Evolutionary Relationships of the Arthropoda II

In the last lecture we concluded that based on the most recent evidence molluscs and annelids are more closely related to each other than either is to arthropods. The molluscs and the annelids are united into the Lophotrochozoa with a number of other phyla and the Arthropoda is the major phylum in another group called the Ecdysozoa. Note that this conclusion assumes that each of these phyla represents a monoplyletic group.

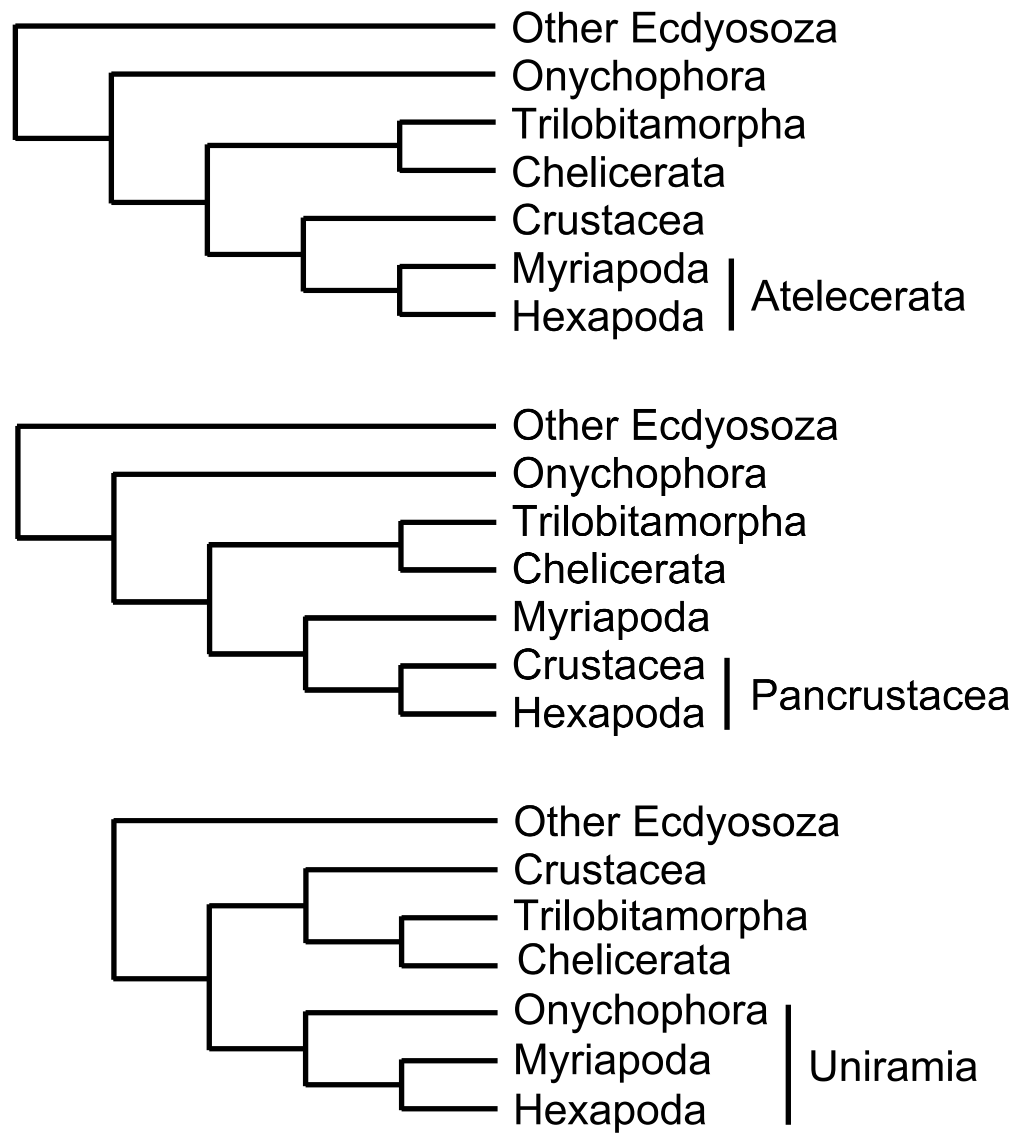
We are now ready to address the other two questions we asked in the previous lecture.

1. Are arthropods a single evolutionary lineage, or have the characteristics that “unite” them evolved multiple times?

2. What is the evolutionary relationship of insects to the other major groups (subphyla) in the Arthropoda?

Arthropoda and Related Phyla

- Based on the evidence presented in the last lecture the Arthropoda is more closely related to the phyla Onychophora and Tardigrada, which together comprise the Panarthropoda.
- The sister-group relationships among these three phyla are still debated. Some studies place the tardigrades as the sister group to the arthropods and others place the onychophora as the sister group of the arthropods.
- There are also competing hypotheses for the relationships among the various subphyla within the Arthropoda, primarily concerning the placement of the Myriapoda and the Onychophora.
- We will examine the evidence for these hypotheses by looking at some of the characters shared by these various groups.

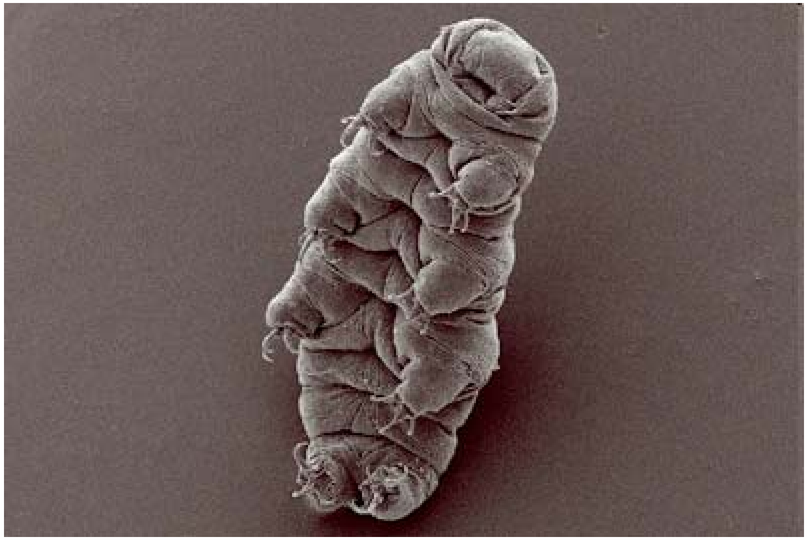


Onychophora: The Velvet Worms

- Approximately 100 species worldwide living among moist leaf litter in forest.
- Species are predatory, spraying a proteinaceous "glue" from the oral papillae that ensure prey such as snails, worms and small arthropods.
- Body segments have a pair of distinct, unjointed lobopods with terminal claws. The head segment also has one set of paired appendages which forms sensory structures superficially similar to the antennae of arthropods.
- The phylum unites primitive features of typical "worms" (e.g., Nematoda and Nematomorpha) with those of other panarthropods.
- Onychophores were present in the Cambrian and several enigmatic fossil forms from the Burgess Shale are place in the Onychophora, including *Hallucigenia*. Unlike the modern members of the phylum, these forms were entirely marine.
- The first terrestrial forms are known from the Upper Carboniforous about 300 mya.

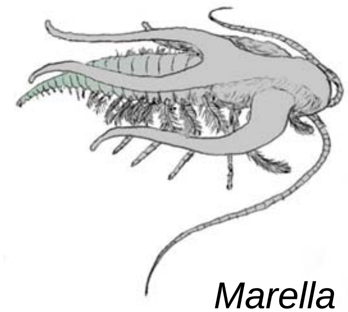
Tardigrada: The Water Bears

- Tardigrades are small animals (200-500 μm in length) that live in moss, lichens, leaf litter and freshwater and marine habitats. There are about 850 species worldwide.
- Species feed on mycelia, algae, plant cells, rotifers and nematodes.
- The best know feature of the phylum is the ability of some species to endure extreme conditions in a dormant, or cryptobiotic state: years, probably even decades of complete desiccation, and at temperatures well above boiling and near absolute zero. Tardigrades inhabit some of the harshest regions on earth, including Antarctica.
- Tardigrade-like forms have been found in mid-Cambrian deposits in Siberia.
- Tardigrades have shown very little change over their evolutionary history (bradytely).

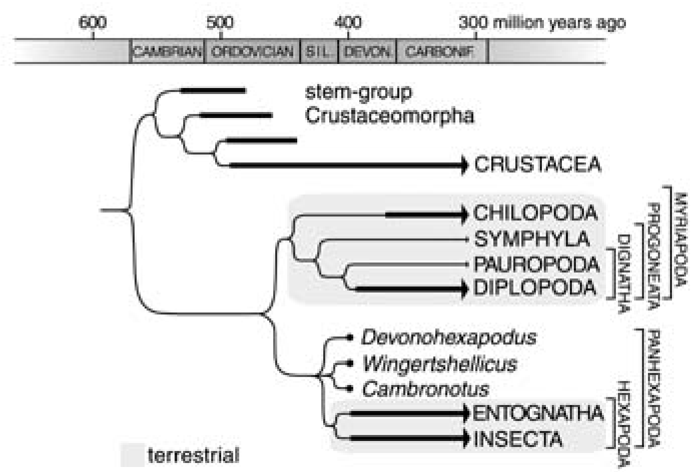


Early History of Arthropods and Insects

- Arthropods were very diverse in the Cambrian oceans, undergoing an explosive radiation in the mid-Cambrian (600 mya). This diversification included the trilobites and the lace crab (*Marella*) common in the Burgess Shale of British Columbia. These organisms were extinct by the end of the Paleozoic (250 mya).
- Trilobites and Marellomorphs were replaced in marine habitats by the Crustacea as dominant invertebrates.
- The earliest assemblages of terrestrial arthropod fossils are from the Late Silurian (415 mya), but fossilized trackways of arthropods on land are known from the Early to mid-Ordovician (480-460 mya). These trackways appear to be from early Chelicerates. The earliest evidence of insects is form the Early Devonian (410-400 mya).
- Invasion of land occurred independently in the Myriapoda and Hexapoda and in the Crustacea (Isopoda), Chelicerata, Tardigrada and the Onychophora.
- Arthropods were the earliest know terrestrial animals. The fact that these early land animals were all predatory indicates that the selective pressure for terrestrial living was perhaps not an herbivorous diet of land plants.
- Early, amphibious arthropods may have ventured on to land as part of their reproductive cycle. They may have sought temporary refuge on land from predators in the coastal waters or to feed upon worms and other animals feeding on microbial and algal mats growing at the water's edge.

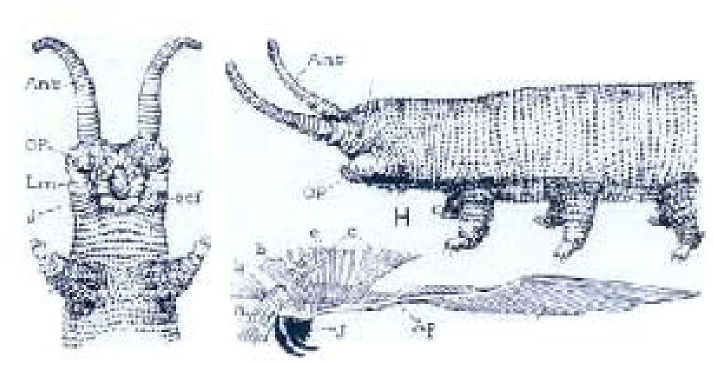


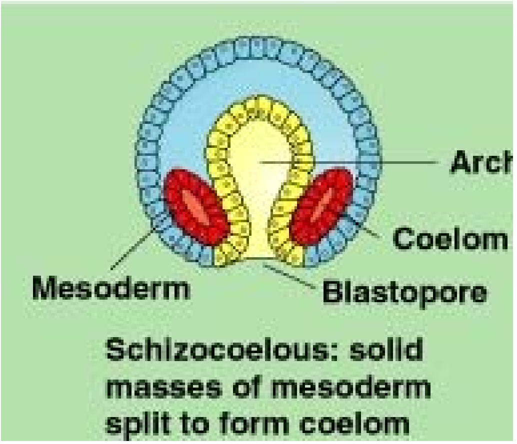
Marella



Characters shared by the Panarthropoda (Onychophora, Tardigrada & Arthropoda)

- Segmentally repeated limbs with terminal claws. Onychophora means “clawed foot”.
- Limbs straddle parasegmental boundaries marked by the expression of the segment polarity gene *engrailed*.
- Segmental paired nephridia as an excretory system.
- Open circulatory system characterized by the fusion of the coelomic cavity and the body cavity (a mixocoel) and a dorsal heart with openings to the haemocoel.
- Nephridia, the mixocoel and heart are absent in the Tardigrada, presumably as a result of their small size.





Polyphyletic Origin of the Arthropoda?

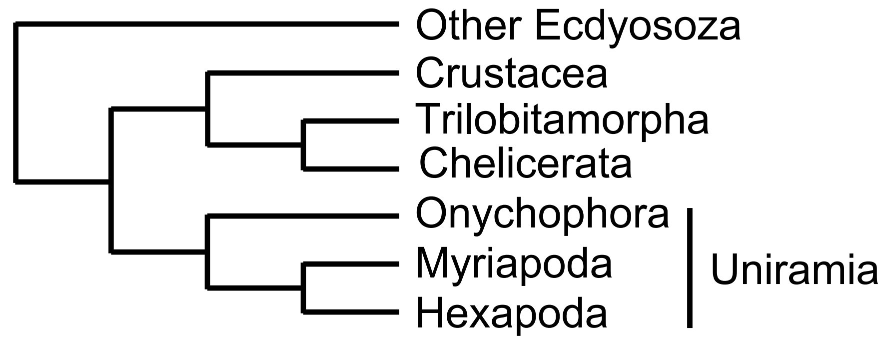
- O. W. Tiegs and S. M. Manton argued that the Arthopoda were an artificial combination of two unrelated groups: the Myriapoda, Hexapoda and Onychophora (the “Uniramia”) and the Trilobita, Crustacea and Chelicerata (“TCC”). According to this hypothesis the Uniramia and the TCC originated independently from worm-like ancestors and converged on “arthropod” traits. They based their argument on two separate character systems.

- The presence of uniramous appendages in the Uniramia and biramous in the appendages (TCC).

- The presence of whole-limb jaws in the Uniramia and gnathobasic jaws in the TCC.

- Their theory ignored all the other derived characters shared by arthropods and focused on the differences among groups.

- Recent work has shown the mandibles of onychophorans and insects develop on different body segments and the musculature of crustaceans and uniramous arthropods are homologous. Fossil evidence indicates that both biramous and uniramous appendages arose from an ancestoral polyramous leg.



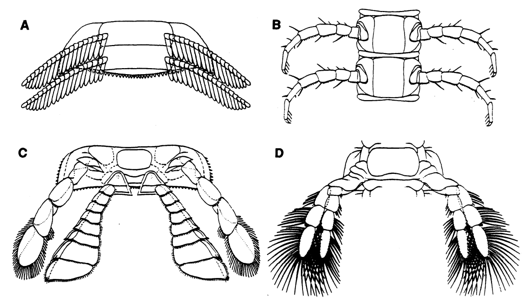
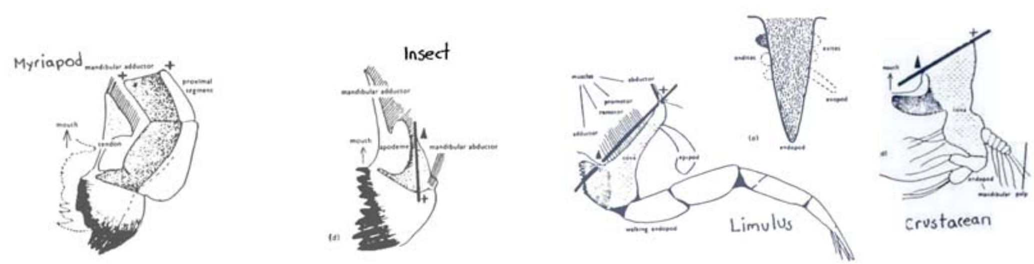
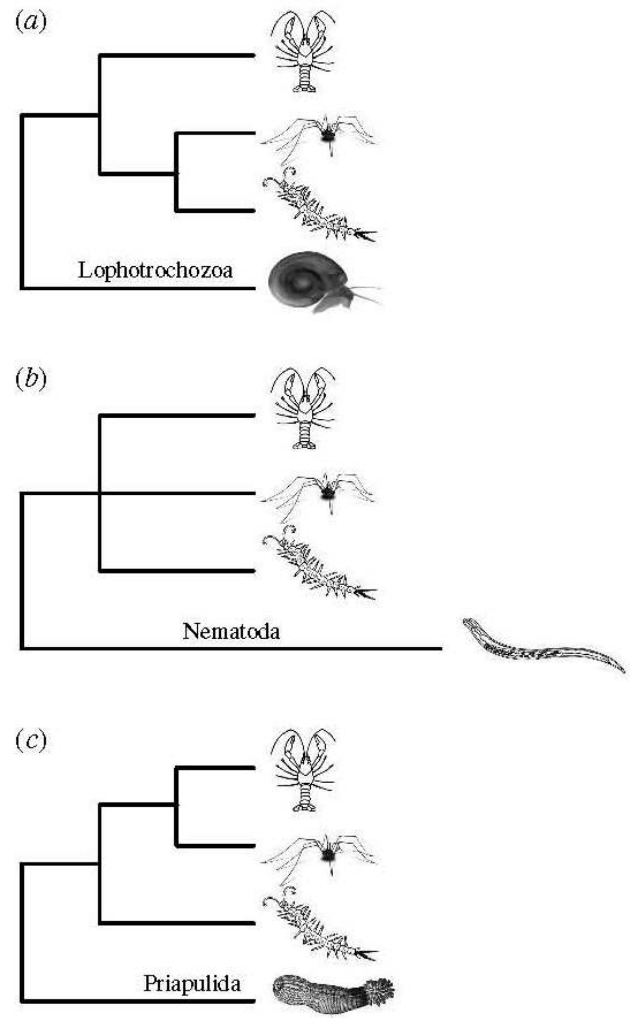


Fig. 2. Semidiagrammatic, ventral views of body segments from representative uniramians and crustaceans. (**A**) Diplosegment of a generalized fossil euthycarcinoidean with uniramous limbs. (**B**) Two segments of a geophilomorph centipede, each with uniramous limbs. (**C**) Segment of the enantiopodan remipede, *Tesnusocaris*. (**D**) Segment of a nectiopodan remipede.



Mandibulata versus Myriochelata

- Myriapoda share numerous similarities of head organization with insects and crustaceans, including the presence of a mandible on the third, appendage-bearing head segment, two pair of antennae (at least primitively), two pair of maxillae and paired gnathobasic mandibles. This group has been referred to as the Mandibulata.
- Recent molecular studies, however, place the Myriapoda closer to the Chelicerata than to the crustacea and the insects. But, the placement of the Myriapoda depends on the outgroup used. Distance outgroups place them near the Chelicerata, whereas more closely related outgroups place them closer to the crustacea.
- Proper phylogenetic reconstruction needs to what outgroup to use. Outgroups should be closely related to the taxa understudy (the ingroup).



Atelecerata versus Pancrustacea

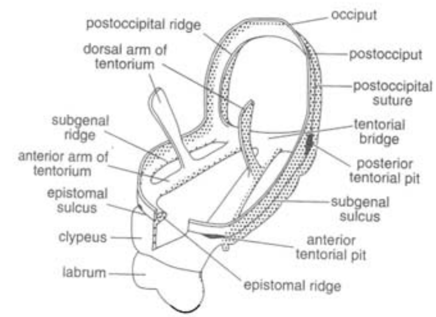
- Myriapoda and Hexapoda share several morphological characters including the loss of the second antennal pair, presence of a tentorium (internal head skeleton), uniramous appendages, a respiratory system involving fine tubules or tracheae, and Malpighian tubules. These shared characters support a sister group relationship between Myriapoda and Hexapoda refered to as the Atelecerata.

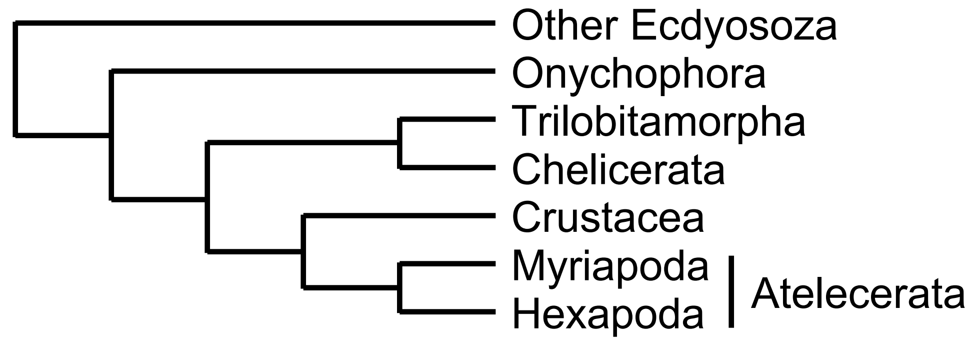
- Some recent molecular studies support a closer relationship between Hexapoda and Crustacea, but morphological traits are not outwardly apparent.

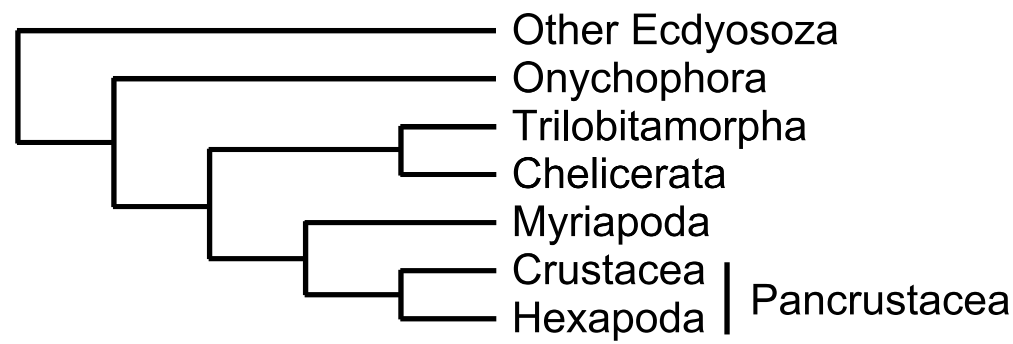
- Grouping the Hexapoda and the Crustacea together as the Pancrustacea would require that several complex morphological features (the tentorium, trachaea and Malpighian tubules) evolved independently in the Hexapoda and the Myriapoda. This seems unlikely.

- A recent combined approach (Edgecombe et al 2000) supported the retention of the Atelecerata and the supression of the Pancrustacea. Still other recent studies support the retention of the Pancrustacea and the supression of the Atelecerata (Dunn et al 2008 and Telford et al 2008).

Tentorium of Grasshopper Head







Conclusions

- The first question we asked in this lecture was whether the Arthropoda was a monophyletic group and thus a single evolutionary lineage or whether it is polyphyletic with more than one independently evolved lineages. Overwhelming evidence indicates that the Arthropoda is monophyletic and that the sister group to the Arthropoda is the phylum Tardigarda or Onychophora, with the weight of evidence in support of the Tardigrada.
- The second question we asked concerned the evolutionary relationship of the Hexapoda to the rest of the Arthropoda. Here the definitive answer is not so clear. Some studies place the Hexapoda and the Myriapoda as sister groups (Atelecerata), while others place the Hexapoda and the Crustacea as sister groups (Pancrustacea). The weight of evidence now available favors the Pancrustacea, but that could change in the future. If true, this means that several complex structures shared by hexapods and myriapods evolved convergently.