae) and is absorbed into the tissues across the moist surfaces. However, unlike the insects, Onycophora have no control on the spiracles and they are always open, making the animal extremely vulnerable to desiccation, so high levels of humidity are required.

Contemporary Onycophorans are able to predate organisms several times larger than themselves by immobilizing it with a gluey secretion from glands in its head, projected up to 30cm. The secretion holds the prey while the animal approaches it, bites through the cuticle, and injects a toxic, digestive saliva into the wound.

Onychophorans themselves have few predators, except perhaps insect carnivores such as centipedes, birds and rodents. - - Chris Clowes - Peripatatus

Fossil Record

All living onychophorans are relatively conservative morphologically. Reconstruction of the stem-group, and erection of successive scions leading down towards the basal node is, however, more difficult, due to the poor fossil record. The Carboniferous *Helenodora* has been assigned to the Onychophora, but the critical head region is missing. Onychophorans have been described from Tertiary Baltic and Dominican amber, and show that the very short slime papillae and the distinct foot of extant Onychophora are derived crown-group features, as some of the fossils lack them. These Tertiary fossils are likely to lie in the Onychophoran stem group. - Budd 2001

Descriptions

Euonychophora **Phylogenetic definition:** here defined as all species closer to .*Peripatus* (Euonychophora) than to *Echiniscus* (Tardigrades) or *Drosopholia* (Arthropoda)

Range: Carboniferous to Recent

Phylogeny: Onychophora : *Antennacanthopodia* + * : *Helenodora* + *Succinipatopsis* + *Tertiapatus* + (Peripatidae + Peripatopsidae)

Comments: around 10 genera and 110 species recognized within two extant families: the Peripatidae (known from the circumtropical regions of Mexico, Central and northern South America, equatorial West Africa, and South East Asia) and the Peripatopsidae (found in Chile, South Africa, Australia including Tasmania, and New Zealand).Chris Clowes - Peripatatus

Euperipatoides rowelli; photo by Andras Kesze Flikr archive, Creative Commons Attribution Non-Commercial Share Alike

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Helenodora inopinata Thompson and Jones, 1980

Range: Carboniferous Mazon Creek of northern Illinois

Phylogeny: Euonychophora : *Succinipatopsis* + *Tertiapatus* + + (Peripatidae + Peripatopsidae) + *

Comments: Earliest known Euonychophoran

Succinipatopsis balticus Poinar, 2000

Range: Eocene Baltic amber

Phylogeny: Stem group Euonychophora

Tertiapatus dominicanus Poinar, 2000

Range: Eocene Baltic amber

Phylogeny: Stem group Euonychophora

Peripatopsidae Bouvier 1907

Range: Recent

Phylogeny: Euonychophora **:** *Helenodora* + *Succinipatopsis* + *Tertiapatus* + (Peripatidae + *)

Comments: The Peripatopsidae exhibit relatively many characteristics that are perceived as original or "primitive". They have between 13 and 25 pairs of legs, behind or between the last of which is the genital opening (gonopore). Both oviparous and ovoviviparous, as well as genuinely viviparous, species exist, although the Peripatopsidae essentially lack a placenta. Their distribution is circumaustral, encompassing Australia, Tasmania, New Zealand, New Guinea, South Africa and Chile. - Wikipedia.

Peripatidae Evans 1901

Range: Cretaceous to Recent

Phylogeny: Euonychophora **:** *Helenodora* + *Succinipatopsis* + *Tertiapatus* + (Peripatopsidae + * **:** *Cretoperipatus* + *Peripatus*)

Comments: The Peripatidae exhibit a range of derivative features. They are longer, on average, than the Peripatopsidae and also have more leg pairs, numbering between 22 and 43—the gonopore is always between the penultimate pair. There are no oviparous species—the overwhelming majority are viviparous. The females of many viviparous species develop a placenta with which to provide the growing embryo with nutrients. Distribution of the Peripatidae is restricted to the tropical and subtropical zones; in particular, they inhabit Central and northern South America, several Caribbean islands, West Africa, northern India, Malaysia and various Indonesian islands. Wikipedia. The only extant family witha fossil record, *Cretoperipatus* from Cretaceous amber of Burma

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Cretoperipatus burmiticus Engel and Grimaldi, 2002

Range: Cretaceous Amber of Kachin state, Myanmar (Burma)

Phylogeny: Peripatidae **:** *Peripatus* <+ */p>

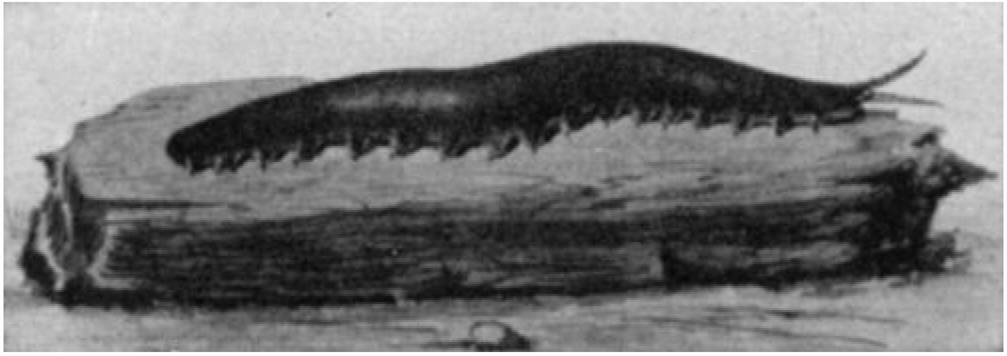
Comments: Unlike other fossil forms, Cretoperipatus can be assigned to a modern family. But while only five leg pairs can be discerned, the information gained from the fossil is enough to preclude assignment to any known modern genus. (Wikipedia)

Peripatus Guilding 1825

Range: Recent

Phylogeny: Peripatidae **:** *Cretoperipatus* + *

Comments: "A widely distributed



old-fashioned type of animal, somewhat like a permanent caterpillar. It has affinities both with worms and with insects. It has a velvety skin, minute diamond-like eyes, and short stump-like legs. A defenceless, weaponless animal, it comes out at night, and is said to capture small insects by squirting jets of slime from its mouth." J. Arthur Thomson. 1922. *The Outline of Science,*

Graphic: from above reference (Public domain, via Wikipedia)

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Onychophora: References

Abbreviated Dendrogram

```
PANARTHROPODA
|--Aysheaia
`--+--TARDIGRADA
   |
   `--+--ONYCHOPHORA
      |  |--Antennacanthopodia
      |  `--Euonychophora
      |     |--Helenodora
      |     `--+--Peripatopsidae
      |         `--Peripatidae
      `==DINOCARIDIDA
            `--ARTHROPODA
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