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Arthropoda

Abbreviated Dendrogram

```
ECDYSOZOA
|==Dinocaridida
|
`--ARTHROPODA
   |--Fuxianhuiida
   `--+--Candaspidida
      `--+--Megacheira
         `--+-Chelicerata
            `--+--Marellomorpha
               `--+--Trilobita
                  `--Mandibulata
                     |--Myriapoda
                     `--+--Crustacea
                        `--Hexapoda
```

Contents

Arthropoda collage. From left to right and from top to bottom: *Kolihapeltis* (trilobite), *Stylonurus* (eurypteryid), Scorpion, Crab, Centipede, Butterfly
Wikipedia, Creative Commons Attribution Share Alike

Arthropoda

One of the most significant inventions of the animal kingdom, the jointed exoskeleton, enabled the arthropods to become the second most abundant form of multicelluar life on Earth (the most abundant being the nematodes). Here we look at the various groups of arthropods, and their evolutionary history and success (or at least we ecventually will, when all the pages have a reasonable amount of content. The most primitive arthropods of all, the Paleozoic Dinocaridida, are equally included under the more inclusive clade Panarthropoda, and so are considered separately. After the dinocaridids, the fuxianhuiids, arre the most primitive arthropods known. The folllowing groups are considered in roughly phylogenetic order, as described in the abbreviated dendrogram above. But as not only the details but even the main lines of arthropod phylogeny remain controversial, our own interpretation here should only be seen as one possible hypothesis among many MAK120520

Most of these pages are still under construction and revision. Note that most of the links here will only work when the other pages are uploaded. MAK120515

Contents

Stem arthropods:

Fuxianhuiida - very primitive or basal early Cambrian arthropods
Candaspidida - very primitive, Cambrian, carapaced arthropods, superficially resembling crustaceans
Megacheira - "great appendage" arthropods with large spiny foreleg in place of antennae, limited to the Cambrian

Chelicerates:

Chelicerata - arthropods with chelicera rather than antennae
Pycnogonida - sea spiders, a poorly known group of basal chelicerates)
Xiphosura - horseshoe crabs and their Paleozoic ancestors
Eurypterida - "sea scorpions", medium-size dto gigantic chelicvcerates, which include the largest arthropods to ver live
Chasmataspidida - early chelicerates related to xiphosurans and eurypterids
Arachnida - spiders, scorpions, and kin
Acari - mites - microscopic arachnids
Araneae - spiders

Stem Mandibulates:

Marellomorpha - very primitive trilobite-like arthropods
Aglaspidida - yet another of those small early paleozoic arthropod groups, until recently thought to be related to chelicerates
Trilobitomorpha - assorted and miscellaneous trilobite-like forms, often included under the paraphyletic taxon "Arcahnomorpha"
Trilobita - the trilobites, armoured forms with three-lobed bodies and primitive limbs, abundant during but limited entirely to the Palaeozoic era
Mandibulata - arthropods with jaws

Myriapods:

Myriapoda - the many legged - millipedes, centipedes, and their relatives

Crustaceans:

Crustaceomorpha - ancestral or proto-crustaceans
Crustacea - the Crustaceans, an extremely important and diverse group
Phosphatocopida - a group of ostracod-like but very primitive Crustacea with phosphatic carapaces
Branchiopoda - fairy shrimps, water fleas and their kin, the most primitive extant crustaceans.
Remipedia - long-bodied many legged types that may (molecular phylogeny) or may not (morphology) be related to insects.
Maxillopoda - a "wastebasket taxon" for Crustaceans that don't fit into the other categories - includes barnacles, copepods, and many more; retained for now pending revision
Ostracoda - "seed shrimps" - tiny bivalved crustaceans with a rich fossil record
Malacostraca - paleozoic carapaced and shrimp-like types, along with extant sand hoppers, pill bugs, krill, and other assorted types
Decapoda - the ten legged: shrimps, lobsters, crabs; the most recognisable and most successful of the crustaceans

Insects:

Hexapoda - six legged arthropods (includes all the following units)
Insecta - the insects, the most important clade of hexapods. This unit introduces the insects and includes primitive wingless forms
Pterygota - winged insects. This unit introduces the Palaeoptera (dragonflies, mayflies, and their Paleozoic relatives)
Palaeodictyopteroida - extremely primitive but succesful Paleozoic beaked insects
Ephemeroptera - the mayflies, one of the four original branches of winged insects
Odonatoptera - dragonflies and their giant paleozoic relatives; darting aerial predators of the insect world
Neoptera - insects that can fold their wings, one of the great evolutionary adaptions of the insect world (includes all the following units)
Polyneoptera - those jumpers and singers the grasshoppers and crickets, the misunderstood earwigs, and the titanic (in insect terms at least) Triassic Titanoptera and extant and equally impressive stick insects
Dictyoptera - the indomitable cockroaches of the Paleozoic undergrowth and their more recent desecndents the crown group cockroaches, termites, and praying mantises
Paraneoptera - lice, thrips, aphids, plant hoppers, cicadas, and true bugs
Holometabola - insects that undergo a larval, pupal, and adult life-cycle - this unit includes a number of minor groups; in addition there are the following four units
Coleoptera - the beetles, who God has an inordinate fondness for (as there are so many different types)
Hymenoptera - ants, bees and wasps, both social insects and solitary types
Diptera - the two wings: flies of all sorts; one of the four largest insect groups
Lepidoptera - moths and butterflies, much beloved of Victorian naturalists, and the second most speciose insectgroup

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The Arthropoda

animals with jointed exoskeletons

Abbreviated Dendrogram

```
ECDYSOZOA
|==Dinocaridida
|
`--ARTHROPODA
   |--Fuxianhuiida
   `--+--Candaspidida
      `--+--Marellomorpha
         |--Megacheira
         `--+-Chelicerata
            `--+--Trilobita
               `--Mandibulata
                  |--Myriapoda
                  `--+--Crustacea
                     `--Hexapoda
```

Contents

Taxa on This Page

1. Arthropoda

This page is still under construction and revision, but has been erected as a provisional and partial updating of the earlier Palaeos pages on this subject. Note that most of the links here will only work when the other pages are uploaded. MAK120515

The Arthropods

The arthropods constitute the most successful and diverse form of life on Earth, constituting millions of species in a diverse range of habitats, and varying in size from microscopic to quite large.

The name "arthropod" comes from the Greek, *arthros* jointed, and *podes*, feet. Hence, jointed feet. All arthropods possess a jointed rigid exoskeleton, which both supports the musculature and protects the animal. The exoskeleton is formed by the cuticle, a protective layer composed mostly of chitin, long chained molecules of the sugar acetyl glucosamine, which when cross-linked form tough fibers embedded in a protein matrix

As the animal grows it has to shed its exoskeleton at regular intervals, a process known as *molting*. During this time it is vulnerable to predators and disease, and also to desiccation if it is a terrestrial form like an insect or spider. Because the larger the animal the longer it takes for the new molt to harden, and hence the longer the time it is vulnerable, this process imposes limits on the size arthropods grow to. Another limit with terrestrial forms like insects is that breathing is through pores in the side of the body. Hence arthropods are mostly small, even microscopic, with very few growing to giant size. Science fiction giant ants and the rest are simply physiologically impossible (though that never stopped sci fi writers in the past).

Primitive arthropods, like trilobites and some crustaceans, have many body segments and many pairs of similar legs. In more advanced forms there is the tendency of the segments to fuse into functional groups, called *tagmata* (sing. *tagma*) such as the head and thorax of an insect or the carapace of a crab.

Taxonomy/Systematics

Arthropods are variously classified. For example the "mandibulates" (e.g. insects) posses jaws (mandibles) and so are distinguished from the "chelicates" which developed pincers instead (e.g. spiders). Conversely, there are those arthropods that possess two pairs of antennae (biramous) as opposed to those with one pair ("uniramous"). There are also embryonic differences as well. crustaceans for example have a unique type of larvae, called the *nauplius*.

Because of all these differences there was for some time a controversy over whether the arthropods constitute a valid monophyletic group, or whether they evolved from separate, even unrelated. soft-bodied ancestors. The late English zoologist S. M. Manton **ref**, **[ref]** argued persuasively that the arthropods consist of three distinct groups that evolved from separate ancestors - the Uniramia, Biramia (Crustacea), and Chelicerata, each of which constitutes a distinct phylum. Others have argued on the basis of molecular and anatomical evidence that the arthropods did indeed evolve from a common ancestor. Nowadays Manton's polyphyletic view of the arthropods is out of favor. One of the more recent theories of arthropod relationships has even involved splitting up the Uniramia by aligning the Hexapoda with the Crustacea rather than the Myriapods (the Pancrustacea hypothesis) [2].

Today there is still little agreement regarding arthropod phylogeny between what could be called the minority paleontological and the majority molecular paradigms

Evolution and Fossil Record

The first arthropods appear in the early Atdabarian epoch (early Cambrian) although arthropod tracks are known from the Tommotian. It is almost certain that the first arthropods evolved around the Poundian-Tommotian boundary (some 545 million years ago). For the first ten million years or so they were probably soft-bodied forms. During the Atdabarian the first hard-bodied armoured trilobites appeared, but these were still a minority in relation to the soft-skinned forms. The various lineages of arthropods underwent an explosive evolutionary radiation, but many of these types died out at the end of the Cambrian. The survivors flourished and have made up the bulk of invertebrate faunas ever since - Trilobites and then Crustacea in the seas, and Chelicerates (especially mites and spiders) and myriapods and hexapods (especially insects) on land.

Descriptions

Arthropoda von Siebold and Stannius 1848 (= Euarthropoda Lankester 1904)

Range: Fr ECambrian

Phylogeny: Panarthropoda **:** *Aysheaia* + (Tardigrada + (Cambrian lobopodians + Onychophora + (more Cambrian lobopodians + (Siberiids + (Dinocaridids + (*Schinderhannes* + * **:** Fuxianhuiida + (Candaspidida + (Marellomorpha + Megacheira + (Chelicerata + (Trilobita + Mandibulata)))))))))

Description: Arthropoda distinguished by hardened body covering composed largely of chitin; body usually well-segmented and jointed externally, and commonly divided into head, thorax, and abdomen; with rather highly developed sensory organs, circulatory and nervous systems; sexes usually separate; young mostly passing through a number of larval stages before gradually or abruptly attaining adult form; growth accommodated by molting of the exoskeleteon (after Moore 1959, p. O21).

Further apomorphies, as noted in Maas & Waloszek 2001, include "a head tagma with one pair of antennae (first antenna, antennula of Crustacea) and 3 pairs of biramous limbs covered by a uniform shield, a segmented, limb-bearing body, and all post-antennular limbs comprising a well-sclerotised basipod carrying two rami. The inner ramus is 7-segmented (endopod) and the outer one is a seta-bearing flap (exopod)" (p. 453).

Whereas the phylogenies proposed up to this point are relatively uncomplicated, even if they are not universally agreed, relationships within the Euarthropoda are particularly fraught. "Novel hypotheses such as a crustacean-hexapod affinity were based on analyses of single or few genes and limited taxon sampling, but have received recent support from mitochondrial gene order, and eye and brain ultrastructure and neurogenesis. Here we assess relationships within Arthropoda based on a synthesis of all well sampled molecular loci together with a comprehensive data set of morphological, developmental, ultrastructural and gene-order characters. ... The optimal 'total evidence' cladogram supports the crustacean-hexapod clade, recognizes pycnogonids as sister to other euarthropods, and indicates monophyly of Myriapoda and Mandibulata" (Giribet et al. 2001). - Chris Clowes

Links: Phylum Arthropoda: Glasgow University Zoology Museum, Scotland; Introduction to the Arthropods; Phylum Arthropoda - brief but useful overview of various groups, especially Crustacea - part of the MEER site; Arthropoda Phylum Overview; Arthropoda - Tree of Life project; Phylum Arthropoda Animal Diversity Web; Arthropoda (jointed-leg animals) - Specimens database at Marine Biological Lab (MBL), Woods Hole

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checked ATW050515, revised MAK120514
page by M. Alan Kazlev

Arthropoda: Classification

Abbreviated Dendrogram

```
ECDYSOZOA
|==Dinocaridida
|
`--ARTHROPODA
   |--Fuxianhuiida
   `--+--Candaspidida
      `--+--Marellomorpha
         |--Megacheira
         `--+-Chelicerata
            `--+--Trilobita
               `--Mandibulata
                  |--Myriapoda
                  `--+--Crustacea
                     `--Hexapoda
```

Contents

The following are two recent classifications of arthropods, one emphasising Cambrian taxa, the other a more generic approach in a recent palaeontological text on insects. It is intended at some point to include our own classificxation scheme, but this has not been done so far due to limitations of time MAK120512

Evolutionary-Linnanean classification from Hou, X. & Bergström J., 1997. Arthropods of the Lower Cambrian Chengliang fauna, southwest China. *Fossils & Strata*, No.45: 1-116 - copied from Nomina Circumscribentia Insectorum

```
phylum Schizoramia Bergstrom 1976
  superclassis Proschizoramia n. supercl.   (:12)
    classis Yunnanata n. cl.  (:12)
      ordo Fuxianhuiida Bousfield 1995 u87
    classis Paracrustacea n. cl.  (:22)
      ordo Canadaspidida Novozhilov in Orlov 1960 Canadaspis
      = Hymenostraca Rolfe 1969
      = Prophyllocarida Simonetta & Delle Cave 1975
    classis Megacheira n. cl.  (:26)
      ordo Leanchoiliida Stormer 1944 Leanchoilia
      ordo Yohoiida Simonetta & Delle Cave 1975 Yohoia
      ordo Fortiforcipida n. ord. Fortiforceps
    classis Sanctacaridea Bousfield 1995 Sanctacaris
      ordo Sanctacarida Bousfield 1995 Sanctacaris
    classis * (classes uncertain)
      ordo Acanthomeridiida n. ord.  Acanthomeridion
      ordo Vetulicolida n. ord. Vetulicola
         fam. Habeliidae Simonetta & Delle Cave 1975 Habelia
         fam. Molariidae Simonetta & Delle Cave 1975 Molaria
      ordo Tuzoiida Simonetta & Delle Cave 1975 Tuzoia
      ordo Bradoriida Raymond 1936 Bradoria
  superclassis Crustaceomorpha Chernysheva 1960
```

```
      classis Pseudocrustacea Størmer 1944
        ordo Agnostida Salter 1864 Agnostus
        ordo Waptiida Strømer 1944 Waptia
        ordo Phosphatocopida Muller 1964
      classis Crustacea Pennant 1777
    superclassis Lamellipedia n. supercl.   (:42)
    = subphylum Arachnomorpha Heider 1913, emend. Størmer 1944 [as phylum]
    = subphylum Trilobitomorpha Størmer 1944
      classis Marellomorpha (Beurlen 1934) Størmer 1944 Marella
      classis Artiopoda n. cl.  (:43)
        subclassis Nectopleura n. subcl.  (:43)
          ordo Nectaspidida Raymond 1920 (nom. corr. herein, ex Nectaspida)
          ordo Acercostraca Lehmann 1955
          ordo Halicyna Gall & Grauvogel 1967 Halicyne
          ordo Retifaciida n. ord. Retifacies
        subclassis Conciliterga n. subcl.  (:60)
          ordo Helmetiida Novozhilov 1969 Helmetia
        subclassis Trilobita Walch 1771
        subclassis Petalopleura n. subcl.  (:73)
          ordo Xandarellida Chen, Ramskold, Edgecombe & Zhou in Chen et al. 1996 Xandarella
          ordo Cheloniellida Broili 1933 (emend.) Cheloniellon
          ordo Sinoburiida n. ord. Sinoburius
        subclassis Xenopoda Raymond 1935
          ordo Emeraldellida Størmer 1944 Emeraldella
          ordo Limulavida Walcott 1911
        subclassis Aglaspidida Bergstrom 1968 Aglaspis
          ordo Aglaspidida Walcott 1911 Aglaspis
          ordo Strabopida n. ordo Strabops
             fam. Strabopidae Gerhardt 1932 Strabops
    superclassis Chelicerata
```

The following classification is from Grimaldi & Engels, *Evolution of the Insects*, 2005 and is copied from Wikispecies

```
Subphylum: †Marellomorpha
Subphylum: Arachnomorpha
   Infraphylum: †Trilobita
   Infraphylum: Cheliceriformes
      Superclassis: †Sidneyiida
      Superclassis: †Emeraldellida
      Superclassis: †Sanctacarida
      Superclassis: Chelicerata
         Epiclassis: Pycnogonida
         Epiclassis: †Aglaspidida
         Epiclassis: Euchelicerata
            Classis:Xiphosura
            Classis:†Eurypterida
            Classis:Arachnida
               Subclassis: Micrura
                  Ordo: Palpigradi
                  Ordo: †Haptopoda
                  Ordo: †Trigonotarbida
                  Ordo: Araneae
                  Ordo: Amblypygida
                  Ordo: Uropygida
                  Ordo: Schizomida
                  Ordo: Ricinulei
                  Ordo: Acari
               Subclassis: Dromopoda
                  Ordo: †Phalangiotarbida
                  Ordo: Opiliones
                  Ordo: Scorpiones
                  Ordo: Pseudoscorpionida
                  Ordo: Solfugida
Subphylum: Mandibulata
   Infraphylum: Crustaceomorpha
      Superclassis: Crustacea
         Epiclassis: †Phosphatocopida
         Epiclassis: Eucrustacea
            Classis:Branchiopoda
               Subclassis: Sarsostraca
               Subclassis: Phyllopoda
            Classis:Remipedia
            Classis:Maxillopoda
               Subclassis: Thecostraca
               Subclassis: †Ascothoracida
               Subclassis: †Orstenocarida
               Subclassis: Tantulocarida
               Subclassis: Branchiura
               Subclassis: Pentastomida
```

```
               Subclassis: †Skaracarida
               Subclassis: Mystacocarida
               Subclassis: Copepoda
            Classis:Ostracoda
               Subclassis: Myodocopa
               Subclassis: Podocopa
            Classis:Malacostraca
               Subclassis: †Nahecarida
               Subclassis: Phyllocarida
               Subclassis: Hoplocarida
               Subclassis: Eumalacostraca
   Infraphylum: Atelocerata
      Superclassis: Myriapoda
            Classis:Chilopoda
            Classis:Progoneata
            Classis:Symphyla
         Epiclassis: Dignatha
            Classis:Pauropoda
            Classis:Diplopoda
               Subclassis: Pselaphognatha
               Subclassis: †Arthropleuridea
               Subclassis: Chilognatha
      Superclassis: Panhexapoda
                        Genus: †Devonohexapodus
         Epiclassis: Hexapoda
            Classis:Entognatha
            Classis:Insecta (=Ectognatha)
```

Note that *Devonohexapodus bocksbergensis*, known from a single specimen, has since been shown to be a synonym of the contemporary *Wingertshellicus backesi*, a Devonian arthropod of uncertain relations, but not a stem hexapod (Kühl, & Rust, 2009) MAK120514

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page MAK120514 from various sources

Arthropod Phylogeny

Abbreviated Dendrogram

```
ECDYSOZOA
|==Dinocaridida
|
`--ARTHROPODA
   |--Fuxianhuiida
   `--+--Candaspidida
      `--+--Marellomorpha
         |--Megacheira
         `--+-Chelicerata
            `--+--Trilobita
               `--Mandibulata
                  |--Myriapoda
                  `--+--Crustacea
                     `--Hexapoda
```

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Problems in Arthropod Phylogeny

As with many large and complex taxa in which the earliest forms are poorly known (if known at all), the arthropods present particular difficulties as far as phylogeny goes. Molecular evidence remains ambiguous, due perhaps to the fact that many clades diverged rapidly within a very short space of time (the Cambrian Explosion). Many fossil forms are known, but it is always difficult to make assertions regarding what little can be gleaned from the gross morphology preserved.

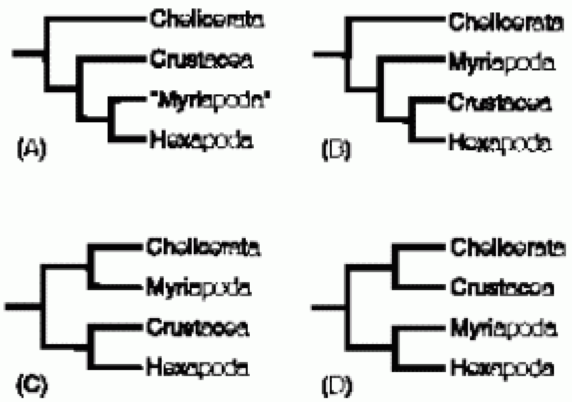


FIG. 1. Main hypotheses of internal relationships for the Arthropoda. (A) Mandibulata and Atelocerata (Snodgrass, 1938; Weygoldt, 1979; Wägele, 1993; Wheeler *et al.*, 1993; Wheeler, 1995, 1998a,b); (B) Mandibulata and Pancrustacea (Zrzavý *et al.*, 1998a; Giribet *et al.*, 1996; Giribet and Ribera, 1998); (C) Pancrustacea and (Myriapoda + Chelicerata) (Turbeville *et al.*, 1991; Friedrich and Tautz, 1995; Giribet *et al.*, 1996); (D) Schizoramia (Cisne, 1974; Briggs *et al.*, 1992; Budd, 1993).

Polyphyly or Monophyly?

Arthropod polyphyly was popularized by Sidnie Manton. Although a popular view for a while, and still found in many zoology textbooks even today, as well as widely on the Web, it's basic premise - that of three distinct phyla (see above cladogram), is no longer considered tenable by most researchers in the field of high-level arthropod systematics. The consensus is now that arthropods are monophyletic, but the exact order of relationships is in dispute (**ref**). it seems like every possible alternative has been offered (*left* - from Giribet and Ribera 2000).

Mandibulata

The Mandibulata are described in more detail elsewhere. As originally proposed by Snodgrass, one of teh great early to mid 21st century scholars of arthropod systematics and evolution, the arrangement of the Mandibulata looked like this:

```
<==o Arthropoda
   |-- Chelicerata
   `--o Mandibulata
      |--Crustacea
      `--o Atelocerata
         |-- Myriapoda
         `-- Hexapoda
```

The above morphology-based hypothesis still has supporters today, and although the status of the Mandibulata is secure, the Atelocerata as we shall see is less so.

Uniramia

The Uniramia are one of the three main phyla proposed by S. M. Manton as part of a paradigm of Arthropod polyphyly. The name Uniramia means "single branch"; as opposed to other arthropod types, which are schizoramous (having branched limbs), the limbs are unbranched, hence the name of the group. They are also identified by their single pair of preoral antennae, possibly homologous with the antennae of trilobites. The body divided into a distinct cephalon (head) and metameric (segmented) trunk. There are three pairs of postoral appendages on head; chewing mouthparts (mandibles) on the second postantennal segment, and compound eyes. They seemed to have evolved a hard exoskeleton later than other groups, but were quick to colonize the land (during the Silurian period). Breathing is by special gas exchange organs along the side of the body called *tracheae* and *malpighian tubules*.

There are three taxa conventionally included: the Onychophora (velvet worms, which do not posses an exoskeleton, and were previously considered a distinct phylum), and the superclasses Myriapoda and Hexapoda. These would seem to represent an evolutionary sequence, from many-legged soft-bodied forms through many-legged hard-bodied types to few legged forms with fused segments (insects). The poorly known *Cambropodus* may also be an early uniramian, but this is not certain.

This hypothesis, were it translated into dendrogrammatic form, could be presented as follows:

```
--Trilobita
|--Chelicerata
|--Crustacea
`--o Uniramia
   |--Onychophora
   `--+--Myriapoda
      `--Hexapoda
```

Recently however the status of the Uniramia as a valid taxon has been increasingly questioned and evidence presented suggesting the Crustacea are the stock from which the Hexapoda arose (i.e. Hexapods and Crustacea form a monophyletic group apart from the Myriapoda) - the Pancrustacea hypothesis, although this is still controversial. Equally if not more damaging is fossil research that shows that transitional lobopod-arthropod-like forms reveal a continuity between lobopodians proper and Euarthropods, thus supporting the monophyly of the Arthropoda and invalidating the Uniramia. A limited version of the Uniramia, the Atelocerata, includes only euarthropodic Uniramia, but this would also be invalidated if the Pancrustacea theory turns out to be correct.

Schizoramia

By "Schizoramia": is meant those arthropods that possess branched appendages as opposed to those with only a simple unbranched limb (variously referred to as "uniramous", Tracheata, or Atelocerata). That arrangement looked like this:

```
<==o Arthropoda
   |--o Schizoramia
   |   |--Trilobita
   |   |--Chelicerata
   |   `--Crustacea
   `--o Atelocerata
       |--Myriapoda
       `--Hexapoda
```

The above cladogram shows the Schizoramia as sister group to the Myriapoda + Hexapoda . However, we follow the "Pancrustacea" school of thought, which unites hexapods and crustaceans. To provide some stability to the region, it is useful to have a clade which unites all four living branches of the arthropods. This is it.

The Schizoramia hypothesis is argued strongly by paleontologists, such as Jan Bergström and Hou Xianguang , although, but are not committed as to whether the arthropoda are monophyletic or diphyletic (Schizoramia + Uniramia/Atelocerata). Many forms that occur in the Chengjiang lagerstätten have been described by Bergström and Hou (the latter the discoverer of the Chengjiang fauna), who follow an intuitive "key-character" approach; In their comprehensive monograph, Hou & Bergström describe many little known forms in detail, and present the following subdivisions of the Schizoramia, including two new superclasses, the Proschizoramia and the Lamellipedia:

Superclass: Proschizoramia
          Class: Yunnanata
          Class: Paracrustacea
          Class: Megacheira
          Class: Sanctacaridea

Superclass: Crustaceomorpha
          Class: Pseudocrustacea (incl. Agnostida)
          Class: Crustacea

Superclass: Lamellipedia
          Class: Marellomorpha
          Class: Artiopoda
          Class: Trilobita
          Class: Chelicerata

Note that much of this arrangement is not accepted by many workers in this field

Atelocerata

Atelocerata - also called Tracheata and Uniramia, although Atelocerata is more correct (ref) - is a daughter clade of the Mandibulata of Snodgrass 1938 and others that unites hexapods (insects and their kin) and myriapods. The taxon went out of favour when S. M. Manton erected the Uniramia, but with the more recent rejection of Arthropod polyphyly it has become more popular again.

With the rise of molecular sequencing and the Pancrustacea hypothesis, which says that the Crustacea are the stock from which the Hexapoda arose (i.e. Hexapods and Crustacea form a monophyletic group apart from the Myriapoda) it has once again gone out of favour. If the Pancrustacea hypothesis is correct then the characteristics uniting Myriapoda with Hexapoda might have evolved independently as adaptations to terrestrialism (1, 2). see also **note** MAK020507

The poorly known middle Cambrian *Cambropodus gracilis* has been suggested as an ancestral ateloceratan (Robison 1990) , although this assignment has been criticised. The Paleozoic Euthycarcinoidea would also seem to be safely uniramian but their exact relationships are not clear.

Pancrustacea

In the 1990s, many studies used molecular analysis to unite crustaceans with atelocerates (hexapods and myriapods) in the old established taxon Mandibulata, there are also many that align crustaceans with chelicerates and trilobites (as the "Schizoramia"). Supporters of Mandibulata can't agree whether Atelocerata is monophyletic and sister to Crustacea (the majority position), or whether crustaceans are sister to hexapods (the Pancrustacea hypothesis).

These conflicting results are influenced by the fundamentally different classes of evidence on which they are based, as well as reliance largely or wholly on recent forms to reconstruct ancient events.

The relative infancy of molecular systematics during the 1990s and turn of the 21st century meant that the data may not be adequate to the task, and produce misleading results. An rRNA study by Giribet and Ribera 2000 was inconclusive, as the high level of sequence heterogeny made placement of some taxa difficult and showed the importance of combining ribosomal gene data with other sources of information.

More recent studies however strongly support several clades such as Chelicerates, Mandibulata, Hexapoda (in some studies reso;lved as diphyletic) and, most controversially, Pancrustacea

,

The term Pancrustacea "All the Crustacea" is used to designate the clade uniting insects and Crustacea. This is the opposite of the Atelocerata hypothesis, and while for some time a minority position, came increasing into favour in the late 90s / early 2000s, and in the last few years become established as the majority paradigm in this field

As with the Mandibulata and Atelocerata, the evidence for a Pancrustacea is from neontological (molecular analysis and soft part anatomy) than paleontological grounds (Friedrich and Tautz 1995; Dohle 1998; Kraus 1998). For example

> "The homology of characters brought forward in favour of a close relationship between myriapods and insects (absence of second antennae, formation of malpighian tubules, postantennal organs and tracheae) cannot well be established. These characters may be due to convergence. This is especially true for the tracheae.
>
> In contrast, the...characters combining insects and crustaceans, malacostracans in particular, (axonogensis in early differentiating neurons, formation of neuroblasts, fine structure of ommatidia, expression patterns of the engrailed gene) seem to be much better substantiated."

Wolfgang Dohle, "Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship"

and

> "Despite the diversity of their limbs and lifestyles, the nervous systems of insects and crustaceans share many common features both in development and in function....Examples include the basic ganglionic architecture and the strikingly similar pattern of GABAergic inhibitory enervation of leg muscles in Crustacea and insects. These and other examples...argue against the idea that these two groups of arthropods evolved independently from separate non-arthropod

> ancestors....Myriapods are often regarded as being more closely related to the insects than are the crustaceans. However, we find that myriapods show substantial differences, for example in the pattern of early axon growth, to the common pattern of early neural development seen in the Crustacea/insecta."

"The Organization and Development of the Arthropod Ventral Nerve Cord: Insights into Arthropod Relationships" Paul M. Whitington and Jonathan P. Bacon

Suggestive as these facts may be, they are not totally persuasive, for the Uniramia hypothesis is also built on factors of similarity in embryology and physiology. Clearly, there has been a great deal of parallelism and convergence in the evolution of the arthropods.

And from the 13 September 2001 issue of *Nature*:

> "Most recent studies suggest a close link between insects and crustaceans, but the relationships of myriapods (centipedes and millipedes) and chelicerates (spiders and allies) with this 'Pancrustacea' group have been contentious. Hwang *et al*. present molecular evidence for a close link between myriapods and chelicerates. In contrast, Giribet *et al*. mix molecules and morphology in a bold 'total evidence' approach that produces a more traditional arrangement, with myriapods closer to insects and crustaceans, and chelicerates lying further away."

"Cladistics: Web of relations"

At first, insects and cruastacea were considered sister taxa, as shown in the following cladograms.

```
<==o Arthropoda
   |--+-- Myriapoda
   |  `-- Chelicerata
   `--o Pancrustacea
      |-- Hexapoda
      `-- Crustacea
```

Molecular phylogeny of Arthropoda after Hwang, et al., 2001

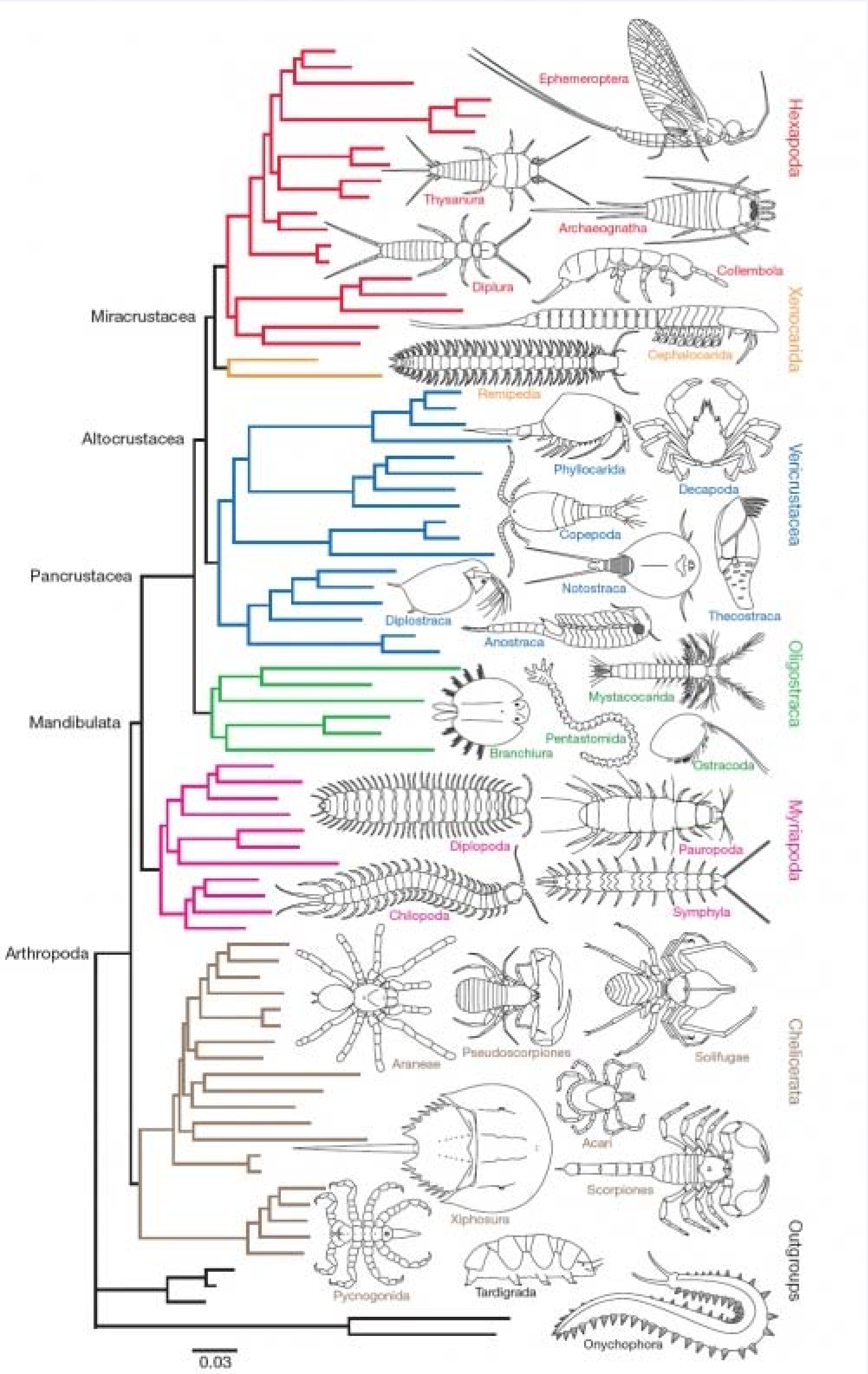
```
<==o ARTHROPODA  (sensu Panarthropoda)
   |-- Lobopodia
   `--+-- Tardigrada
      `--o Euarthropoda
         |-- Pycnogonida
         `--+-- Euchelicerata
            `--o Mandibulata
               |-- Myriapoda
               `--o Pancrustacea
                  |-- Hexapoda
                  `-- Crustacea
```

Molecular phylogeny of Arthropoda after Giribet, et al., 2001

More recently, a definitive molecular study by Regier et al 2010 (*right*) goes much further, by nesting insects (hexapoda) deep within Crustacea.

The main problem with the Pancrustacea theory is the lack of transitional forms, especially in the fossil record, where one would expect to find them most. Not surprisingly, Conway Morris and Hou & Bergström, who adopt a wholly paleontological approach, retain the old taxon Uniramia.

Presumably (assuming insects do derive from Crustacea) primitive hexapods evolved from marginal marine and amphibious crustaceans during the late Silurian or early Devonian



An ironic twist, if this hypothesis does turn out to be true, will be that Crustacea will then become a paraphyletic taxon, and hence invalid under the cladistic system, perhaps to be replaced by a confusing array of smaller clades. Or insects will have to be called "crustacea", just as many vertebrate paleontology enthusiasts now refer to birds as dinosaurs, thus confusing the fact that birds, while evolving from dinosaurs, really have become a distinct form of animal. The same can be said of insects and crustaceans.

Morphologically, insects as crown group crustaceans make about as much sense as turtles as crown group archosaurs (which is also what molecuilar seuencing unanimously asserts). Of course, the question remains, why should the phylogenetic signal from molecular sequencing be considered so much more relaible than that from either fossils, embryology, or extant morphology

Complexes of Characters

Over the last two decades, along with the rise of molecular systematics and interest in high-level arthropod phylogeny, there has been a revival of interest in fossil forms, as well as the discovery and description of several important Cambrian lagerstätten with their spectacular early arthropod faunas. This palaeontological research has resulted in cladistic analyses completely different to those based on neontological (recent taxa) evidence alone, and offers no support at all for popular taxa like the Mandibulata but suggest instead an Arachnomorpha that combines chelicerates and trilobites

But even here the situation is more complex and ambiguous than it may at first appear, due to the difficulty of interpreting often fragmentary and poorly preserved forms known only from thin carbon films or impressions in shale. Often interpretation of characteristics becomes a purely arbitrary, and the same taxon can be given totally different relationships, depending on how it is interpreted. As Professor Geoffrey Fryer (an advocate of arthropod polyphyly) argues:

> Affinities among Cambrian arthropods, deduced by cladistic methods on the assumption of monophyly, are unreliable, and some are certainly erroneous. For example, *Sarotrocercus*, said at different times to be close to *Limulus* and a eurypterid, then to *Yohoia* and *Sanctacaris*, and most recently to *Molaria* and *Leonchoilia*, bears little resemblance to any of these very different animals and is in fact one of the most primitive arthropods yet discovered.
>
> Single characters...can be misleading and, not surprisingly, are often less informative than complexes, which arthropods display in profusion and whose changes during the course of evolution can sometimes be followed in detail." -- Geoffrey Fryer, Arthropod Polyphyly

For these various reasons it would seem advisable to take many of the cladograms and phylogenetic hypotheses dealing especially with earlier and less well-known taxa, with a small Siberian salt mine. The closer one gets to modern taxa, the more reliable findings may be, but even there is an element of uncertainty (as shown by the rival interpretations regarding myriapod, insect, and crustacean relationships, which may remain for some time to come.

Notes

"Myriapod-insect relationships as opposed to an insect-crustacean sister group relationship" - Wolfgang Dohle, Berlin (from abstract of paper)

> "The homology of characters brought forward in favour of a close relationship between myriapods and insects (absence of second antennae, formation of Malpighian tubules, postantennal organs and tracheae) cannot well be established. These characters may be due to convergence. This is especially true for the tracheae.
>
> In contrast, the homology and synapomorphy of characters combining insects and crustaceans, malacostracans in particular, (axonogensis in early differentiating neurons, formation of neuroblasts, fine structure of ommatidia, expression patterns of the engrailed gene) seem to be much better substantiated. "

Links

Book Review - Arthropod Fossils and Phylogeny - reviewed by Jonathan Adrain (Palaeontologica Electronica)

A Review of Arthropod Phylogeny- New Data Based on Ribosomal DNA ...

S413_13d 157..161

Systematics of the Arthropoda

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ARTHROPODA
DENDROGRAM

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Arthropoda

Abbreviated Dendrogram

```
ECDYSOZOA
|==Dinocaridida
|
`--ARTHROPODA
   |--Fuxianhuiida
   `--+--Candaspidida
      `--+--Marellomorpha
         |--Megacheira
         `--+-Chelicerata
            `--+--Trilobita
               `--Mandibulata
                  |--Myriapoda
                  `--+--Crustacea
                     `--Hexapoda
```

Contents

The following provisional dendrogram is by Christopher Taylor and is copied without modification from Palaeos org. It is intended at some point to upgrade it

Due to limitations of time, rthis page has not been formatted (hence no italics etc) MAK120512

```
Arthropoda (see below for synonymy)
   |  i. s.: Dictyocaris Salter 1860
   |         Urokodia Hou, Chen & Lu 1989
   |         Tontoia Walcott 1912
   |         Retifacies Hou, Chen & Lu 1989
   |         Rhombicalvaria Hou 1987
   |         Helmetia Walcott 1917
   |         Corcorania Jell 1980
   |         Serracaris Briggs 1978
   |           `--S. lineata [=Anomalocaris lineata]
   |         Cambropodus gracilis
   |         Protocaris Walcott 1884
   |         Achanarraspis Anderson et al. 2000
   |         Arthrogyrinus Wilson & Almond 2001
   |           `--*A. platyurus Wilson & Almond 2001
   |--Sidneyia Walcott 1911 [Limulavida, Sidneyidea]
   |    `--S. inexpectans
   `--+--Leanchoiliidacea
      `--+--Yohoiidea [Protochelicerata, Yohoiidacea]
         |    |--Jiangfengia Hou 1987 [Jianfengiida]
         |    `--Yohoia Walcott 1912 [Yohoiida]
         |        `--Y. tenuis
         `--+--Sanctacaris Briggs & Collins 1988 [Sanctacarida, Sanctacaridea]
            |    |--'Utahcaris' orion Conway Morris & Robison 1988
            |    `--Sanctacaris uncata Briggs & Collins 1988
            `--+--+--Fortiforceps
```

```
|  `--+--Occacaris
|     `--+--Clypecaris
|        `--+--+--Pectocaris
|           |  `--Fuxianhuiida [Fuxianhuiata]
|           |       |--Fuxianhuia protensa Hou 1987
|           |       `--Changjiangocaris longiformis Hou & Bergström 1991
|           `--Canadaspidida
|                |  i. s.: Rehbachiella kinnekullensis Müller 1983
|                |--Perspicaris Briggs 1977
|                `--+--Canadaspis Novoshilov 1960
|                   |    `--C. perfecta (Walcott 1912)
|                   `--Brachiocaridea
|                        |--Odaraia Walcott 1912 [Odaraiata, Odaraiida]
|                        |    `--O. alata
|                        `--Branchiocaris Briggs 1976 (see below for synonymy)
|                             `--B. pretiosa (Resser 1929) [=Protocaris pretiosa]
`--Euarthropoda [Emeraldellacea]
     |--Arachnomorpha
     `--+--Emeraldella Walcott 1912 [Emeraldellida]
        `--+--Cambropachycope
           `--Mandibulata [Antennata, Atelocerata, Biantennata, Tracheata]
                |  i. s.: Euthycarcinoidea [Archicopepoda, Euthycarcinata]
                |            |  i. s.: Synaustrus brookvalensis (Riek 1964)
                |            |         Schramixerxes gerem (Schram & Rolfe 1982)
                |            |         Kalbarria brimmellae
                |            |--Sottixeriformes
                |            |    |--Pieckoxerxes piekoae (Schram & Rolfe 1982)
                |            |    `--Sottyxerxes multiplex Schram & Rolfe 1982
                |            `--Euthycarciniformes
                |                 |  i. s.: Euthycarcinus
                |                 |            |--E. ibbenburensis
                |                 |            `--E. kessleri Handlirsch 1914
                |                 `--Kottixerxidae
                |                      |--Kottixerxes Schram 1971
                |                      |    |--*K. gloriosus Schram 1971
                |                      |    `--K. anglicus Wilson & Almond 2001
                |                      `--Smithixerxes Schram & Rolfe 1982
                |                           |--*S. juliarum Schram & Rolfe 1982
                |                           `--S. pustulosus Wilson & Almond 2001
                |         Marrellomorpha
                |            |--Vachonisia Lehmann 1955 (see below for synonymy)
                |            `--Marrellidea
                |                 |--Mimetaster Gurich 1931 (see below for synonymy)
                |                 `--Marrella Walcott 1912 [Marrellata, Marrellida]
                |                      `--M. splendens
                |--Myriapoda
                `--Pancrustacea [Tetraconata]
                     |--Crustacea
                     `--Hexapoda
```

Synonymy:

Arthropoda [Burgessidea, Canadaspididea, Cheliceromorpha, Emeraldellidea, Euthycarcinomorpha, Merostomoidea, Schizoramia, Trilobitoidea, Trilobitomorpha] Branchiocaris Briggs 1976 [Branchiocarata, Branchiocarida] Mimetaster Gurich 1931 [Mimetasterata, Mimetasterida] Vachonisia Lehmann 1955 [Vachonisiata, Vachonisiida]

* Type species of genus indicated

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Arthropoda: References

Abbreviated Dendrogram

```
ECDYSOZOA
 |==Dinocaridida
 |
 `--ARTHROPODA
    |--Fuxianhuiida
    `--+--Candaspidida
       `--+--Marellomorpha
          |--Megacheira
          `--+-Chelicerata
             `--+--Trilobita
                `--Mandibulata
                   |--Myriapoda
                   `--+--Crustacea
                      `--Hexapoda
```

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> The results show that arthropods are monophyletic. Tardigrades represent the sister group of arthropods (in parsimony analyses) or they are related with crustaceans (distance analysis and PRN). Arthropoda are divided into two main evolutionary lines, the Hexapoda + Crustacea line (weakly supported), and the Myriapoda + Chelicerata line. The Hexapoda + Crustacea line includes Pentastomida, but the internal resolution is far from clear. The Insecta (Ectognatha) are monophyletic, but no evidence for the monophyly of Hexapoda is found. The Chelicerata are a monophyletic group and the Myriapoda cluster close to Arachnida.

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Trilobita : The Trilobites

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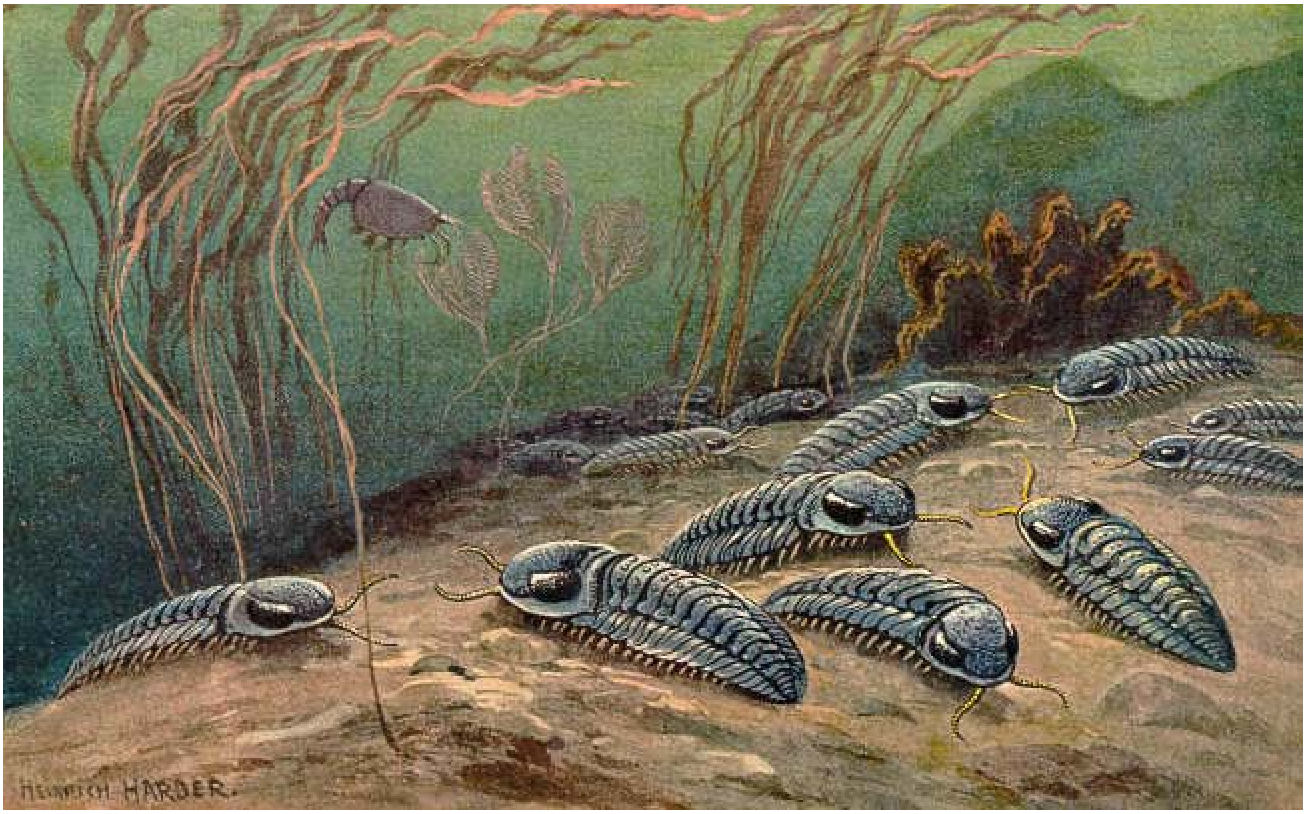

Middle Cambrian trilobites (Artwork by Heinrich Harder, 1916, from Geology in Art)

Trilobites comprise a complex and huge clade of arthropods with estimates of number of species ranging up to 20,000 thousand among some 5000 genera, 150 families, and nine distinct orders. There are 10 orders if Odontopleurida is erected from Order Lichida, and 11 if the Nektaspida (commonly called soft-bodied trilobites are classified as a trilobite order). Trilobites burst into amazingly diversity in the fossil record within some five million years of the base of the Cambrian. Such diversity is evidence that trilobites had a past dating long before this famous period and its apparent explosion of life known as the Cambrian Explosion. What made them seem new was that they had acquired a readily preserved skeleton, one they had to be shed to grow. Trilobite progenitors with soft bodies had died and decomposed leaving no trace. Trilobites radiated into the most diverse class of extinct creatures during the Paleozoic, but the Cambrian marked their middle age, not their beginnings. Their size ranged from less than a mm to over one meter in length. The made their living in diverse ways, some crawling, some swimming ,and some living a planktonic existence. They were detritivores, predators, and scavengers, and evolved stealthy and defensive phenotypic characteristics in order to survive in an evolutionary arms race between predator and prey. When they appearin the Cambrian fossil record they are not only diverse in form, and dispersed in geography across all continents. Among the Cambrian fauna, the crystal eyes of trilobites are unique. In the eyes is a strong clue of their ancestry in deep time of the Precambrian, since the fossil record indicates pre-sight neural tissue existed in forms of worms that also contain segmented morphology retained in the trilobite body plan.. RGP111204

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&nbsp;&nbsp;&nbsp; Order <a href="lichida.htm">Lichida</a><br> &nbsp;&nbsp;&nbsp;Order <a href="proetida.htm">Proetida</a><br>
&nbsp;&nbsp;&nbsp;Order <a href="harpetida.htm">Harpetida</a><br> &nbsp;&nbsp;&nbsp;Order <a
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&nbsp;&nbsp;&nbsp;Order <a href="odontopleurida.htm">Odontopleurida</a><br> &nbsp;&nbsp;&nbsp;Order <a
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Palaeos: TRILOBITA
ARTHROPODA AGNOSTIDA

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Trilobita : Agnostida

Class Trilobita Order Agnostida
Order Redlichiida
Order Corynexochida
Order Phacopida
Order Lichida
Order Proetida
Order Harpetida
Order Ptychopariida
Order Asaphida
Order Odontopleurida
Order Nectaspida

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The trilobites of Order Agnostida (pronounced Ag-nós-t-eh-da) appeared in the Lower Cambrian where they were diverse and ubiquitous. They then declined to become rare in the Ordovician prior to their complete extinction by the end of the Ordovician. There is debate about whether agnostids were benthic (living in the lowest level of a body of water and upper sediment) or pelagic (living in water not close to the bottom or near to the shore). Additionally, the systematic position of Order Agnostida remains unsettled, if not contentious. The agnostids were mostly blind and exhibited a strong symmetry of cephalon and pygidium size, making it hard to distinguish front from rear.

There are two Suborders. Members of Suborder Agnostina have two segments between the cephalon and pygidium, and lack sutures on the cephalon. In contrast, members of Suborder Eodiscina may have two or three body segments, and some have small eyes and proparian sutures ending forward of the genal angle. Among trilobites, the Agnostida are so relatively unusual that some researchers have suggested, based on meraspis phase larval limb structure differing markedly from what is prototypical for trilobites (Muller and Walossek, 1987), that one of the two suborders, Agnostina, should not be included in Class Trilobita; the Agnostina have been proposed as a stem group separately descended from Crustaceans. Such a conclusion would be premature, since fossils showing limbs from adults have yet to be discovered (Fortey, 2001). There has also been speculation that agnostids might be paedomorphic due to their superficial resemblance to the meraspis phase of some trilobites; this would suggest precocious sexual maturity, which could include retention of a larval limb structure. Jell (2003) proposes a progenesis from the Ellipsocephaloidea family of Order Ptychopariida as the origin of the members of Suborder Eodiscina, from which the Agnostina descended. Additionally, cladistic analysis (Cotton and Fortey, 2005) strongly supports the continued unification of Suborders Agnostina and Eodiscina as true trilobites based on exoskeleton morphology, despite an obvious specialized body plan.

A highly widespread paleo-geographic dispersion was long considered consistent with a pelagic, planktonic lifestyle.

In contrast, a lack of eyes in most species suggests a benthic lifestyle in deep, cold water on the ocean floor in minimal or no light where they fed on detritus. The agnostids are often found in dense mass mortality assemblages and in association with other benthic trilobites, particularly those of Order Ptychopariida. Additionally, their diminutive size, low mass and general morphology are hydrodynamically inconsistent with a swimming pelagic mode of life. A weight of evidence tends to support that the Agnostida were benthic, but more data are needed; perhaps the little Agnostida made their living in different or multiple ways, depending on their age, or on the paleoenvironment where they lived.

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Trilobita : Agnostida

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- Order Redlichiida
- Order Corynexochida
- Order Phacopida
- Order Lichida
- Order Proetida
- Order Harpetida
- Order Ptychopariida
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- Order Odontopleurida
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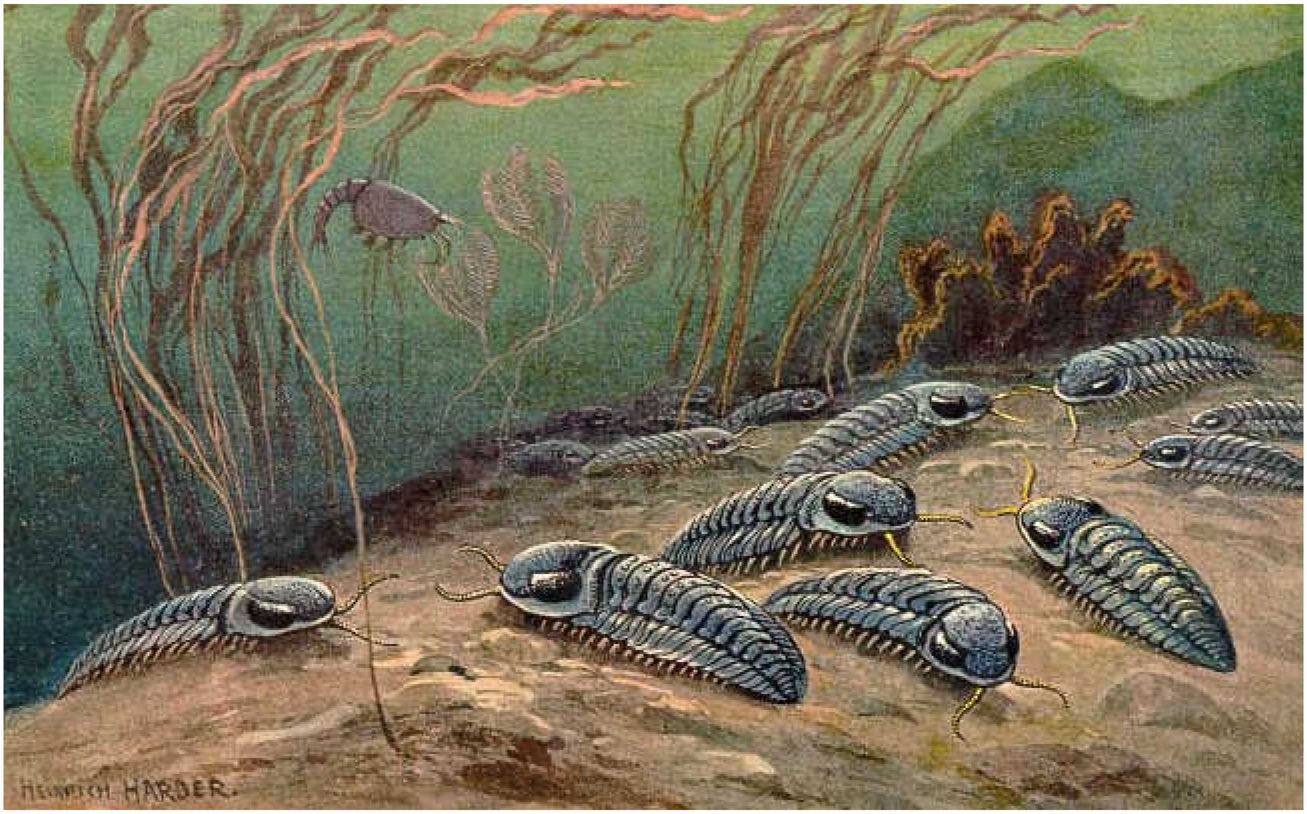

Middle Cambrian trilobites (Artwork by Heinrich Harder, 1916, from Geology in Art)

Trilobites comprise a complex and huge clade of arthropods with estimates of number of species ranging up to 20,000 thousand among some 5000 genera, 150 families, and nine distinct orders. There are 10 orders if Odontopleurida is erected from Order Lichida, and 11 if the Nektaspida (commonly called soft-bodied trilobites are classified as a trilobite order). Trilobites burst into amazingly diversity in the fossil record within some five million years of the base of the Cambrian. Such diversity is evidence that trilobites had a past dating long before this famous period and its apparent explosion of life known as the Cambrian Explosion. What made them seem new was that they had acquired a readily preserved skeleton, one they had to be shed to grow. Trilobite progenitors with soft bodies had died and decomposed leaving no trace. Trilobites radiated into the most diverse class of extinct creatures during the Paleozoic, but the Cambrian marked their middle age, not their beginnings. Their size ranged from less than a mm to over one meter in length. The made their living in diverse ways, some crawling, some swimming ,and some living a planktonic existence. They were detritivores, predators, and scavengers, and evolved stealthy and defensive phenotypic characteristics in order to survive in an evolutionary arms race between predator and prey. When they appearin the Cambrian fossil record they are not only diverse in form, and dispersed in geography across all continents. Among the Cambrian fauna, the crystal eyes of trilobites are unique. In the eyes is a strong clue of their ancestry in deep time of the Precambrian, since the fossil record indicates pre-sight neural tissue existed in forms of worms that also contain segmented morphology retained in the trilobite body plan.. RGP111204

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Trilobita : Asaphida

Class Trilobita
- **Order Agnostida**
- **Order Redlichiida**
- **Order Corynexochida**
- **Order Phacopida**
- **Order Lichida**
- **Order Proetida**
- **Order Harpetida**
- **Order Ptychopariida**
- **Order Asaphida**
- **Order Odontopleurida**
- **Order Nectaspida**

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The trilobites of order Asaphida are notably diverse in number of species and morphology, and interestingly contains about 20% of known species. The most differentating morphological feature of the Asaphid trilobites is the smooth and isopygous (similar in size) cephalon and pygidium, an evolutionary adaptation called effacement believed to have helped trilobites more easily burrow into and hide in sediment. Another theory is that the smoothing of the exoskeleton streamlined the trilobite for locamotion. Effacement is also evident among the Agnostids, and Suborder Illaenina of Order Corynexochida. The Asaphids appeared in the Middle Cambrian and persisted to the Lower Silurian. Order Asaphida comprises six Superfamilies: Anomocaroidea; Asaphoidea; Cyclopygoidea; Trinucleioidea; Dikelokephaloidea; and Remopleuridoidea listed at the bottom of this page. .

The major extinction event concluding the Ordovician Period markedly reduced trilobite diversity across all the orders. Among the Asaphids, only some members of superfamily Trinucleioidea survived, and they too met extinction near the end of the Silurian.

Trilobita : Corynexochida

Class Trilobita
  Order Agnostida
  Order Redlichiida
  Order Corynexochida
  Order Phacopida
  Order Lichida
  Order Proetida
  Order Harpetida
  Order Ptychopariida
  Order Asaphida
  Order Odontopleurida
  Order Nectaspida

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The members of trilobite Order Corynexochida (pronounced Cory-nex-o-chee-da) comprise a large and morophologically diverse and complex trilobite clade with a biostratigraphy range from the Lower Cambrian to the Middle Devonian. The Corynexochida are divided into three suborders, Corynexochina, Illaenina and Leiostegiina that have distinct differentiating characteristics. Strong evidence supports the well-accepted phylogeny that the corynexochids descended from the Redlichiina in the Lower Cambrian.

Order Corynexochida was greatly expanded by Fortey (1990) from the 1959 Treatise (Rasetti in Moore, 1959), where it contained only Cambrian families, to include Leiostegioidea and Scutelluina. To unite the expanded order, Fortey used the characteristically clavate glabellar shape, often concavesided, and frequently with splayed glabellar furrows, and conterminant hypostomal attachment. Because Ontogenies are well known for a number of genera (e.g., Chatterton, 1980), including late protaspides very like those of Illaenidae, the Illaenids were incorporated in the Corynexochida; hypostomes and rostral plate structures were also noted to be comparable between the two groups. Fortey also notes the primary differentiating characteristic between Cambrian and later corynexochids. Cambrian corynexochids are typified by the rostral plate that is fused to the hypostome, in contrast to Ordovician and younger representatives.

With the 1990 revisions, the morphological features uniting the Corynexochids are: opisthoparian sutures; elongate pestle-shaped glabella, played furrows (unless effacement evident) with typically backward-pointing hind pair and anterior pairs pointing increasingly forward toward the cephalon; sometimes with pit-like furrows; ledge like cranidial borders, either conterminant or (in derived forms) impendent hypostome, and large eyes (sometimes arcuate). The Corynexochid thorax typically has 7 to 8 segments, often with spinose pleural tips, but species with from 2 to12 segments are known. The pygidium is usually large, isopygous or subisopygous, of variable form, and sometimes spinose.

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Trilobita : Harpetida

Class Trilobita
  Order Agnostida
  Order Redlichiida
  Order Corynexochida
  Order Phacopida
  Order Lichida
  Order Proetida
  Order Harpetida
  Order Ptychopariida
  Order Asaphida
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  Order Nectaspida

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Trilobites of Order Harpetida are mainly differentiated from others by a semicircular brim around the front of the cephalon (head). The brim is often contains small holes that are believed to have served as a feature for filtering food. The brim surround the cephalon extending backward from the front on both sides, and normally has a prominent suture along the outer edge. Harpitids typically have small eyes on prominent ridges, twelve or more thoracic segments, and a small pygidium.

Order Harpetida was formerly allied with Ptychopariida, until Order Harpitida was erected by Ebach and McNamara in 2002. The subclass Librostoma was created in 1990 by Richard Fortey to cover the orders formally included with the Ptychopariida (i.e., Ptychopariida, Harpetida, Asaphida, and Proetida). The Harpetids are now most often considered to be descendents of Order Ptychopariida, appearing in the upper Cambrian period and going extinct along with many other trilobite orders in the late Devonian period.

Trilobita : Lichida

Class Trilobita
  Order Agnostida
  Order Redlichiida
  Order Corynexochida
  Order Phacopida
  Order Lichida
  Order Proetida
  Order Harpetida
  Order Ptychopariida
  Order Asaphida
  Order Odontopleurida
  Order Nectaspida

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Trilobita : Nectaspida

Class Trilobita
- Order Agnostida
- Order Redlichiida
- Order Corynexochida
- Order Phacopida
- Order Lichida
- Order Proetida
- Order Harpetida
- Order Ptychopariida
- Order Asaphida
- Order Odontopleurida
- Order Nectaspida

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Trilobita : Odontopleurida

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Trilobita : Phacopida

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  Order Redlichiida
  Order Corynexochida
  Order Phacopida
  Order Lichida
  Order Proetida
  Order Harpetida
  Order Ptychopariida
  Order Asaphida
  Order Odontopleurida
  Order Nectaspida

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Trilobita : Proetida

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Order Redlichiida
Order Corynexochida
Order Phacopida
Order Lichida
Order Proetida
Order Harpetida
Order Ptychopariida
Order Asaphida
Order Odontopleurida
Order Nectaspida

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The Proetids persisted the longest and were the last order of the trilobites to go extinct. These last survivors arose in the Ordovician and died out during the great Permian Extinction.

They were relatively smaller trilobites that, like the trilobites of order Phacopida, often exhibited pits and tubercles on their exoskeletons, particularly on their glabella. Unlike some trilobites of the order Phacopida that have schizochroal eyes, the proetids have the more common holochroal eyes. Holochroal eyes closely packed biconvex lenses beneath a single corneal layer covering all lenses. Each lens is roughly hexagonal and thus in direct contact with adjacent ones, and can number into the thousands of lenses. The proetid's thorax of proetids have between some eight to 22 segments. Many have pronounced genal spines resembling those of trilobite order Phacopida.

Proetida (pronounced Pro-eh-tee-da) is often included in subclass Librostoma along with what are now Orders Ptychopariida, Asaphida, and Harpetida that were united as Order Ptychopariida, a huge and paraphyletic group (see the 1959 Treatise on Invertebrate Paleontology). The subclass Librostoma was erected in 1990 by Fortey (1990) to encompass these orders that share a natant hypostomal condition. Subsequently, Ebach & McNamara (2002) erected order Harpetida because its members lack a rostral plate and have a marginal facial suture.

- Ebach, M.C. & K.J. McNamara. 2002. A systematic revision of the family Harpetidae (Trilobita). Records of the Western Australian Museum 21:135-67.
- Fortey, R.A. 1990. Ontogeny, hypostome attachment and trilobite classification. Palaeontology 33:529-76.

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Trilobita : Ptychopariida

Class Trilobita
  Order Agnostida
  Order Redlichiida
  Order Corynexochida
  Order Phacopida
  Order Lichida
  Order Proetida
  Order Harpetida
  Order Ptychopariida
  Order Asaphida
  Order Odontopleurida
  Order Nectaspida

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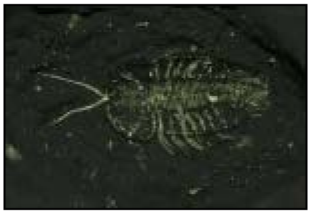

Ptychopariida (pronounced Pity-cho-pa-ree-da) is a huge and morphologically diverse order of trilobite that has largely defied science's attempts to unravel its phylogeny through cladistics. Many ptychopariids were among the most primitive trilobites dating to the early Cambrian. The order persisted through to the late Ordovician. Fortey (2001), posited that Ptychopariida arose out of the paraphyletic suborder Redlichiina. Ptychopariida is a critical grouping in that the order likely gave rise to the great plurality of post-Cambrian trilobites (Edgecombe, 1992; Eldredge, 1977; Fortey and Chatterton, 1988; Fortey and Owens, 1997; Fortey, 2001; Jell and Adrain, 2003). Order Ptychopariida is often described as a catch-all bucket for trilobites from the middle through upper Cambrian.

Interestingly, there has been some speculation that diminitive trilobites of order Agnostida may have evolved as a offshoot of the Ptychopariida due to progenesis, the retention by an organism of juvenile or even larval traits into later life.

What are now trilobite Orders Ptychopariida, Asaphida, Proetida, and Harpetida were grouped together as Order Ptychopariida in the 1959 Treatise on Invertebrate Paleontology. The subclass Librostoma was erected in 1990 by Fortey (1990) to unite these orders that are allied at least in more primitive genera by a natant hypostomal condition where the Hypostome is free of the anterior doublure, and aligned with anterior edge of glabella. Subsequently, Ebach & McNamara (2002) raised Harpetida to an order status because its members lack a rostral plate and have a marginal facial suture.

The thorax is usually large, much longer than the normally small pygidium and has eight or more segments. In some species the pygidium has a flattish border. Ptychopariida trilobites typically have opisthoparian facial sutures, with a forward angled simple glabella with a rounded front. Order Ptychopariida includes what is arguably the most common trilobite, Elrathia kingii that is prodigious in the House Range of Utah.

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Trilobita : Redlichiida

Class Trilobita
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  Order Redlichiida
  Order Corynexochida
  Order Phacopida
  Order Lichida
  Order Proetida
  Order Harpetida
  Order Ptychopariida
  Order Asaphida
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Members of trilobite Order Redlichiida (pronouced Red-li-chee-da) are the oldest trilobites known from the fossil record. The Redlichiids appear in the Cambrian Epoch 2 and disappear from the fossil record prior to the Furongian at the end of the Cambrian. The order is believed to contain the progenitors of members of Order Corynexochida, and Order Ptychopariida.
A number of morphological features in the Redlichiids are considered to be the characteristics of the earlier and more primitive trilobites. These include: 1) numerous thoracic segments having spinose tips; 2) large and semicircular cephalon; 3) large crescent-shaped eyes; 4) and a diminutive (micropygous) pygidium having one to a few segments

Order Redlichiida is divided into two suborders, Olenellina and Redlichiina. Of the two, the Olenellina are considered to be the earliest trilobites. Primarily due to their lack of facial sutures, some scientists have argued unsuccessfully for their separation from Trilobita. In all likelihood, Olenellina is most closely related to the last arthropod common ancestor of the trilobites.

The Olenellids are restricted to what was Laurentia in the Lower Cambrian, which now includes part of North America. In contrast, the Redlichiina are found in numerous Lower Cambrian locations that were not part of Laurentia. The different stratigraphical ranges are important as they form the basis for the phylenogy of Redlichiida. In fact, Lieberman (2002) has argued that cladistic analysis together with the biogeographic data supports the notion that early trilobite cladogenesis (i.e., the evolutionary splitting) occurred about coincident with the breakup of Pannotia sometime between 600–550 million years ago. Lieberman also conducted cladistic analyses among a group of basal trilobites within the Redlichiina, and the paraphyletic Fallotaspidoids. The group had primitive characteristics, such as the absence of facial sutures allying them with the Olenellina, and other characteristics allying them with the Redlichiina. Shared characteristics supported a phylogenetic position of the fallotaspids as transitional to all or almost all other trilobites except the Olenellina.

The Olenellid Fallotaspis from Morocco at about 540 mya has been cited by Fortey (2000) as the oldest trilobite in the fossil record. This Fallotaspis possessed relatively large holochroal eyes. Redlichids are found in two of the world's famous Cambrian Lagerstätten, the Maotianshan Shales near Chengjiang in China, as well as Emu Bay in Southern Australia. They are also commonly found in many sites in the western part of the United States and Canada. Many examples from these and other various fossil sites are shown below.

The members of Family Olenellidae have been proposed as chemoautotrophic symbionts (Fortey, 2005). Their wide thoraces, large numbers of thoracic segments, remarkably thin exoskeletons and, in some species, degenerate hypostome, and the occasional development of brood pouches are all consistent with this hypothesis. The Olenids appear well adapted to anoxic. Their extended pleural areas could have provided area for the cultivation of sulfur bacteria. It is feasible that the bacteria were grown on the ventral membrane beneath the extended pleurae and/or on the appendages. Among living animals, the gills of bivalves or the appendages of carideans are modified in chemoautotrophic symbionts for bacterial growth.

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Grandagnostus, Largest Known Agnostid Trilobite

Grandagnostus sp

Trilobites Order Agnostida, Family Agnostoidea

Geologic Time: Middle Cambrian

Size: 13 mm in length

Fossil Site: Upper Fauna, Cassis or Agra Zone, Christmas Hills, Smithton, Tasmania

Grandagnostus is the world's largest known Agnostid trilobite.. The meaning of the genus name, Grandagnostus, is pretty self evident. It is a positive and negative specimen that of a fully mature adult with excellent preservation.

RGP120609

Trilobites Family Album

Crotalocephalus Phacopid Trilobite

Crotalocephalus sp

Trilobites Order Phacopida, Family Family Cheiruridae

Geologic Time: Middle Devonian

Size: 60 mm in length

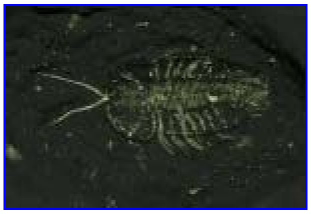
Fossil Site: Oufaten, Alnif, Morocco

The most diagnostic features of this taxon are the sharp pleural and pygidial spines and the distinctive cephalic projections. The spines may have aided it in staying at the surface of the soft seafloor.

RGP120902

Trilobites Family Album

Triarthrus eatoni Ptychopariid Trilobite with Preserved Soft Tissue



Triarthrus eatoni

Trilobites Order Ptychopariida, Family Olenidae

Geologic Time: Late Ordovician

Size: 13 mm in length

Fossil Site: Lorraine Shale, Lewis County, New York

Theis trilobite was buried rapidly, resulting in an anxonic environment which allowed for infilling with fine-grained pyretic deposits that preserved the soft tissue details seen here. The rich gold color is a striking contrast to the deep black matrix.

RGP120903

Trilobites Family Album

Xiphosura

```
Chelicerata
|--Merostomata
|   |--Xiphosura
|   |   |--Bunodidae
|   |   `--+--Bellinurina
|   |      `--Limulina
|   |         |--Paleolimulidae
|   |         `--Limulidae
|   `--+--Chasmataspida
|      `--Eurypterida
`--Arachnida
```

Limulus polyphemus

The horseshoe crab *Limulus polyphemus*
Photo by Jir� Bukovsk�, Encyclopedia of Life, - Limulidae, Creative Commons Attribution Non-Commercial

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Xiphosura

```
Chelicerata
|--Merostomata
|   |--Xiphosura
|   |   |--Bunodidae
|   |   `--+--Bellinurina
|   |      `--Limulina
|   |         |--Paleolimulidae
|   |         `--Limulidae
|   `--+--Chasmataspida
|      `--Eurypterida
`--Arachnida
```

Taxonomy

Class Xiphosura Latreille, 1802

(Horseshoe crabs and their extinct relatives)

Limulus polyphemus (Linnaeus)

Limulus photo from Paul D. Bell's Insects Classification - Arthropoda page family Limulidae - "tribe Limulini"

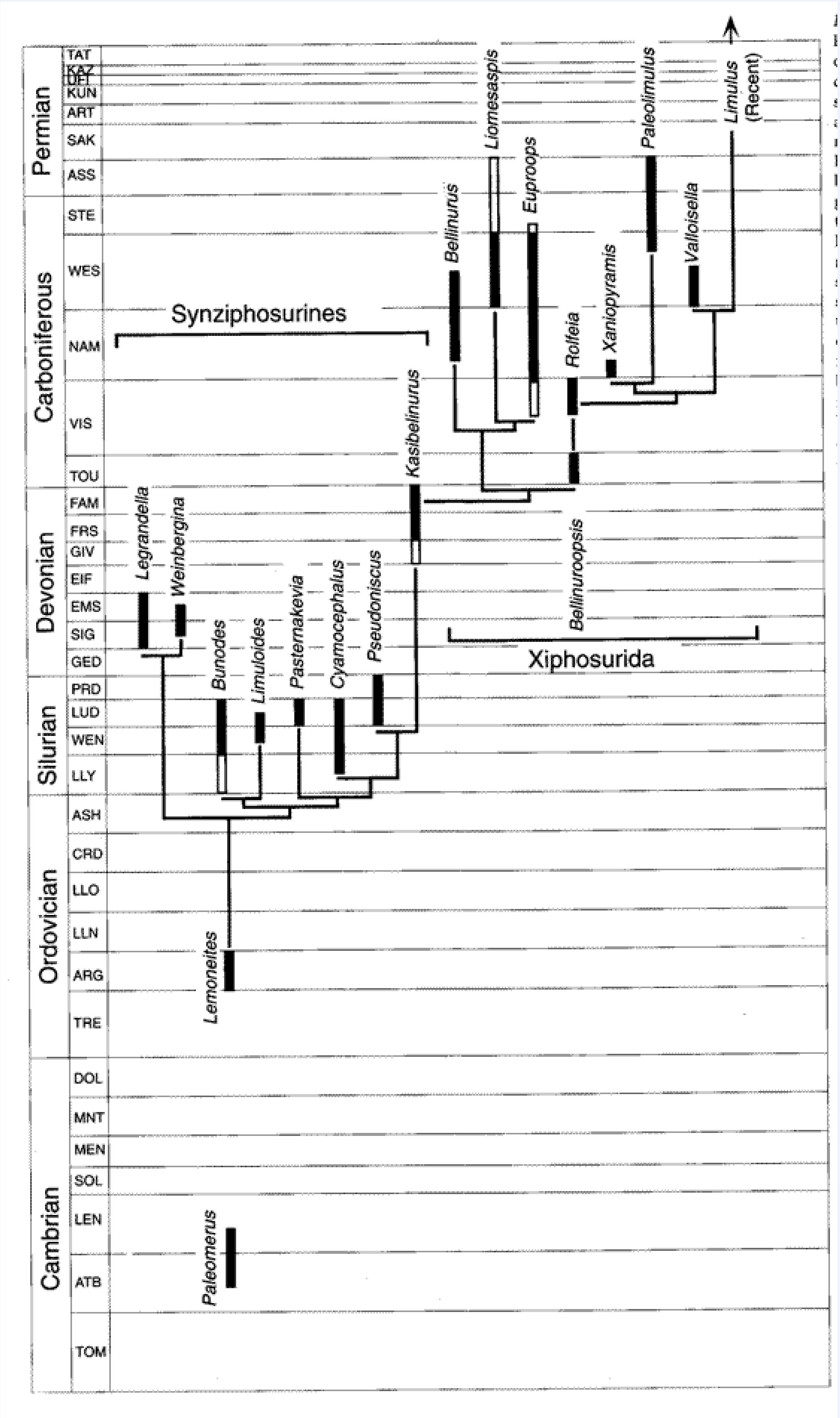
Contents

Remarks

There are only 3 genera and 5 species of Xiphosura left alive today, but they were much more numerous and diverse during the Palaeozoic era. The surviving horseshoe crabs (*Limulus*) are 'living fossils', barely changed in some 250 million years (since early Triassic time). Members of this class have a large shield that covers the cephalothorax; the carapace is hinged between the cephalothorax and abdomen. The exoskeleton generally consists of three parts, the large, semicircular cephalothorax, or prosoma, the usually smaller, subtriangular and in earlier forms "trilobite"-like opisthosoma, and the long stout tail-spine or telson (which is actually the end part of the opisthosoma).

The prosoma contains both head and visceral organs. The compound eyes are small (and absent in some early forms), and there are six pairs of legs (in the living *Limulus*) but no antennae. The second pair of appendages, the pedipalps, resemble walking legs. Respiration is via 5 pairs of book gills, the flaps of which beat in a metachronal rhythm to produce a vigorous current. Recent xiphosurids (Horseshoe crabs) feed on worms and other small invertebrates. They are often used as laboratory animals by physiologists. It has been argued that because of their unique status as prehistoric "living fossils" they deserve special conservation status.

Evolution



The Evolution of the Xiphosura during the Paleozoic era, showing representative genera. This cladogram is from Anderson & Selden, reproduced courtesy Lyall Anderson.

Paleomerus and *Lemoneites* are very early forms that were either Aglaspids or transitional between the Aglaspida and the Xiphosura. The Furongian (Caerfai epoch) marine family Eolimulidae is generally considered a true Xiphosuran, but again more research needs to be done if more is to be known about the early history of this interesting group.

Systematics

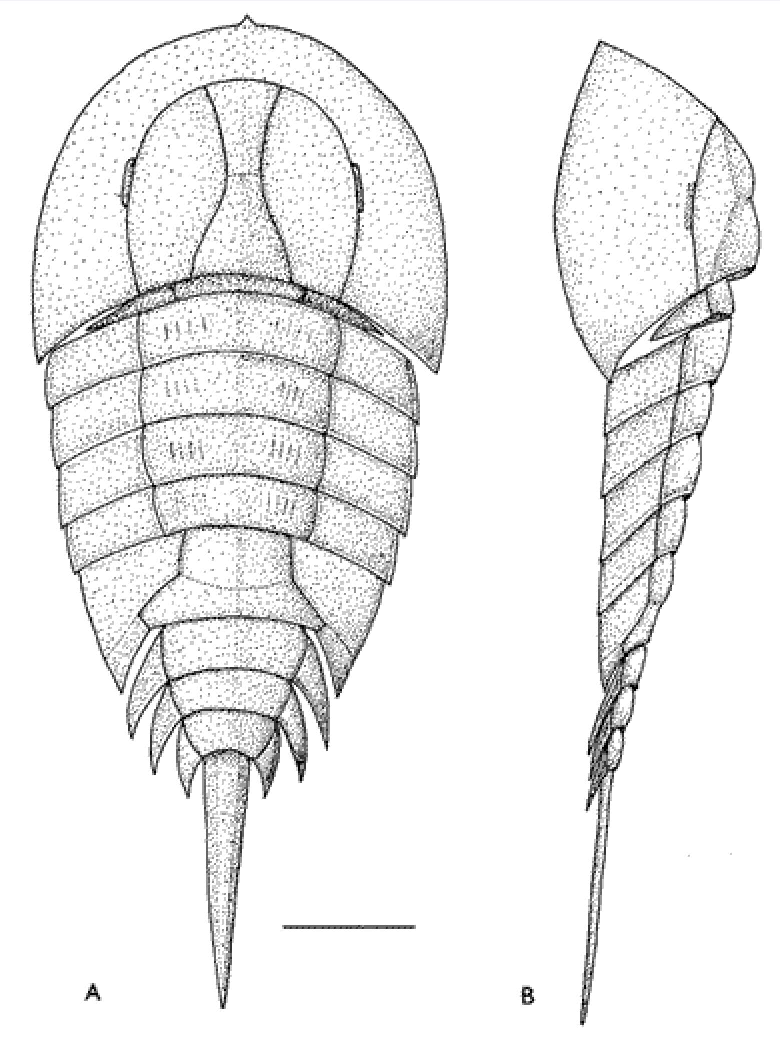
There are only two orders (or sub-orders, depending on your preference) of Xiphosura, the primitive and ancestral Synziphosurina/-ida, and the Lumulina/-ida/Xiphosurida/-ina. The latter group includes modern horseshoe crabs and their immediate ancestors.

The Aglaspida, for a long time considered a very primitive order of Xiphosura, are now thought to be a distinct group, and may actually be closer in fact be closer to the trilobites, or alternatively an ancestral lineage of Merostomata. The Chasmataspida, previously considered Xiphosura, appear to be closer to the Eurypterida, or possibly represent an independent subclass. With modern cladistic analysis even this Linnean arrangement is being discarded.

The following family level Linnean classification presented here is a sort of compromise between the *Treatise of Invertebrate Paleontology*, the *Fossil Record* I and II, and the recent work of Lyall Anderson (who presents a cladistic arrangement of the group). In view of the fact that this material is taken hither-thither from other sources it should not be considered an authoritative review of the group.

Order Synziphosurida (Basal Xiphosura)

Silurian to Early Devonian.

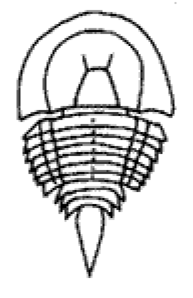


Cyamocephalus loganensis Currie 1927
Length about 5 cm - family Pseudoniscidae
Late Llandovery or possibly early Wenlock, Silurian period, Scotland (Euramerica)

image by, and courtesy of, Lyall Anderson.

The Synziohosurida are a small, fairly diverse, paraphyletic / ancestral group of primitive Xiphosura. Rather trilobite-like in appearance. Large prosoma (headshield), simple eyes only. 9 or 10 opisthosomal (abdominal) segments, most or all of which are free (unfused). The segments are not chelate. Mostly brackish or freshwater environments, although some forms were marine (marginal marine?). Usually found in association with eurypterids and ostracoderms.

Family Weinberginidae



Family Weinberginidae Richter and Richter, 1929

time range: (Pragian to Emsian

habitat: Marine

representative taxa: *Weinbergina opitzi* Richter and Richter, 1929, *Willwerathia laticeps* (Størmer, 1936); *Legrandella lombardi* Eldredge, 1974

status: monophyletic

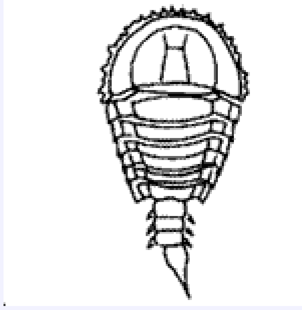
description: Medium-sized forms with large semicircular smooth prosoma, short 10-segmented Small trilobite-like abdomen, post-abdomen with 3 segments, 5 pairs of walking legs, spines. These late surviving forms seem to be among the most primitive of the Synziphosurida, or in any case they represent a side branch away from the main axis of Xiphosuran evolution. They are also the only Synziphosurines found in a proper marine environment.

Family Bunodidae

family Bunodidae Packard 1886

Small elongate forms, ornamented prosoma, abdomen with broad axis, 9 free segments, post-abdomen with 3 or 4 segments.

Subfamily Limuloidinae



new ranking; formerly family Limuloididae Størmer, 1952

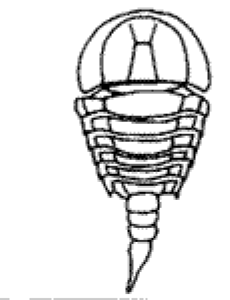
time range: Wenlock to Ludlow

habitat: Marginal Marine

representative taxa: *Limuloides limuloides* Woodward, 1865

description: Small forms, ridged and spiny prosoma, post-abdomen with 3 segments. Only one genus.

Subfamily Bunodinae



new ranking; family Bunodidae Packard 1886

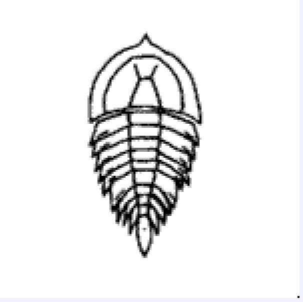
time range: Llandovery to Ludlow

habitat: Marginal Marine

representative taxa: *Bunodes lunula* Eichwald, 1854

description: Small trilobite-like forms, vaulted, radially-lobed prosoma, post-abdomen with 3 to 4 round segments.

Family Pseudoniscidae



family Pseudoniscidae Packard 1886

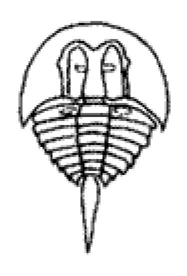
time range: Llandovery to Pridoli

habitat: Marginal Marine

representative taxa: *Pasternakevia podolica* Selden and Drygant, 1987, *Cyamocephalus loganensis* Currie, 1927, *Pseudoniscus aculeatus* Nieszkowski, 1859

description: Small forms with large, somewhat flat, smooth prosoma, 9 or 10 free segments with pleural (marginal) spines, no post-abdomen. *Pasternakevia* is transitional between the Bunodidae and Pseudoniscidae proper.

Family Kasibelinuridae



Family Kasibelinuridae Pickett, 1993

time range: Givetian to Famennian

habitat: Marginal Marine

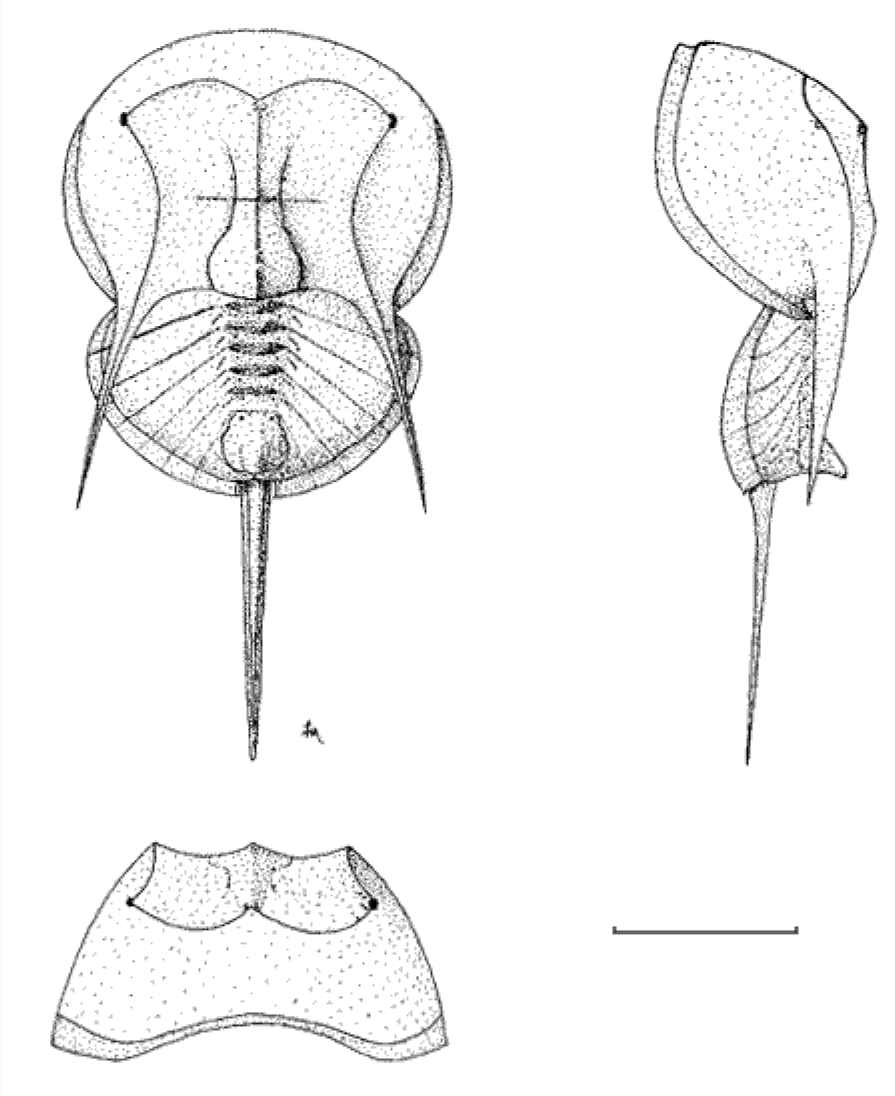
representative taxa: *Kasibelinurus amicorum* Pickett, 1993

description: The last of the synziphosurnes, and also the most derived (advanced). Live in south-East Gondwanaland (Australia). Presumably ancestral to the Xiphosurida.

status: monospecific

Order Xiphosurida

Devonian to Recent.



Liomesaspis laevis Raymond 1944
Length about 4 cm
A common coal swamp form - Family Euproopidae
Late Bashkirian ? and early Moscovian to early Gzhelian (Euramerica)

image by, and courtesy of, Lyall Anderson.

The Order Xiphosurida/Limulida includes most Xiphosura, and all post-Devonian forms. These animals were quite common during the Carboniferous, and some forms seem to have been amphibious, although other types (e.g. *Paleolimulus*) were fully marine. Beginning from small ancestral types they increased in size through the Mesozoic and Cenozoic, and modern horseshoe crabs are giants compared to Paleozoic forms (the horse also has shown a similira tendency to increase in size but reduce in diversity throughout the Tertiary and Quaternary periods), There is the tendency towards fusion of the opisthosomal tergites (free abdominal segments) to form a thoracetron or fused plate. There are several superfamilies and a greater number of families, but only one lineage made it into the post-Paleozoic world. Cladistic analysis so far indicates that the Xiphosurida are a monophyletic taxon.

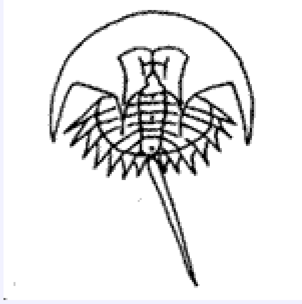
Suborder Bellinurina

Anderson and Selden consider the Bellinuroidea a suborder (Bellinurina) which contains only two families, the Bellinuridae and the Euproopidae. His Euproopidae would seem to be equivalent to the *Treatise*'s Euproopacea, as it includes the genera *Euproops* and *Liomesaspsis* (usually each put in a seperate family of the Euproopacea). These were small animals, with short bodies, only partially fused abdominal segments, and wide rounded horseshoecrab-like headshields, giving them a rather trilobite-like resemblence, apart from the long tail-spine or *telson*. They frequented the coal swamps and were in all likelihood amphibious, perhaps living part of their life-cycle on land.

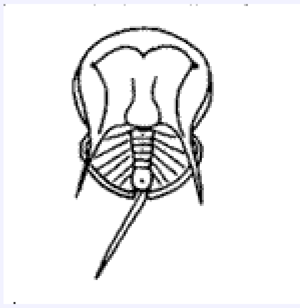
Elleriidae?

time range: Frasnian
habitat: Marginal Marine ? Brackish and Fresh water. Amphibious?
representative taxa:
description: Abdominal axis and pleural area segmented; the rear of the abdominal shield deeply indented. In the *Treatise* placed in the superfamily Euproopacea. In view of the early date this group may perhaps turn out to be a separate early off-shoot.

Family Euproopidae



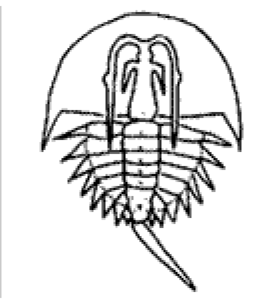
Family Euproopidae Eller, 1938 (junior synonym: family Liomesaspidae Raymond 1944
time range: Vis�an to Artinskian
habitat: Marginal Marine, Brackish and Fresh water. Amphibious.
representative taxa: *Euproops anthrax* Prestwich, 1840, *Euproops danae* Meek and Worthen, 1865, *Euproops rotundatus* Prestwich, 1840, *Liomesaspis laevis* Raymond, 1944
description: Small, common forms with well-marked cardiophalmic horseshoe crab "head" area, the cardiac lobe bordered by distinct axial furrows. The abdomen broad and rounded, abdominal shield with annulated (ringed) axis and a boss or knob on the last segment. Like Bellinurids, Euproopids were a common element in the great coal swamps of the Carboniferous tropics.



Taxanomic note: In the *Treatise* this family is separated from the Bellinuridae by being placed in the superfamily Euproopacea. *Liomesaspis* is placed in the family Liomesaspidae, superfamily Euproopacea, and there is also a seperate listing for the family in the Fossil Record II (time range: Bashkirian to Asselian). However Anderson and Selden include *Liomesaspis* in the family Euproopidae, and Anderson points out that Raymond's initial diagnosis of Liomesaspidae as lacking axial furrows does not apply to the specimens of the genus he has studied. There seems no reason therefore in retained it as a valid family.

time range: Bashkirian to Asselian
habitat: Marginal Marine, Brackish and Fresh water. Amphibious.

Family Bellinuridae



Family Bellinuridae Zittel and Eastman, 1913
time range: Givetian? Serpukhovian to Moscovian
habitat: Marginal Marine, Brackish and Fresh water. Amphibious.
representative taxa: *Bellinurus trilobitoides* Buckland, 1837.
tentative taxa: *Bellinuroopsis rossicus* Chernyshev, 1933 (=*Neobelinuropsis*) may represent a distinct family and superfamily. *Protolimulus eriensis* (Williams) is a small poorly known Devonian form.
description: The most primitive Xiphosurid family, evolving from a *Kasibelinurus*-like ancestor, representing an ancestral type from which more advanced forms may have developed. The forward abdominal segments are free, but the last two or more rear ones may be fused. This fusing of the abdominal segments is a common and defining tendency among the Xiphosurida.

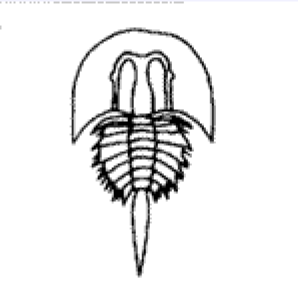
Suborder Limulina

superfamily Limuloidea Zittel 1885

The Limulina represent the most advanced lineage of the group, descended from early Carboniferous transitional forms like *Rolfeia*. The cephalothorax is wide and arched, with the cardiophthalmic region poorly defined. . The abdominal segments are usually fully fused, although the marginal spines are movable. Includes the 5 living species of "horseshoe crabs" (*Limulus*). These creatures live in a shallow marine environment (although some Paleozoic forms may have been brackish water inhabitants). Jurassic Xiphosurids are extremely similar to those found today.

Anderson and Selden distinguish between the superfamily Paleolimuloidea - defined by the pyramidal cheek node on the carapace - and the superfamily Limuloidea (which Includes all Mesozoic and Cenozoic Xiphosura).

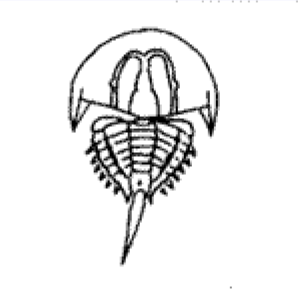
Family Rolfeiidae



Rolfeiidae Selden and Siveter, 1987
time range: Tournaisian - Visean
habitat: Marginal Marine
representative taxa: *Rolfeia fouldenensis* Waterston, 1985

These are paraphyletic basal limulines.

Family Paleolimulidae



Family Paleolimulidae Raymond, 1944
time range: Serpukhovian to Asselian (*not* Hettangian, *"Paleolimulus" fuchsbergensis* does not belong in the genus)
habitat: Marine, Marginal Marine, Brackish and Fresh water
representative taxa: *Paleolimulus avitus* Dunbar, 1923
description: Small forms with ophthalmic ridges meeting in front of the cardiac lobe; carapace with pyramidal cheek node; abdominal axis distinctly annulated.

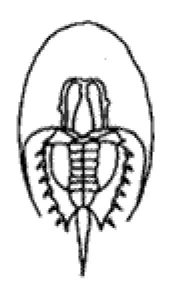
Family Moravuridae

Family Moravuridae Pribyl, 1967

time range: Serpukhovian
habitat: Marginal Marine
representative taxa: *Xaniopyramis linseyi* Siveter and Selden, 1987

Probably a branch of the Paleolimulidae

Family Undetermined (New family? - "Valloisellidae")



time range: Bashkirian to Moscovian
representative taxa: *Valloisella lievensis* Racheboeuf, 1992
description: sister taxon to the Limulidae and their relatives. Represent the ancestral type from which modern horseshoe crabs evolved. Basically similar to modern forms.

This, and the following two families are staem limulids, of uncertain monophyly.

Family Austrolimulidae

time range: Ladinian
habitat: Fresh water

Family Heterolimulidae

time range: Ladinian
habitat: Marine

Family Limulidae

Family Limulidae Zittel, 1885
time range: Scythian - Recent
habitat: Marginal Marine, Brackish, and Fresh water
description: Small to large forms; prosoma with ophthalmic ridges not meeting in front of the cardiac lobe; no annulation of abdominal axis; conventional horseshoe crabs.

Subfamily Mesolimulinae Størmer, 1952

In the *Treatise* this taxon is considered a family.
time range: Scythian to Tithonian (or Cretaceous?)
habitat: Coastal/Marginal Marine, Brackish, and Fresh water
representative taxa: *Mesolimulus walchi* (Demarest) is known from the Solnhofen late Jurassic. *Psammonlimulus gottingensis* Lange and *Limulitella bronni* (Schimper) are early and late Triassic forms respectively.
description: Small to medium-sized forms; genal angles moderately prolonged backwards; axial furrows distinct.

Subfamily Limulinae Zittel, 1885

In the *Treatise* this taxon is considered a family.
time range: Tertiary to Recent
habitat: Coastal Marine and Brackish water
description: Medium to large forms; hexagonal-shaped abdomen; genal angles strongly prolonged backwards; axial furrows indistinct; "modern" horseshoe crabs.

Tribe Tachypleini Pocock, 1902

new ranking - in the *Treatise* this taxon is considered a subfamily.
time range: Tertiary to Recent
habitat: Living forms coastal Marine; although the Miocene *Tachypleus dechneni* of Germany may have inhabited brackish water.
representative taxa: *Tachypleus dechneni* Zinken (Miocene); *Tachypleus gigas* (Muller) and *Carcinoscorpius rotundatus* (Latrieille) both Recent of Asian Pacific.
description: Prosoma slightly vaulted, movable lateral spines of equal length.

Tribe Limulini Zittel, 1885

In the *Treatise* this taxon is considered a subfamily.
time range: Recent
habitat: Coastal Marine

representative taxa: *Limulus polyphemus* (Linnaeus)
description: Prosoma vaulted, movable lateral spines decreasing in length backwards.

Links and References

Links and References

Xiphosura - Horseshoe crabs presents the best general introduction to the group on the Web

Lyall I. Anderson's Home Page - excellent material on Paleozoic Xiphosura, and heaps of links

Anderson, LI (1997), *The xiphosuran **Liomesaspis** from the Montceau-les-Mines Konservat Lagerstatte, Massif Central, France*. **N. Jahrb. Geol. Palaontol., Abh.** 204: 415-436. **abstract**

Anderson, LI (1998), *A new specimen of the Silurian synziphosurine **Cyamocephalus***. **Proc. Geol. Assoc.** 110: 211-216. **abstract**

Anderson, LI & PA Selden (1997), *Opisthosomal fusion and phylogeny of Palaeozoic Xiphosura*. **Lethaia** 30: 19-31. **abstract**

Euproops danae, from the Mazon Creek deposits of Illinois (Moscovian age) *Euproops danae* was a small form, length about 2 cm, that is relatively common in the Mazon Creek deposit. It seems to have been freshwater or even semiaquatic, living part of its life on land

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Chasmataspida

Cambrian to Devonian

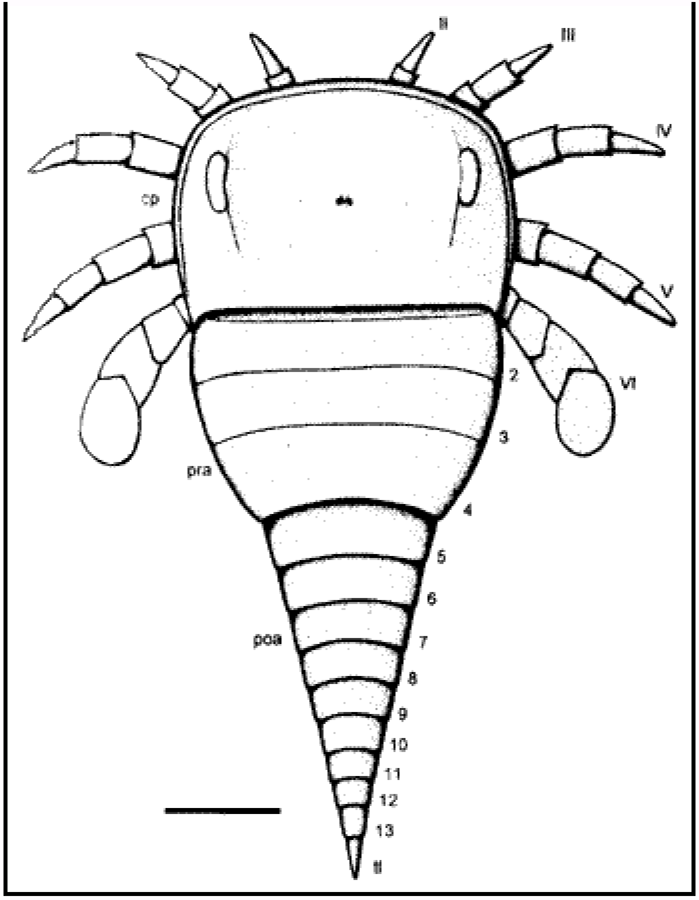
```
Chelicerata
|--MEROSTOMATA
|   |--Xiphosura
|   |   |--Bunodidae
|   |   `--+--Bellinurina
|   |      `--Limulina
|   |         |--Paleolimulidae
|   |         `--Limulidae
|   `--+--Chasmataspida
|      `--Eurypterida
`--Arachnida
```

Introduction to the Chasmataspida

```
<==o �CHASMATASPIDA
   |--o �Chasmataspidae
   |   `-- �Chasmataspis laurencii Caster & Brooks, 1956
   |--o �Diploaspididae
   |   |-- �Diploaspis casteri Stormer, 1972
   |   `-- �Forfarella mitchelli Dunlop et al., 1999
   `-- �Heteroaspididae
```

Chasmataspida **Caster & Brooks, 1956**

The Chasmataspida are primitive merostomatans, possessing a narrow, eurypterid-like cephalothorax and somewhat trilobite-like appearance. Originally considered rare, a number of recent discoveries suggest that chasmataspids were a more widespread and common group than previously realized. Obviously, the similarity with Eurypterids results in some confusion from both sides (some Eurypterids have turned out to be chasmataspids, while a specimen discovered in 1987 by early fish expert Philippe Janvier, from the Middle Devonian (Givetian/frasnian) Do Son Formation of the Do Son peninsula in northern Vietnam, and tentatively referred to the Chasmataspida turned out to be a eurypterid of the family Carcinosomatidae.)



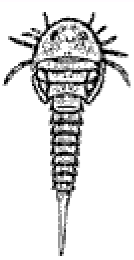
In both *Chasmataspis* and *Diploaspis* at least, the opisthosoma is subdivided into a pre- and postabdomen, with the latter consisting of 9 segments. The number of post-cephalic segments in these animals represents an increase in at least three both on the number of segments of the xiphosurids proper and on the emeraldellids. The respiratory apparatus is limited to the preabdomen.

Caster & Brooks (1956) originally described Chasmataspida as an order within the Xiphosurida (= Xiphosura). Størmer (1972) altered Chasmataspida to Chasmataspidida, though this seems an unnecessary and cumbersome variation. For a while regarded as unusual basal or ancestral xiphosurans, Chasmataspids may actually be closer to Eurypterids. Phylogenetic hypotheses include: the sister group of eurypterids (Eldredge 1974), as both share features such as paddles, a polyphyletic group with *Diploaspis* close to the ancestry of arachnids (Bengström 1979). and sister group to eurypterids and arachnids (Dunlop & Selden 1997). However, recent discoveries have revealed that chasmataspids possess both a metastoma and a genital appendage, both typical diagnostic eurypterid characteristics. This supports Eldredge's thesis that the Chasmataspida and the Eurypterida are sister groups; i.e. that they both shared a common ancestor, together with which they form a single clade. Chasmataspids differ from Eurypterids in their different opisthosomal tagmosis and the presence of genal spines and perhaps also ophthalmic ridges. The position of the scorpions, which some researchers consider as a sister group of eurypterids (see Dunlop & Selden 1997) further complicates things. My own completely unstudied opinion on all this is that either Chasmataspids and the Eurypterids evolved form a common ancestor some time in the Cambrian, or that Eurypterids evolved from Chasmataspids, while scorpions are an early off-shoot of specialized Eurypterids (e.g. *Mixopterus*-like forms). Arachnids in turn (spiders, mites, etc) evolved from early Scorpions (Scorpions are traditionally included within the Arachnida).

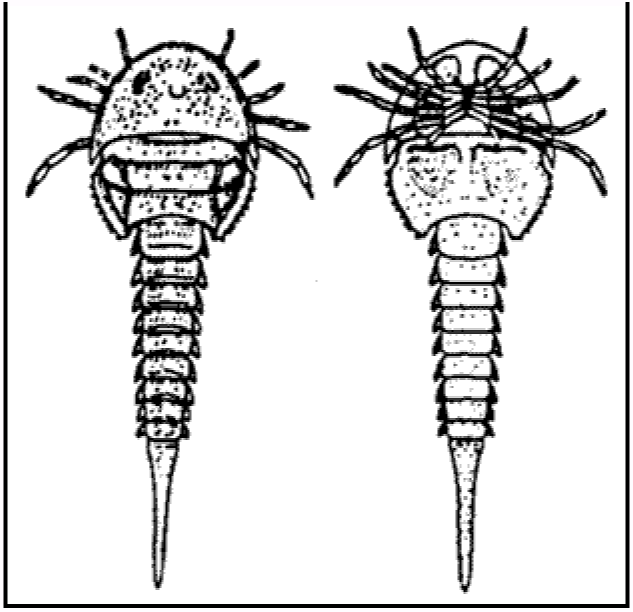
Image: *Forfarella mitchelli*, length about 17 mm (scale bar 2.5 mm). Early Devonian of South Euramerica (Midland Valley of Scotland); family Diploaspididae. From Dunlop *et al*. (1999), by, and courtesy of, Lyall Anderson.

Family Chasmataspidae

Chasmataspis laurencii
Darriwilian Age (Ordovician) of Laurentia
figure from Delle Cave & Simonetta (1991)



Chasmataspidae Caster and Brooks 1956
time range: Darriwilian Age (Ordovician) to Early Devonian
known distribution: Laurentia (Canada and USA (Tennessee)), Euramerica
habitat: Marginal Marine, Brackish water, amphibious

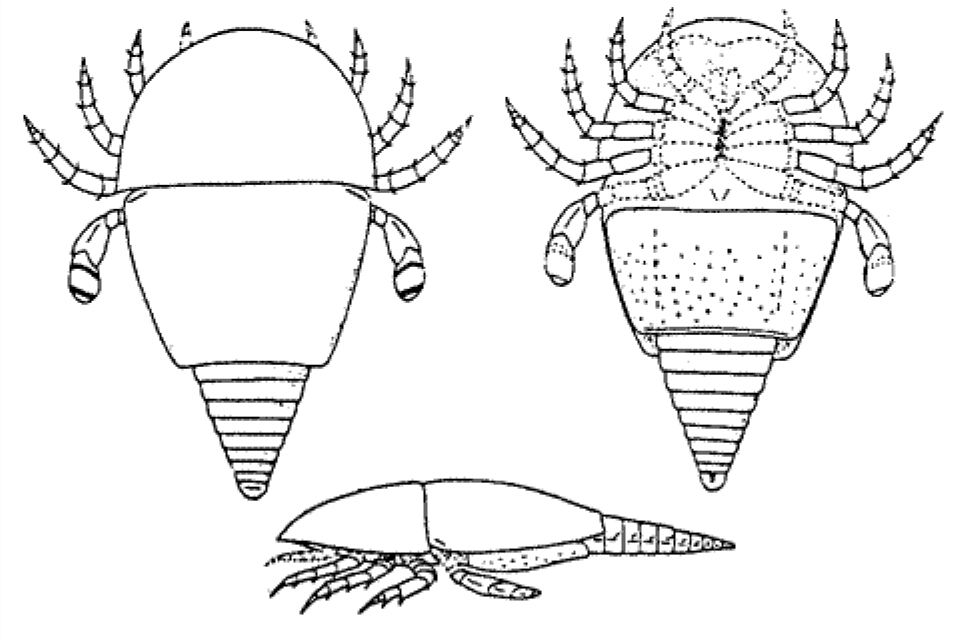


representative taxa: *Chasmataspis laurencii* Caster and Brooks 1956
description: Large chasmataspids with elongate postabdomen and long telson.
reference: Caster & Brooks (1956)
notes: For a long time *Chasmataspis laurencii* was the only known species. However, some Furongian fossils provisionally described as merostomes by Wahlman & Caster (1978) show a rounded prosoma and a long postabdomen, a consistent with them being a series of superimposed resting traces of an animal similar to *Chasmataspis*. There are also two early Devonian species (Størmer, 1972), and some material formerly described as eurypterids from the early Devonian of Siberia may also belong to this group (Størmer, 1972). Delle Cave & Simonetta's reconstruction of *Chasmataspis Iaurencii* is, to quote from their review: "obviously tentative, based as it is on published evidence. The walking legs are very incompletely known: we assumed them to be basically similar, but to be progressively longer caudally in order to balance the animal when walking. The eurypterid *Mixopterus kiasri* Størmer, though of much larger size, has a shape recalling that of *Chasmataspis* and the proportions of the legs have been based on this indirect evidence. As is clear from the figure, the tagmosis of *Chasmataspis* may be compared with the tagmosis of the later, Devonian, *Diploaspis*....The opisthosoma is subdivided into a pre- and postabdomen, with the latter consisting of 9 segments. The number of segments incorporated in the preabdomen is not known, but our tentative suggestion (Simonetta & Delle Cave, 1981) of three is still valid."

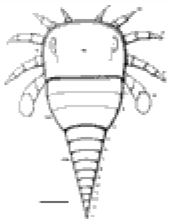
The respiratory apparatus seems to be more sophisticated than that of the Diploaspididae, and apparently includes had a pair of pouches opening by some sort of slits. Such an apparatus, being almost completely closed, certainly could favor life under comparatively dry conditions. Under water it could function only if there was some sort of efficient pumping mechanism. With 3 or 4 preabdomen segments, a modified system of intersegmental muscles and tendons may have been evolved to act as a pump. It is also possible that *Chasmataspis* was an intertidal dweller, foraging at low tide on stranded organisms. The existence of Ordovician (or even Furongian) "strandloopers" does not seem unreasonable, in view of the discovery of truly terrestrial Arachnids in the Silurian, and in fact was a logical step in the progression of life from the ocean to dry land.

Image: *Chasmataspis laurencii* Darriwilian Age (Ordovician) of Laurentia, from Delle Cave & Simonetta (1991).

Family Diploaspididae



Diploaspis casteri
early Emsian epoch (Devonian)
Armorica / tropical South Euramerica (Germany)
figure from Delle Cave & Simonetta (1991)



Family Diploaspididae Størmer, 1972

time range: Early to Middle Devonian

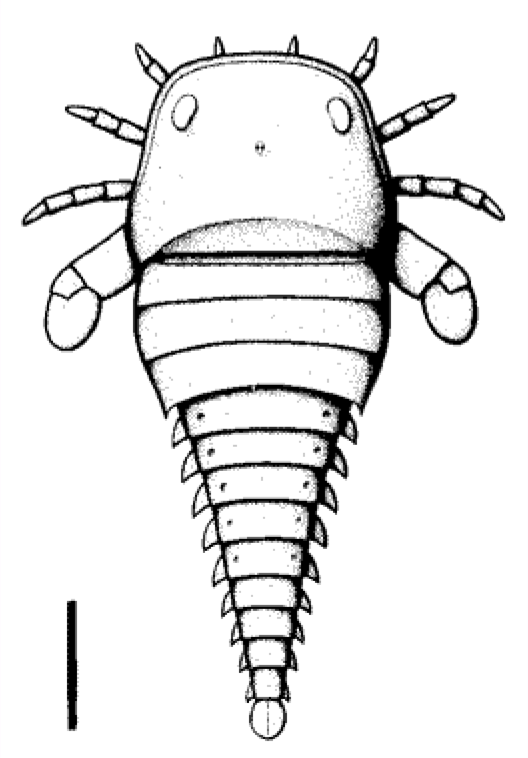
known distribution: Armorica, South Euramerica (Germany and Scotland); Siberia (Severnya Zemla archipelago)

habitat: Marginal Marine to Brackish and Fresh water

representative taxa: *Diploaspis casteri* Størmer, 1972; *Forfarella mitchelli* Dunlop, Anderson, and Braddy, 1999; *Achanarraspis reedi* Anderson, Dunlop, and Trewin, 2000

references: Størmer (1972); Dunlop *et al*. (1999); Anderson *et al*. (2000).

description: Small to very small chasmataspids with semicircular or subrectangular carapace, a distinctly tapering postabdomen and a short telson. The respiratory apparatus is limited to the preabdomen and, in contrast to the Chasmataspidae, constitutes a simple situation recalling that of the Xiphosurans.



Achanarraspis reedi Anderson, Dunlop, and Trewin, 2000
length about 30 mm (scale bar 5 mm)

Late Eifelian of south Euramerica (Caithness, Scotland); family Diploaspididae

This genus is distinguished by a carapace longer than the pre-abdomen, and a spatulate telson (the leaf-like structure at the "tail")
Image from Anderson *et al*. (2000), by and courtesy of, Lyall Anderson.

Family Heteroaspididae

Family Heteroaspididae Størmer, 1972
time range: early Devonian (early Emsian)
known distribution: Armorica / South Euramerica (Germany - Alken)
habitat: Marginal Marine or Brackish Fresh water
representative taxon: *Heteroaspis novojilovi* Størmer, 1972
reference: Størmer (1972)
notes: may turn out to be synonymous with the Diploaspididae

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Merostomata Dendrogram

```
Chelicerata
|--MEROSTOMATA
|  |--Xiphosura
|  |  |--Bunodidae
|  |  `--+--Bellinurina
|  |     `--Limulina
|  |        |--Paleolimulidae
|  |        `--Limulidae
|  `--+--Chasmataspida
|     `--Eurypterida
`--Arachnida
```

```
MEROSTOMATA
|--o XIPHOSURA Latreille, 1802 (Horseshoe crabs)
|  |?- �Palaeomerus
|  |?- �Lemoneites
|  |--o �Weinberginidae Richter & Richter, 1929
|  |  |-- �Weinbergina opitzi Richter & Richter, 1929
|  |  |-- �Willwerathia laticeps (Stormer, 1936)
|  |  `-- �Legrandella lombardi Eldredge, 1974
|  `--+--o �Bunodidae Packard 1886
|     |  |-- �Bunodes lunula Eichwald, 1854 [Bunodidae Packard 1886]
|     |  `-- �Limuloides limuloides Woodward, 1865 [Limuloididae Stormer, 1952]
|     `--+-- �Pasternakevia podolica Selden & Drygant, 1987 [paraphyletic Pseudoniscidae Packard
1886]
|        `--+-- �Cyamocephalus loganensis Currie, 1927 [paraphyletic Pseudoniscidae Packard 1886]
|           `--+-- �Pseudoniscus aculeatus Nieszkowski, 1859 [paraphyletic Pseudoniscidae Packard
1886]
|              `--+-- �Kasibelinurus amicorum Pickett, 1993 [paraphyletic Kasibelinuridae Pickett,
1993]
|                 `--o XIPHOSURIDA Latreille, 1802 (Horseshoe crabs)
|                    |--o �BELLINURINA Zittel & Eastman, 1913
|                    |  |?- �Elleriidae
|                    |  |--o �Bellinuridae Zittel & Eastman, 1913
|                    |  |  |?- �Protolimulus eriensis (Williams, )
|                    |  |  `-- �Bellinurus trilobitoides Buckland, 1837
|                    |  `--o �Euproopidae Eller, 1938
|                    |     |-- �Liomesaspis laevis Raymond, 1944 [Liomesaspidae Raymond 1944]
|                    |     `--o �Euproops Meek, 1867
|                    |        |-- �E. anthrax Prestwich, 1840
|                    |        |-- �E. danae Meek & Worthen, 1865
|                    |        `-- �E. rotundatus Prestwich, 1840
|                    `--o LIMULINA Richter & Richter, 1929 sensu lato?
|                       |-- �Bellinuroopsis rossicus Chernyshev, 1933 [Neobelinuropsis]
|                       `--+-- �Rolfeia fouldenensis Waterston, 1985 [Rolfeiidae Selden and
Siveter, 1987]
|                          `--o LIMULINA Richter & Richter, 1929 sensu Anderson, 1997(?)
|                             |--o �PALEOLIMULOIDEA Anderson, 1997(?)
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|                              |  |-- �Paleolimulus avitus Dunbar, 1923 [Paleolimulidae Raymond,
1944]
|                              |  `-- �Xaniopyramis linseyi Siveter & Selden, 1987 [Moravuridae
Pribyl, 1967]
|                              `--o LIMULOIDEA Zittel, 1885
|                                 |-- �Valloisella lievensis Racheboeuf, 1992 ["Valloisellidae"]
|                                 `--+?- �Austrolimulidae
|                                    |?- �Heterolimulidae
|                                    `--o Limulidae Zittel, 1885 (modern horseshoe crabs)
|                                       |?-o Mesolimulinae Stormer, 1952 (paraphyletic?)
|                                       |  |-- �Psammonlimulus gottingensis Lange
|                                       |  |-- �Limulitella bronni (Schimper)
|                                       |  `-- �Mesolimulus walchi (Demarest)
|                                       `--o Limulinae Zittel, 1885
|                                          |--o Tachypleini Pocock, 1902
|                                          |  |-- Carcinoscorpius rotundatus (Latrieille)
|                                          |  `--o Tachypleus
|                                          |     |-- �T. dechneni Zinken
|                                          |     `-- T. gigas (Muller)
|                                          `--o Limulini Zittel, 1885
|                                             `-- Limulus polyphemus (Linnaeus)
|
(amerikanmolukkirapu; horse-shoe crab)
`--+--o �CHASMATASPIDA
   |  |--o �Chasmataspidae
   |  |  `-- �Chasmataspis laurencii Caster & Brooks, 1956
   |  |--o �Diploaspididae
   |  |  |-- �Diploaspis casteri St�rmer, 1972
   |  |  `-- �Forfarella mitchelli Dunlop et al., 1999
   |  `-- �Heteroaspididae
   `--EURYPTERIDA
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Eurypterida

```
CHELICERATA
|--+--Xiphosura
|  `--EURYPTERIDA
|     |--Eurypteracea
|     |  |--Mixopteracea
|     |  `--Pterygotina
|     `--Stylonuracea
|        |--Dolichopteridae
|        `--+--Stylonuridae
|           `--Hibbertopteroidea
`--Arachnida
   |--Scorpioniformes
   |  |--Opiliones
   |  `--Scorpionida
   |     |--Palaeoscorpiones
   |     `--Orthosterni
   |        |--Chactoidea
   |        `--Scorpionoidea
   `--Araniformes
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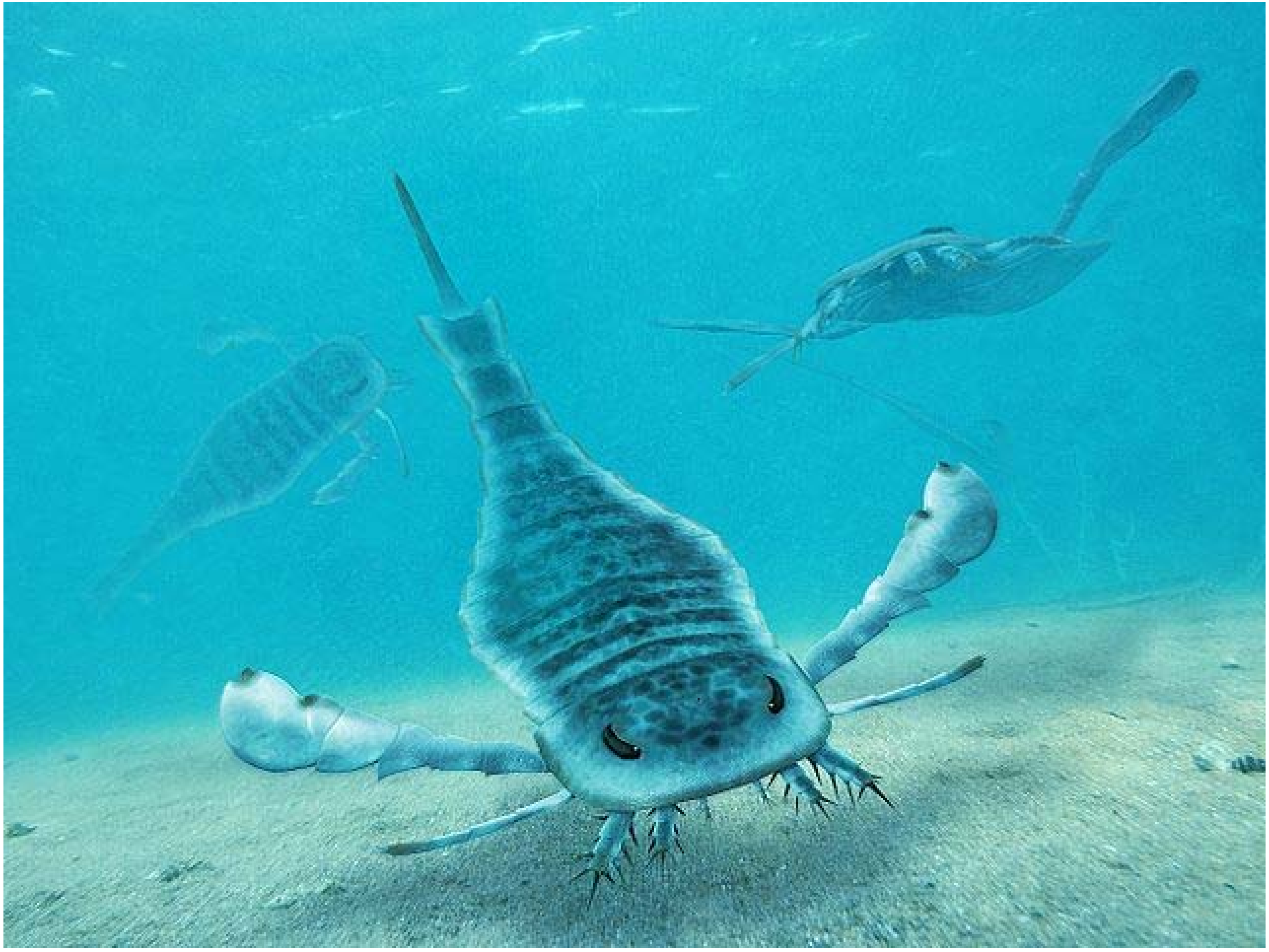

Life reconstruction of *Eurypterus*, a Silurian eurypterid, length about 20 cm.
Artwork by ObsidianSoul, background *Water Floor* by Dimitris Siskopoulos Wikipedia, Creative Commons Attribution

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Eurypterida

```
CHELICERATA
|--+--Xiphosura
|  `--EURYPTERIDA
|     |--Eurypteracea
|     |  |--Mixopteracea
|     |  `--Pterygotina
|     `--Stylonuracea
|        |--Dolichopteridae
|        `--+--Stylonuridae
|           `--Hibbertopteroidea
`--Arachnida
   |--Scorpioniformes
   |  |--Opiliones
   |  `--Scorpionida
   |     |--Palaeoscorpiones
   |     `--Orthosterni
   |        |--Chactoidea
   |        `--Scorpionoidea
   `--Araniformes
```

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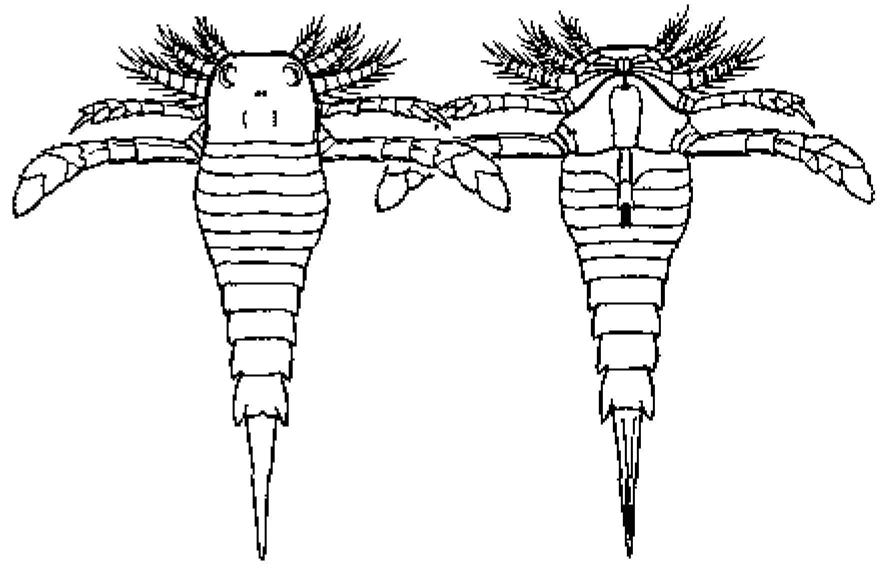
Taxa on This Page

1. Eurypterida X

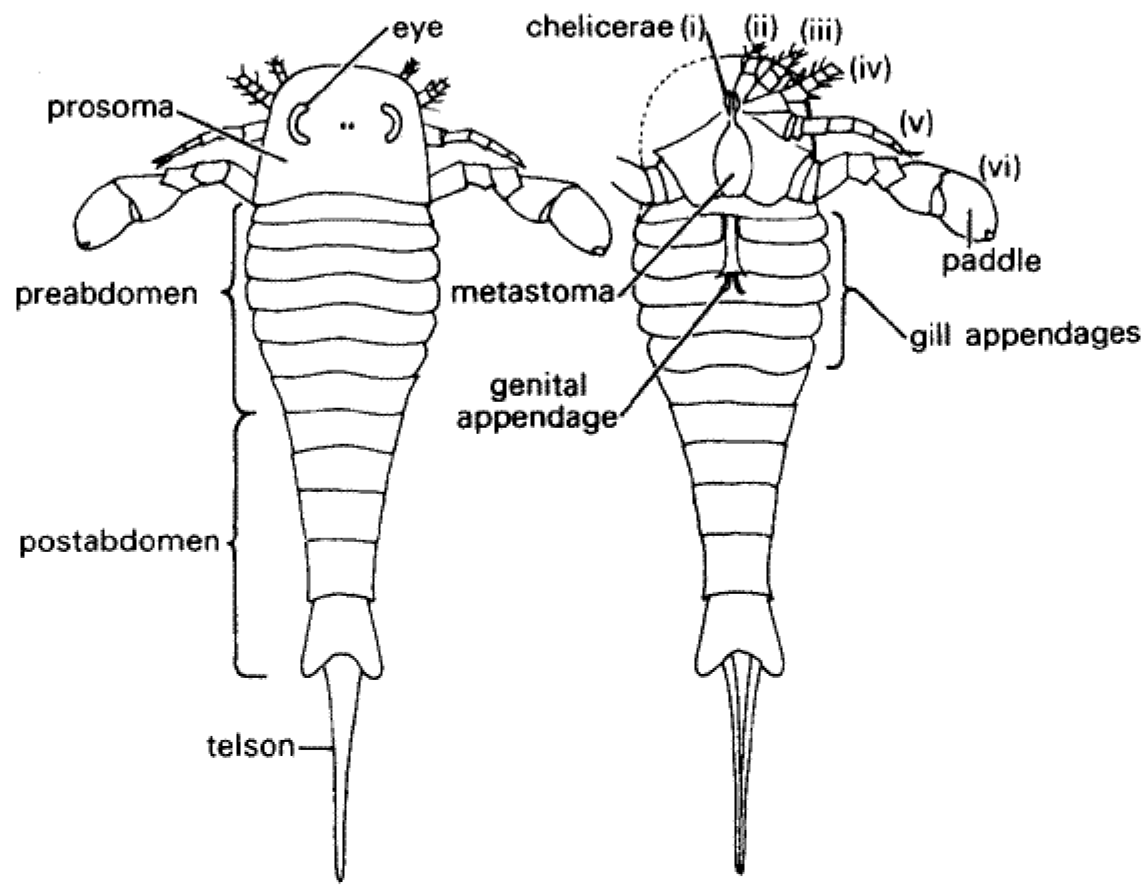
Introduction



Dolichopterus macrocheirus
length 25 to 30 cm
Late Silurian period of west central Euramerica

The Eurypterida are an extinct Paleozoic group of chelicerate arthropods of which 200 fossil species are known. These were spectacular animals, although very rare as fossils. The largest, such as *Pterygotus*; reached 2 meters and more in length, but most species were less than 20 cm. Although called "sea scorpions" only the earliest ones were marine. Most lived in brackish water, sheltered lagoons etc. Many species inhabited shallow aquatic environments and some may have been amphibious, emerging onto land for at least part of their life cycle. They may have been capable of breathing both in water and in air. Their morphology suggests that they fed on a variety of kinds of foods. Some forms like *Mixopterus* were very scorpion-like and may have even been ancestral to scorpions. About two dozen families of eurypterids are known.

Morphology



Baltoeurypterus tetragonophthalmus
left, dorsal (upper) view; right ventral (bottom) view

The morphology of the Eurypterid exoskeleton is very well known, thanks to the work of Holm in 1898, who made a detailed study of the Silurian species *Baltoeurypterus tetragonophthalmus*, formerly known as *Eurypterus fischeri*. He did this by isolating fragments of the exoskeleton from rock, as he did with graptolites, so that they could be studied as transparencies.

The eurypterid body is similar to that of other primitive arthropods, such as trilobites and horse-shoe crabs (Xiphosura). In fact the Eurypterids are rather closely related to the latter. As with the Xiphosura, the long segmented body can be divided into two parts.

The front or "head" part is called the *prosoma*, where the legs are attached and the eyes and mouth are located. As with horseshoe crabs, the prosoma is both the head and thorax of the animal. The upper or dorsal side of the prosoma is equipped with two prominent kidney-shaped compound eyes, and in the middle a pair of small *ocelli* or simple eye-like sense-organs. The mouth is located underneath in the center, and around it the six pairs of legs are attached. Depending on their structure, these were used for walking, swimming, or grasping food. The legs are connected to the body by toothplates or *gnathobases*. These border the slit-like mouth and are lined by teeth.

The first pair of legs are the *chelicerae*, which are the same organs (but differently developed - i.e. *homologous*) as the fangs of spiders. All chelicerate arthropods have this special first set of modified legs. The next four pairs of appendages are the walking legs, These are cylindrical and spiny and increase in size with each pair. Finally there are the very large smooth flattened paddle-like sixth pair of limbs, which were used for swimming. These were capable of being protracted and retracted and were probably used in a breast-stroke-like manner. Note that there are no antennae - Chelicerates do not have antennae. A small U-shaped plate (the *endostoma*) borders the mouth; and is normally covered by a much larger plate, the *metastoma*, which is actually part of the abdomen

The long rear part is the *opisthosoma*, which can be further divided into a broad flattened *pre-abdomen* consisting of seven segments, and a narrower and more cylindrical *post-abdomen* of only five segments. Alternatively it can be divided into the first six (the *mesosoma* - "middle body") and the last six (*metasoma*). All Eurypterid species have a total of twelve flexible opisthomal segments, or *tergites* as they are called. At the end of the last segment is a stout blade-like spine, the *telson*.

The prosoma is actually made up of the first six exoskeleton segments, which have been fused together. The seventh segment has become the metastoma; and the eighth is the genital aperture. Xiphosurans have this same genital aperture but do not have a metasoma. This plate-like eighth segment is also termed the *operculum*. In its center is the *genital appendage*, an elongated and sculptured rod of which there are two kinds always found in a single eurypterid population. Traces of internal ducts have been found in both kinds.

Each of the abdominal segments is composed of a dorsal (upper or back) tergite and a ventral (lower or belly) sternite. The operculum and the following four appendages of the pre-abdomen covered chambers in which the five pairs of gills were located. These were covered by protective plates. The first pair of gills/plates also contain the reproductive organs. In some forms the gills were able to remain moist and so allow the animal to move about on land for short periods

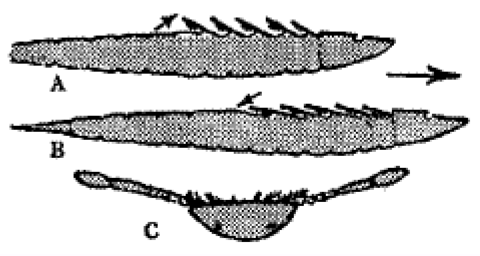
Eurypterid cuticle was chitinous and of varying thickness, but generally very thin, and preserved specimens (which were probably mostly molted skins) are usually crushed. It may bear different kinds of sculpture, such as terrace lines and scale-like ornament. Ultramicrographic work has revealed inner laminations resembling those of *Limulus* the modern horseshoe crab.

Not much is known about the internal organs of eurypterids. There are a few fossils in which part of the intestine is preserved, and this ends in an opening between the final tergite and the telson. It is not unlikely that the internal structure of Eurypterids would have been midway between that of their two closest living relatives - the horseshoe crab and the scorpions. Recently more has been known thanks to exceptionally preserved material from the Late Ordovician of South Africa, displaying internal tissues such as the musculature associated with the appendages and telson. Also, material from the earliest Carboniferous (early Tournasian) of France reveals a possible endosternite, gut trace and lamellate gills.

Locomotion

Swimming

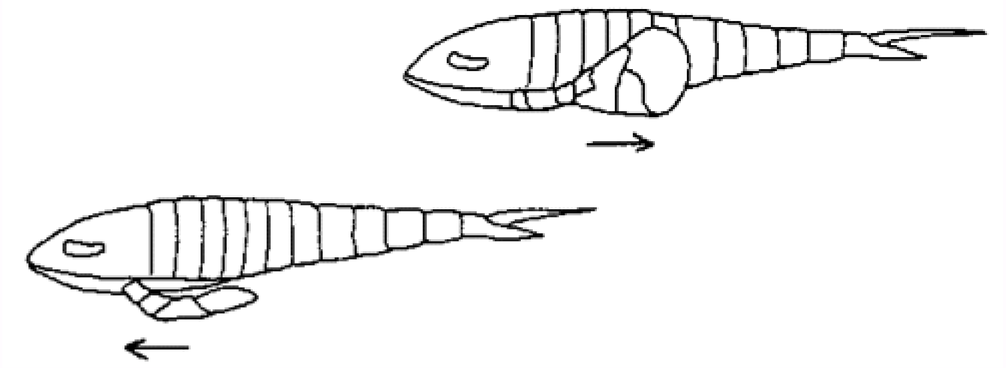
It was originally suggested, e.g. by Størmer, an important authority on the Merostomata, that Eurypterids flipped over and swum on their backs, using their gill plates like huge fairy shrimps.



Upside-down swimming, possibly used by tiny young Eurypterids, but not by adults
(from Moore, Lalicker and Fischer, *Invertebrate Fossils*)

This explanation (see figure above) is unlikely in view of the upward-facing eyes, and recent studies have shown that swimming involved using the large last set of limbs as a paddle or oar.

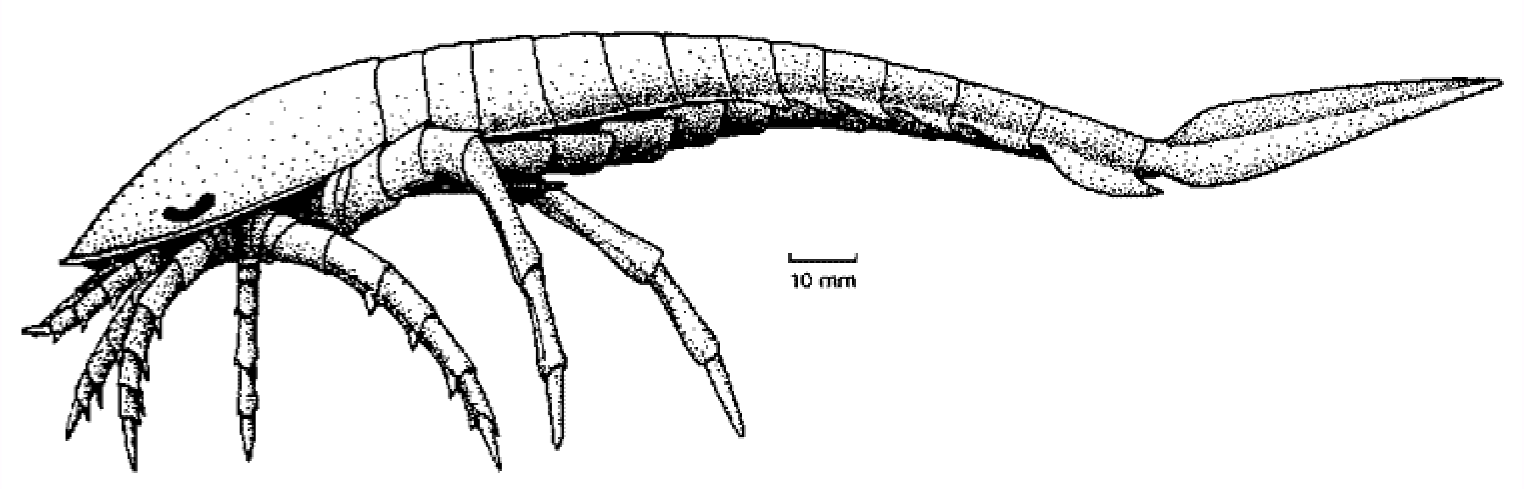
However, it is still possible that young individuals may have practiced upside-down swimming, as young xiphosurans do today.



Baltoeurypterus swimming
from Clarkson's *Invertebrate Paleontology and Evolution*, 3rd ed.

Walking

Although many Eurypterids had legs too tiny to do more than allow them to crawl over the sea bottom, a number of forms had large stout legs, and were clearly capable of terrestrial locomotion (like land crabs today). While functional studies that eurypterids used out-of-phase walking techniques, their trackways indicate that they used in-phase, hexapodous (six-legged) and octopodous (eight-legged) gaits.



Parastylonurus walking
from Clarkson's *Invertebrate Paleontology and Evolution*, 3rd ed.

Sexual Dimorphism and Reproduction

Understanding sexual dimorphism among extinct organisms is one of the many problems that bedevil paleontologists in their attempt to reconstruct organisms known only from bones, shells, or carapaces. In some cases the two sexes of an organism have been interpreted as two distinct species living side by side; in other instances there is not enough difference to even distinguish different sexes. And even when they can be differentiated, there is the problem of figuring out which is the male and which the female.

The eurypterids present a particularly difficult example of this. As mentioned, there are always two kinds of genital appendages found in any Eurypterid population. The original hypothesis has the type A, which is equipped with "clasping organs" on the prosomal appendages, as the male copulatory organ, while the other kind (type B) can be interpreted as the female ovipositor for depositing eggs, and fitting neatly over the male clasper. However, Simon Braddy suggests that eurypterid reproduction occurred via spermatophore (sperm package) transfer on the substrate (in at least *Baltoeurypterus*); the type A appendage is in this case the female who is able to retrieve a spermatophore for storage in her spermathecae ('horn organs'). The 'scimitar lobes' (male) are considered to have been clasping structures.

In any case the variations of form among different taxa are very useful in classification. To avoid the possibility of error, I have simply referred these to "type A" and "type B", leaving open which type belongs to which gender.

Ecology and Lifestyle

Eurypterids inhabited marine, brackish, and freshwater environments. Most were active benthos, although some were nektonic, being able to actively swim. Some may have been able to spend short intervals of time on land. Most eurypterids were probably predatory on other eurypterids or fishes. Eurypterid associations can often be distinguished and related to environmental conditions, such as marine, lagoonal or estuarine, or brackish to freshwater faunas.

Dr Simon Braddy rejects Kjellesvig-Waering�s 'ecological phases' model in favour of a model whereby individual taxa have a palaeoecological range influenced by an�ontogenetic gradient�. A �mass-moult-mate� hypothesis, comparable to the behavior adopted by some extant semi-terrestrial crustaceans, thus explains the occurrence of abundant eurypterid assemblages (e.g. the Bertie Waterlime), previously regarded as mass death assemblages.

Phylogeny and Diversity

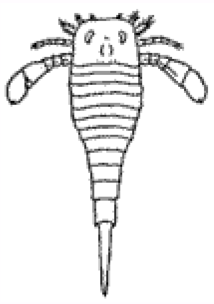
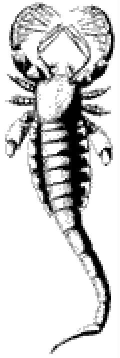
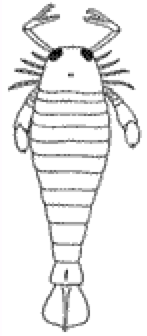
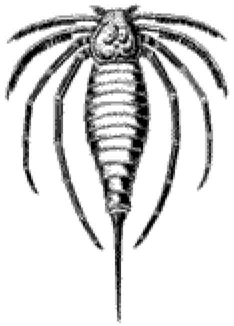
The first certain eurypterids appeared during the Middle Ordovician, although a possible earlier ancestral form (*Kodymirus*, although this may be an aglaspid) dates back to the Early or Middle Cambrian. They seem to have diversified quite quickly, and by the end of the Ordovician almost all the main lineages had appeared. Although the morphology of some genera is well known others are represented only by very poorly preserved material, and there are acute taxonomic problems in classifying such isolated remains. Differences involve adaptive differences in size, prosomal shape, the location of the eyes, and the morphology of the body, the appendages and the telson. The best know classification is the Linnean arrangement given in the *Treatise on Invertebrate Paleontology*, which is now sadly out of date. Dr Simon J. Braddy uses a cladistic analysis of the more completely known eurypterid genera (48 taxa, 19 characters) to give the following model of eurypterid phylogeny:

```
Stylonurina
Eurypteroidea
        Adelophthalmidae
                Hughmilleriidae
                        Mixopterina
                                Carcinosomatidae
                                        Mixopteroidea
                                        Megalograptoidea
                        Pterygotina
                                Slimoniidae
                                Pterygotidae
```

The classification given on the following pages is based on a synthesis of *Treatise on Invertebrate Paleontology*, *The Fossil Record I* (I don't have the revised edition unfortunately), Clarkson's *Invertebrate Paleontology and Evolution*, and the above cladogram of Dr Simon J. Braddy, updated with a few other recent web sources which appear to have some reliability. Combining as it does a number of sources, and as I am unable to acquire more detailed up to date information at the moment, this classification should be taken as being very provisional only. Click on each image and group for more details.

Subclass and Order Eurypterida

Suborder Eurypterina (Ordovician to Permian)			Suborder Stylonurina (Ordovician to Permian)

			
Eurypteracea	Mixopteracea	Pterygotacea	Stylonuracea (*see* Stylonuridae)

Descriptions

Eurypterida Burmeister 1943

Synonyms Gigantostraca Haeckel 1866

Range: Ordovician to Permian, Cosmopolitan

Phylogeny: Chelicerata **:** Xiphosura + (Arachnida + * **:** Stylonuracea + (Eurypteracea + (Mixopteracea + -Pterygotina)

Links: Eurypterida - UCMP; The possible lifestyle of a Late Ordovician eurypterid - by Jeffrey Minicucci - very interesting essay on the mode of life of *Onychopterella augusti*; Faktablad om sjøskorpioner - material on Eurypterids - in Norwegian - includes a photo of a lovely *Mixopterus* specimen; Eurypterida - Dendrogram and genus list, by Mikko K. Haaramo; Dr Simon J. Braddy - research on Eurypterids, and on Paleozoic arthropod trackways as documenting the diversity and palaeoenvironmental distribution of the early terrestrial arthropods.; bulletin board Re: Eurypterid Chat; Where? - some notes on the late Silurian Williamsville formation of Buffalo, New York, and the Eurypterid fauna

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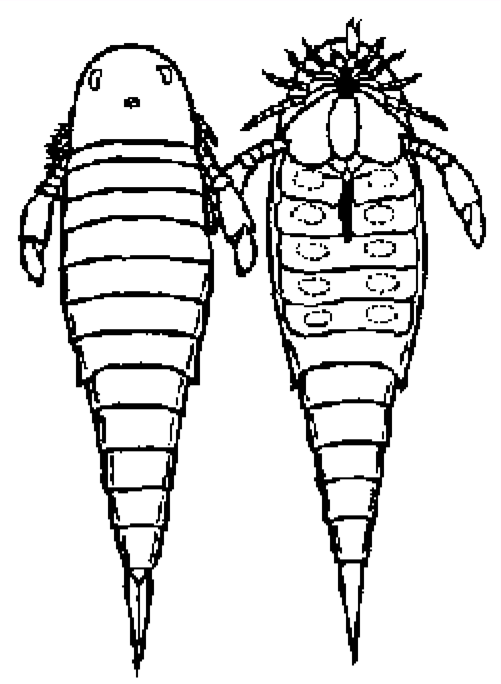
Superfamily Eurypteracea

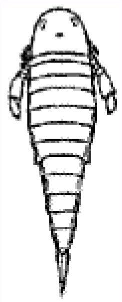
Ordovician to Permian

This superfamily includes the "typical" (unmodified) Eurypterids, in which the last prosomal appendages developed as swimming legs that carry paddles formed by expansion of the two penultimate joints. They can be considered the ancestral lineage from which the other groups evolved.

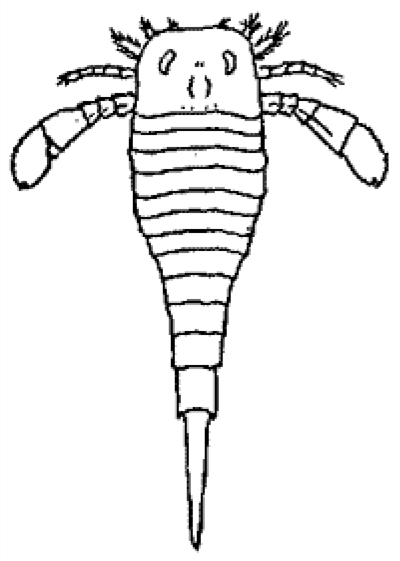


Hughmilleria norvegia (Kiaer)
length about 10 cm
Pridoli or earliest Lokhovian, Norway
illustration from *Treatise on Invertebrate Paleontology*

family Hughmilleriidae

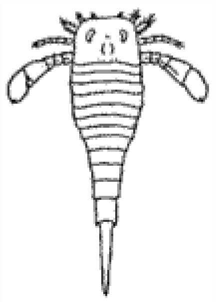


Family Hughmilleriidae Kjellesvig Waering, 1951
time range: ?Floian to Frasnian
known distribution: Euramerica
habitat: Marine to Marginal Marine
representative taxa: *Hughmilleria norvegia*, *Hughmilleria bellistriata* (Silurian)
description: *Hughmilleria* is small form which does not differ from the standard Eurypterid body-plan. The prosoma is rounded, with marginal compound eyes. The chelicarae are medium-sized, with small pincers for grasping food, they are like miniature versions of the large claws of *Pterygotus*. The body is also similar to *Pterygotus*, although the fairly short resembles that of *Eurypterus*. The metastoma ovate; genital appendage is short and broad in the type "B" form, long and narrow in male.

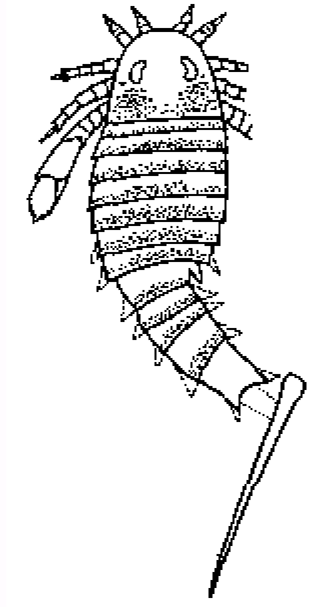


Eurypterus remipes Dekay
length about 20 cm
Ludlow of Western Euramerica (New York)
illustration from Moore, Lalicker and Fischer, *Invertebrate Fossils*

family Eurypteridae



time range: Darriwilian to Frasnian
known distribution: Euramerica , Asia
habitat: Marginal marine and fresh water
representative taxa: *Baltoeurypterus tetragonophthalmus* (= *Eurypterus fischeri*), *Eurypterus lacustris*, *Eurypterus remipes*
notes: typical Eurypterids. The body is fairly elongate; the largest species attaining a length of about a meter but most much smaller (average about 20 cm). The prosoma is squared off, the compound eyes kidney-shaped and placed towards the middle of the head, so they look upwards. Between them are two ocelli or simple eyes.



Lepidoderma mansfieldi
Late Carboniferous - length about 12 cm
illustration from *Treatise on Invertebrate Paleontology*

family Adelophthalmidae

time range: Llandovery to Artinskian
known distribution: Euramerica , Asia
habitat: Marginal marine, brackish and fresh water; amphibious

representative taxa: *Lepidoderma mansfieldi*, *Lepidoderma mazonense* (both late Carboniferous), *Adelophthalmus sellardsi* (early Permian),
notes: Mostly small forms, similar to *Eurypterus* but spiny, the outer surfaces with pointed scales and striae; the elongate body equipped with spurs. The postabdomen is narrow and the telson very long (styliform). The compound eyes are located somewhat towards the center of the head. The walking legs are mostly devoid of spines. In *Adelophthalmus* the genital appendage of the male is long, of the type "B" form short, with spatulate lateral lobes. These creatures seem to have been semi-aquatic swamp dwellers. They were among the last of the Eurypterids.

Links: **Eurypterus remipes Fauna** - Fiddler's Green Formation - Late Silurian - one of the most common eurypterid species is Eurypterus lacustris

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graphics from *Treatise on Invertebrate Paleontology* vol P. - Chelicerata - Merostomata

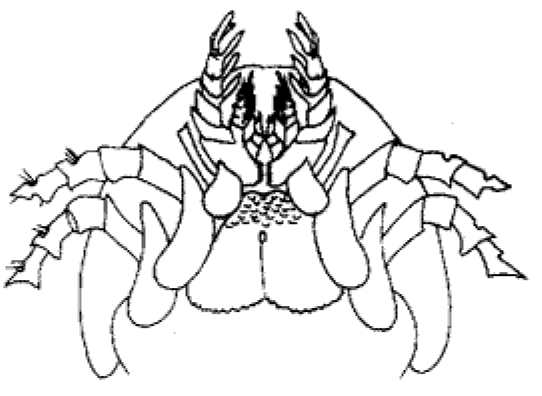
Suborder Hibbertopterina

Late Devonian to Permian

Hibbertopterus scouler

Hibbertopterus scouleri
width 25 cm
early Carboniferous
image from *Treatise on Invertebrate Paleontology* P38

The Hibbertopterina were mostly large animals, many of which may have ventured onto land, flourishing in the moist Permo-Carboniferous coal swamps. The outer surface of the skin is armed with spiny scales. The prosoma is subsemicircular, strongly convex; the compound eyes almost in the middle of the head ("subcentral"), with inflated angular lobes between them. The abdominal tergites are convex. The posterior (last) prosomal legs have a basal extension, which is a distinguishing mark of the group.



Campylocephalus (Carboniferous) ventral (belly) view of prosoma showing large metastoma and basal extensions on posterior legs typical of Hibbertopteridae (redrawn from Waterston, 1957, *Trans. Roy. Soc. Edin.* 63, 265-88) - image and text from Clarkson's *Invertebrate Paleontology and Evolution*.

family Hibbertopteridae

Family Mixopteridae Caster & Kjellesvig Waering, 1955

time range: ?Frasnian / Famennian (Devonian) to Ufimian / ? Kazanian (Permian)
known distribution: Euramerica
habitat: Marginal marine, brackish, and fresh water - amphibious
Representative genera: *Hibbertopterus*, *Campylocephalus*.

"...it was Hibbert (1836) who discovered the first eurypterid in the quarry,*Hibbertopterus scouleri* (above). Under more recent scrutiny there have been three genera of generally poorly preserved eurypterid found in the East Kirkton Limestone [early Carboniferous - Visean epoch - Scotland). Jeram and Selden (1994) suggest that these appear to have been washed into the depositional area, due to the lack of juveniles in the assemblage. They believe that the eurypterids found here are semi aquatic. They cite the rarity of complete specimens and abundance of cuticle fragments in horizons rich in pulverized plant debris as evidence for the eurypterids living immediately around the lake and not permanently within it. Jeram and Selden propose that the eurypterids preyed on small invertebrates (one genera using paddle-like filters to extract them from the sediment) and possibly brine shrimps which would have inhabited pools around the lake." reference

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Superfamily Mixopteracea

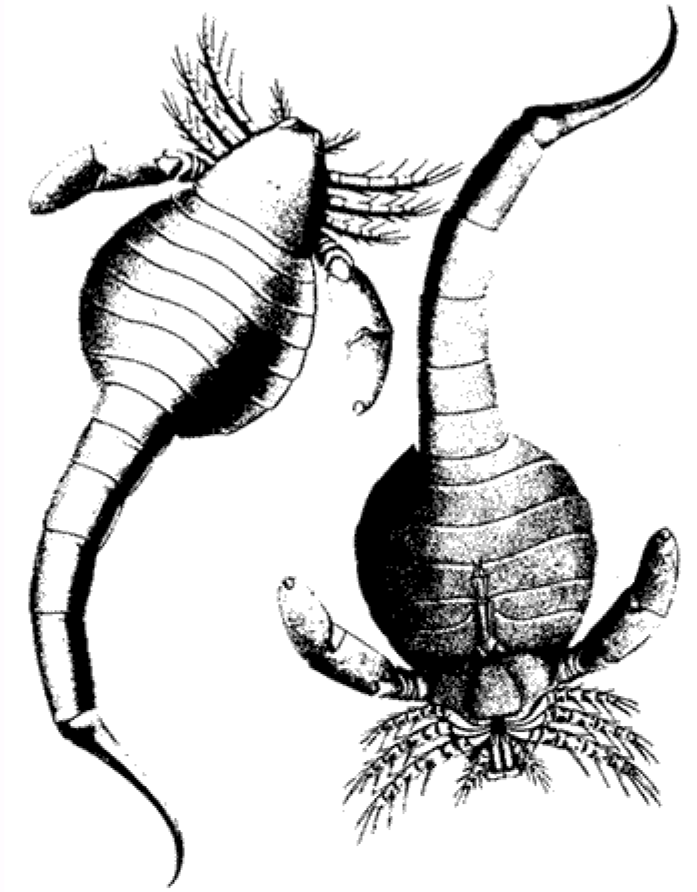
Ordovician to Carboniferous

walking posture

Mixopterus kiaeri - walking posture

Introduction
Carcinosomatidae
Mycteropidae
Megalograptidae
Mixopteridae
Links

The most scorpion-like of the Eurypterids (and possibly ancestral to the scorpions), this is a diverse group of often spiny Eurypterids. Many of these animals were clearly amphibious, as is indicated by a trail in the Silurian of Ringerike, Norway, believed to have been made by a large *Mixopterus*.

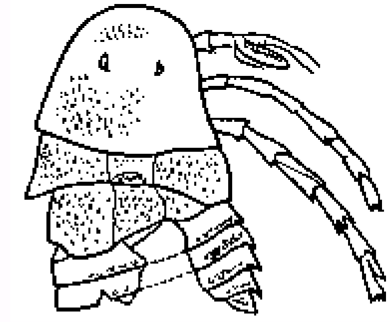


Carcinosoma scorpionis (Grote and Pitt)
length to half a meter
Late Silurian (Ludlow) of New York (west-central Euramerica)
illustration from *Treatise on Invertebrate Paleontology*

Carcinosoma (*above*) has a large discoidal pre-abdomen with a marked waist and a cylindrical post-abdomen and, like the fearsome-looking Mixopterus, it has a telson, like that of a scorpion, apparently modified as a poison spine.

family Carcinosomatidae

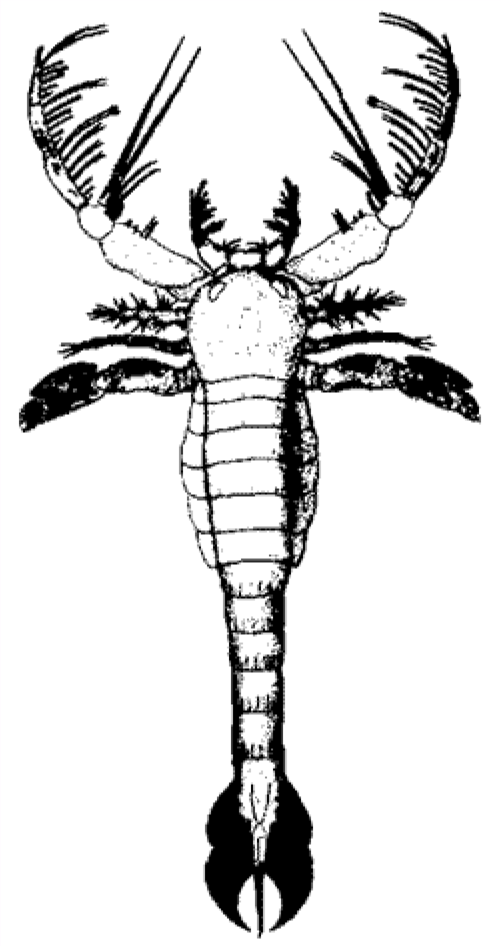
Family Carcinosomatidae Størmer 1934
time range: Floian to Emsian - ? Frasnian
known distribution: Euramerica
habitat: Marginal marine
representative taxa: *Carcinosoma scorpionis* average length about 30 cm; the larger *Carcinosoma grandis* was 60 to 90 cm lo Both from the late Silurian Waterlime of North Buffalo, New York. *Eocarcinosoma ruedemanni* from the Middle Ordovician of New York state is the earliest species.
description: Small to large forms with scattered minute tubercles or raised tongue-shaped scales. The prosoma is subtriangular in shape, with small compound eyes small and located toward the side of the head. The fore part of the abdomen is widened to form a distinct mesosoma, while the postabdomen is narrow and cylindrical with a curved telson, giving the whole body a rather scorpion-like appearance. The chelicerae are small, the walking legs have long spines, with the second pair of legs the longest. The metastoma is subtriangular; genital appendage probably short and broad in type "B" form, long with distal spines in type "A" form. *Carcinosoma* was originally known as *Eusarcus*.



Mycterops? scabrosus
width about 70 cm
Early Carboniferous, Scotland (central Euramerica)
illustration from *Treatise on Invertebrate Paleontology*

family Mycteropidae

Family Mycteropidae Størmer, 1951
time range: Serpukhovian to Moscovian
known distribution: Euramerica
habitat: Fresh water - amphibious
description: Medium to fairly large forms; outer surface decorated with numerous scales and reticulate (cross-hatched) ornamentation; the prosoma subtrapezoid, with the fist and possibly the second tergite of abdomen strongly developed and deep. The legs are of the stylonurid type.



Megalograptus ohioensis
body length about a meter
Hirnantian epoch of Ohio (Laurentia)
illustration from *Treatise on Invertebrate Paleontology*

family Megalograptidae

Family Megalograptidae Caster & Kjellesvig-Waeritag, 1955

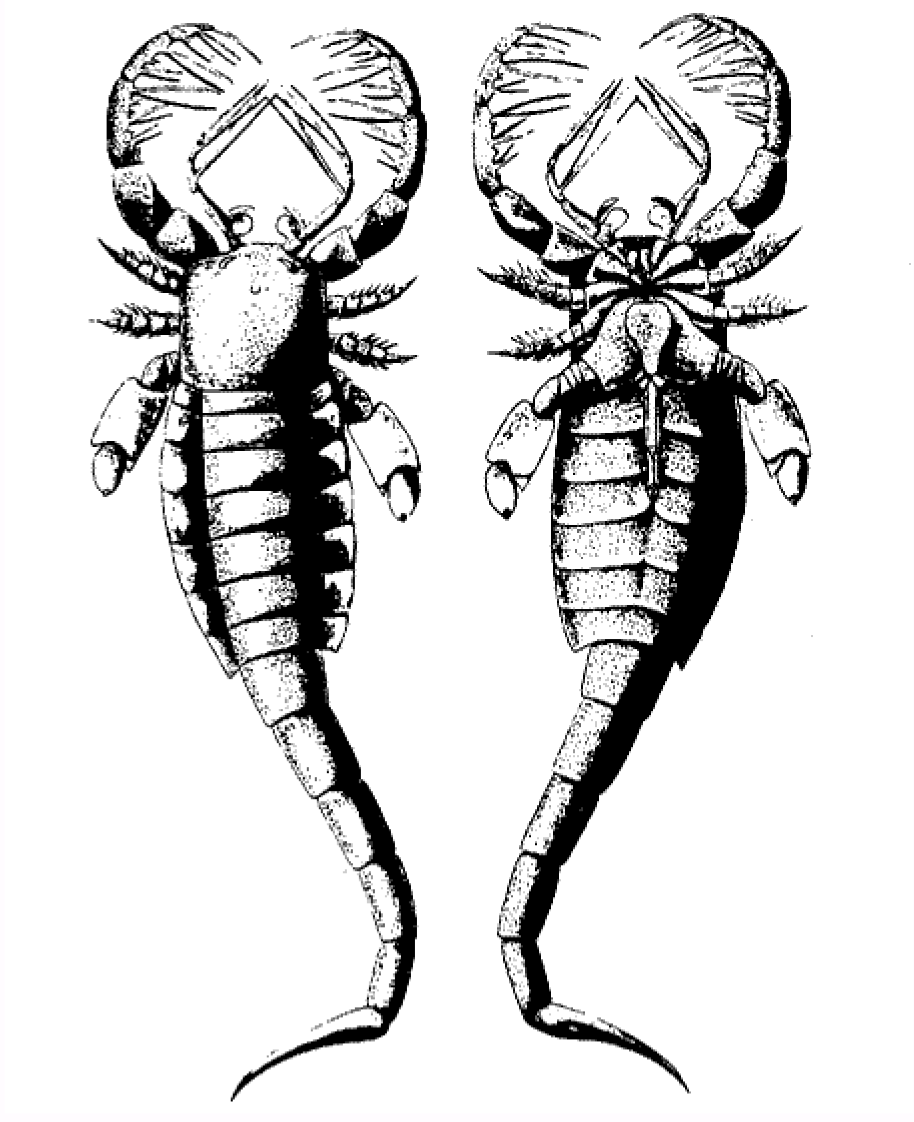
time range: ?Sandbian to Hirnantian

known distribution: Laurentia

habitat: Marine to marginal marine

representative taxa: *Echinognathus* is a large form with appendages armed with curved spines, ?Sandbian of New York; *Megalograptus* from the Richmond series (Latest Ordovician - Hirnantian) of Ohio is another genus. As the name indicates, its fragmentary remains seem to have been originally described as from a graptolite!

description: huge spectacular spiny predatory Ordovician forms, clearly active hunters, seem to have taken over from the waning Endocerid nautiloids as the superpredators of the late Ordovician oceans. Nevertheless they were a short-lived group, geographically restricted, and seem to have been wiped out by the terminal Ordovician mass extinction, although not before giving rise to the Mixopteridae. The compound eyes face forward, and there tongue-like extension at the front of the prosoma bearing large marginal spines. The chelicerae small and short, 1st and 3rd walking legs relatively short, with closely set spines, second pair of legs enormously developed, with long paired spines for snaring prey. The preabdomen narrow with axial furrows; the postabdomen moderately narrow; telson narrow lanceolate, with what seem to be side claspers. The epistoma short and broad; metastoma subovate to cordate; genital appendage of type "B" form club-shaped, of type "A" form short and narrow.



Mixopterus kiaeri Størmer
dorsal and ventral view
body length about 75 cm
Pridoli or early Lokhovian of Norway (north-east Euramerica
illustration from *Treatise on Invertebrate Paleontology*

family Mixopteridae

Family Mixopteridae Caster & Kjellesvig Waering, 1955
time range: Wenlock to Pridoli
known distribution: Euramerica
habitat: Marginal marine to ?brackish - amphibious
description: Large scorpion-like forms, exoskeleton with scattered tubercles or semicircular scales, prosoma squarish (subquadrate) preabdomen fairly narrow, with axial furrows; postabdomen narrow, with a curved telson, possibly bearing a poison sting. First two pairs of legs strongly developed, with paired spines. These were held out in front of the animal to catch prey. Third and fourth pairs of moderate in size, with short spines, used for walking. Metastoma narrow cordate; genital appendage of type "A" form long. It has been suggested that these animals were ancestral to Scorpions, although the two groups probably diverged fairly early.

Links

Faktablad om sjøskorpioner - this site is in Norwegian, it includes a photo of a superb *Mixopterus* specimen

Eurypterida - nice reconstruction of a *Mixopteris* here

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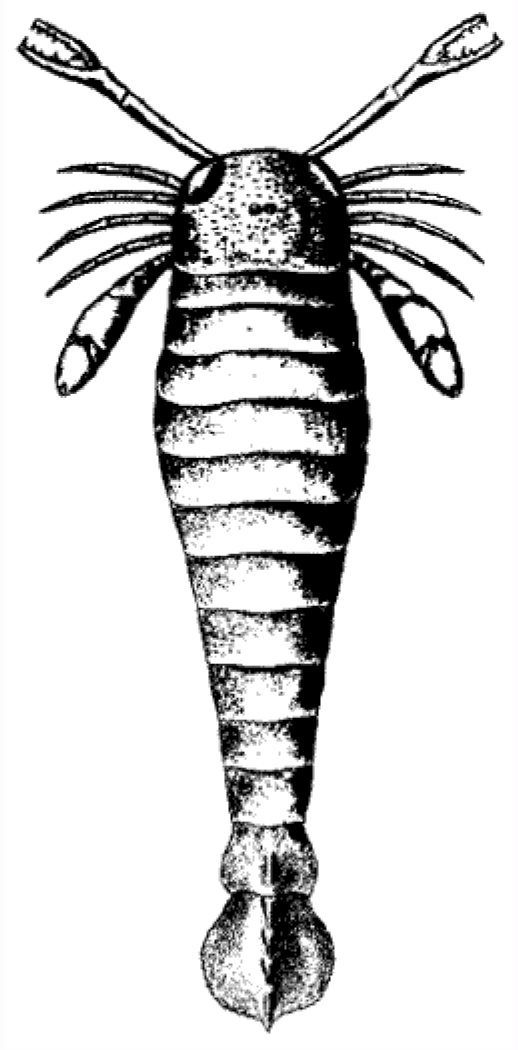
Suborder Pterygotina

Ordovician to Devonian



Pterygotus (Acutiramus) buffaloenisis Pohlman
late Silurian (Ludlow)
New York
length about 2 meters
illustration from Fenton and Fenton *The Fossil Book*

Introduction
Slimoniidae
Pterygotidae
Jaekelopteridae
Links

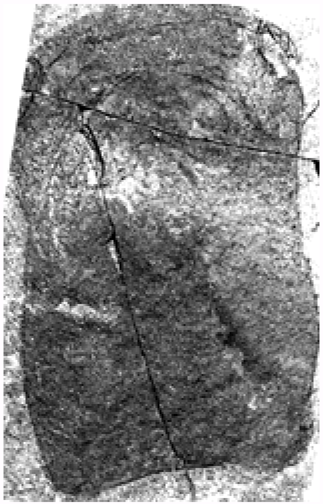
The Pterygotina

The Pterygotids are among the most spectacular of the eurypterids, in the more advanced forms equipped with large chelicerae or "pincers". In most eurypterids, the chelicerae are rather small; only in the Pterygotina do they grow into large pincer-type grasping organs as those shown here. But despite their resemblance, these chelicerae are not *homologous* to the pincers of scorpions (i.e. they are not formed from the same pair of limbs). Scorpion pincers are the second pair of appendages, whereas pterygotid pincers are the first. These animals were active hunting by site predators, as indicated by the large bulbous eyes, located at the side (rather than the middle) of the head, giving superior peripheral vision.

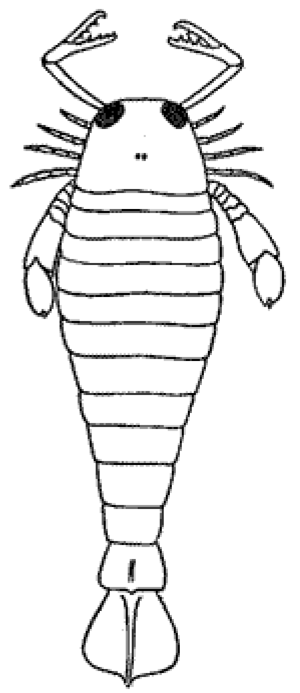
As with most Eurypterid lineages, the Pterygotina reached their acme in the late Silurian and early Devonian, at the time the great deltas of Euramerica and elsewhere were creating a rich near-shore detritus-based food-chain that enabled the armoured ostracoderms and many other prey-animals to flourish.

Slimonia acuminata Salter 1856
length about a meter
Early to Middle Silurian (Llandovery to early Wenlock), Scotland (central Euramerica)
illustration from SENCKENBERG Exponat April 1996

family Slimoniidae



time range: Llandovery to Pridoli
known distribution: Euramerica
habitat: Marginal Marine? Brackish and Fresh water
size: 60 cm to a meter or more in length
description: Large forms with smooth outer surface, quadratic prosoma with small compound eyes at the side of the head; postabdomen narrow, front half of *Pterygotus*-like telson strongly expanded and flattened; walking legs with denticles but lacking spines; The metastoma is narrowly cordate (heart-shaped) in outline; the genital appendage is long and narrow in both sexes.
notes: Previously included under the family Hughmilleriidae, these primitive Pterygotines lack the distinguishing cheliceratic pincers but in other respects were similar to the typical Pterygotines. The eyes, although smaller than those of Pterygotus, are large in comparison to other Eurypterids, indicating an active predator that hunted by sight. Unlike the more advanced representatives of the group, the Slimoniids inhabited brackish and fresh water



Pterygotus (Pterygotus) rhenaniae Jaekel
early Devonian
Germany
length up to 1.8 meters
illustration from Moore, Lalicker and Fischer, *Invertebrate Fossils*

family Pterygotidae

terygotidae

Family Pterygotidae Clarke & Ruedemann, 1912
time range: - Floian to Famennian
known distribution: Euramerica
habitat: Marginal Marine? Brackish and Fresh water
size: Although some species were small, many grew to great size. The largest known complete specimen is "only" one and a quarter meters in length, but isolated segments and body parts indicate these animals typically reached 1.5 to 1.8 meters, with large forms exceeding 2 meters in length. Rivaled only by the enormous (but harmless) millipede-like arthropleurids of the Carboniferous, this was the largest size ever attained by an arthropod.
representative taxa: *Pterygotus (Acutiramus) buffaloenisis* Pohlman, *Pterygotus (Pterygotus) rhenaniae* Jaekel, *Pterygotus (Pterygotus) anglicus* Agassiz, description: Small to very large forms - distinguished by very large and long chelicerae in the form of "pincers" provided with strong teeth. The exoskeleton ornamented with distinct semilunate scales; and the broad flattened telson, which may have served a stabilizing function when the animal swam. The epistoma is present; the walking legs are generally small, slender, and lacking spines. The metastoma is suboval to heart-shaped in outline; the genital appendage is short and pear shaped in the type "B" form, and somewhat short, narrow and blunt in the type "A" form.
Pterygotids were also unusual among eurypterids in that, although preferring marginal marine (deltaic) environments, also inhabited typically marine environments, where they clearly served the role of top predator in the benthic food-chain. These animals were clearly to large, and their walking legs too small, to have ventured onto land. They did not even move into fresh-water ecosystems.

family Jaekelopteridae

time range: Pragian to Emsian
habitat: Marine
representative taxa: *Jaekelopterus*
description: resemble the Pterygotids in the possession of large "pincer"-like chelicerae.

Links: **Systematics of the Eurypterida**

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graphics from *Treatise on Invertebrate Paleontology* vol. P. - Chelicerata - Merostomata; and Fenton and Fenton *The Fossil Book* (1958, Doubleday & Co., Garden City, New York); and Moore, Lalicker and Fischer, *Invertebrate Fossils*, 1952, McGraw-Hill Book Company, Inc., New York, Toronto, London)

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Eurypterida Dendrogram

```
<==o �EURYPTERIDA (sea scorpions)
   | ?- �Glyptoscorpius
   |--o �EURYPTERACEA
   |  |--o �Eurypteridae
   |  |  |-- �Eurypterus
   |  |  |-- �Onychopterella
   |  |  `-- �Tylopterella
   |  `--+-- �Adelophthalmidae
   |     |--o �MIXOPTERACEA
   |     |  |--o �Carcinosomatidae
   |     |  |  `-- �Carcinosoma
   |     |  `--+--o �Mixopteridae
   |     |     |  `-- �Mixopterus
   |     |     `--o �Megalograptidae
   |     |        |-- �Megalograptus
   |     |        `-- �Echinognathus
   |     `--o �PTERYGOTINA
   |        |--�Hughmilleriidae
   |        |  |?- �Hastimima
   |        |  |-- �Hughmilleria
   |        |  |-- �Salteropterus
   |        |  |-- �Grossopterus
   |        |  `-- �Lepidoderma
   |        `--+--o �Slimoniidae
   |           |  `-- �Slimonia
   |           `--o �Pterygotidae
   |              `-- �Pterygotus
   `--o �STYLONAURACEA
      |--o �Mycteropidae
      |  `-- �Mycterops
      `--+--o �Rhenopteridae
         |  `-- �Rhenopterus
         `--+--o �Dolichopteridae
            |  |-- �Dolichopterus
            |  `-- �Strobilopterus    |
            `--o �Stylonuridae (paraphyletic?)
               |-- �Stylonurus
               |-- �Drepanopterus
               |-- �Brachyopterus
               |-- �Ctenopterus
               |-- �Tarsopterella
               |-- �Melbournopterus
               `--o �Hibbertopteridae
                  |-- �Campylocephalus
                  `-- �Hibbertopterus
```

This phylogeny was revised to revised to reflect newer, but still unpublished sources -- mostly student papers and abstracts. We have also made a wild guess about the position of the Hibbertopteridae. ATW060226.

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Crustacea

```
PROTOSTOMIA
|--ARTHROPODA
|  |--Trilobita
|  `--PANCRUSTACEA
|     |--CRUSTACEA
|     |  |--Pentastomida?
|     |  `--+--Remipedia
|     |     `--+--Cephalocarida
|     |        `--+--Malacostraca
|     |           `--+--Maxillopoda
|     |              `--Branchiopoda
|     `--INSECTA
`--LOPHOTROCHOZOA
   |--MOLLUSCA
   `--ANNELIDA
```

Contents

The California spiny lobster *Panulirus interruptus*
Photo by Ed Bierman, via Flikr, Creative Commons Attribution

With around 35,000 known species (and many more doubtless not yet discovered) the Crustacea are a diverse group. They are so incredibly abundant in marine and freshwater habitats are they that they have been called the insects of the water. A majority of zooplankton are Crustacea - either larvae or tiny adults. A few Crustacea (slaters or sow bugs) even live on land, usually under old logs and leaf litter. The majority of crustaceans are marine and are herbivores, although there are also many species which are carnivores, scavengers, or filter-feeders

The Crustacea are a very ancient group. They first evolved in the earliest Cambrian period, as part of the great evolutionary radiation of that time. By the Jurassic Crustaceans looked pretty much like they do today. Shrimps and lobsters from the famous Solnhofen limestone are hardly distinguishable from modern forms

Crustacea are characterized by two pairs of antennae, three pairs of mouthparts, and a special type of larvae called the *nauplius* (see photo at right) Most crustaceans have jointed appendages which serve as either walking or swimming legs, and some of which have been modified in some way to serve a special function, such as the claws of lobsters and crabs. The number of body segments varies widely among the different groups. They generally also have a carapace and compound eyes .

Crustacean Diversity

The following is a list of classes of this diverse group

Remipedia
Cephalocarida
Branchiopoda
Ostracoda
Mystacocarida
Copepoda
Branchiura
Cirripedia (Barnacles)
Tantulocarida
Malacostraca

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Crustacea - 1

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PROTOSTOMIA
|--ARTHROPODA
|  |--Trilobita
|  `--PANCRUSTACEA
|     |--CRUSTACEA
|     |  |--Pentastomida?
|     |  `--+--Remipedia
|     |     `--+--Cephalocarida
|     |        `--+--Malacostraca
|     |           `--+--Maxillopoda
|     |              `--Branchiopoda
|     `--INSECTA
`--LOPHOTROCHOZOA
   |--MOLLUSCA
   `--ANNELIDA
```

Contents

Introduction

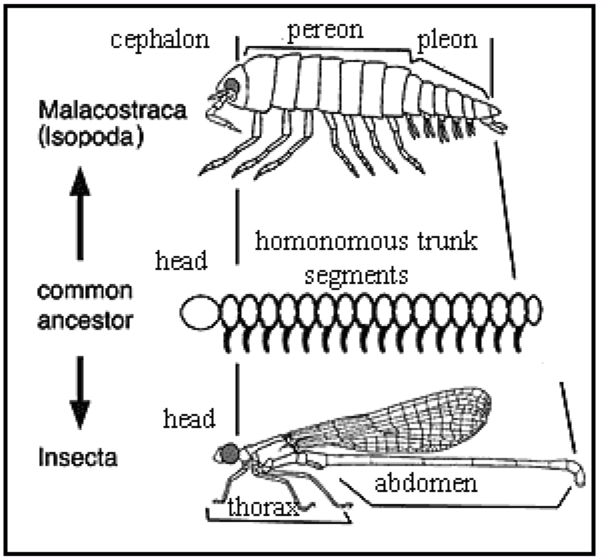
This page introduces the crown group Crustacea, sometimes defined as the last common ancestor of all living crustaceans and all of its descendants. This is, of course, a circular definition. We normally try to give a somewhat more explicit definition of a clade, but that's admittedly difficult for the Crustacea. Nothing remotely resembling a consensus phylogeny of the main crustacean groups has emerged from 250 years of *carcinology*. Martin & Davis (2001). In fact, we even lack agreement on what the "main crustacean groups" might be. For example, a respectable minority holds that Crustacea itself is *paraphyletic* and includes the insects. *See, e.g.*, Cook *et al*. (2005); Regier *et al*. (2005) and discussion below.

The Crustacea are both diverse and common. The usual estimate of 50,000+ known species is probably a gross underestimate. Martin & Davis (2001). Actual diversity is certainly many times that number. The standing crop of just one species, the Antarctic krill *Euphausia superba*, is said to approach 500 million tons. *Id*. Indeed, the majority of zooplankton are Crustacea - either larvae or tiny adults. Martin & Davis (2001) quote Geoffrey Fryer for the proposition that the characteristic crustacean *nauplius* larva is "the most abundant type of multicellular animal on earth."

The vast majority of crustaceans are marine. Crustaceans are typically benthic filter feeders who use various appendages to force water through setae attached to other limbs. Virtually all other modes of life may also be found in any reasonably large taxon of Crustacea. A few (slaters or sow bugs) even live on land, usually under old logs and leaf litter.

But to really appreciate the Crustacea, you have to see them from a *carcinologist's* point of view. To the carcinologist, crustaceans are not simply one of the four main arthropod lineages. The carcinologist recognizes that the arthropods hit the Middle Cambrian running and very quickly produced side branches leading to the chelicerates, myriapods, and various extinct groups. Somewhat later, the Hexapoda went off to handle some terrestrial arthropod niches. The Crustacea, however, are the main line and torch-bearer of arthropod evolution; and have carried that torch since the Cambrian "explosion" of metazoans.

There is something to be said for this point of view. It isn't the usual parochialism of monomaniacal specialists. Crustaceans have no single body plan, no ubiquitous limb specialization, and no consistent number of segments per major body division. Perhaps that isn't quite true. The crustacean head is fairly stereotyped. However, none of the recent papers we examined would even *propose* a list of *synapomorphies* for Crustacea. A good many characteristics are common among Crustaceans, but we are unsure if *any* are both universal and unique to the Crustacea. If you're interested, it should be possible to derive some synapomorphies from the data in Giribet *et al*. (2005). In any event, there is a very reasonable case to be made that the arthropods include (a) various small stem groups, mostly extinct, (b) two larger specialized groups, the chelicerates and myriapods, and (c) the insects, with their stem group (Hexapoda). Everything else is Crustacea.



This state of affairs is a recent improvement. Up until a few years ago, it was unclear which of the major arthropod taxa was the sister-group of the Crustacea; but essentially all of the studies published since the late 1990's favor the hexapod-crustacean clade called Pancrustacea or, sometimes, Tetraconata. In fact, as mentioned earlier, it is no longer completely clear that insects are separate from crustaceans. Most (but not quite all) molecular phylogenies in the last few years show Hexapoda as a group within Crustacea. See, for example, Lavrov *et al*. (2004); Cook *et al*. (2005); Regier *et al*. (2005). Then again, *some* molecular phylogeny can usually be found to support almost any phylogenetic hypothesis, no matter how demented.

Both molecules and (to a lesser extent) morphology, also suggest a particular connection between the most successful groups of aquatic Crustacea, the Malacostraca, and the most successful group of terrestrial hexapods, the Insecta. This putative insect/malacostracan relationship is probably a mirage caused by *Williston's Law* applied to similar patterns of *tagmosis*. We may get to that issue in more detail below. The important point is that, putting aside these peculiar notions (although we may well come to regret our skepticism), recent reports contain a goodly number synapomorphies which unite the hexapods and crustaceans, to the exclusion of everyone else.

The factor which has propelled this recent flurry of interest (and progress) in Crustacean phylogeny is the maturing business of "evo-devo." After writing that last sentence, we thought we'd better work up a short background piece on the evo-devo of *hox genes*, since they are important to what follows. That was almost six months ago. Hopefully, you are already a haruspice of hox, or at least have ready access to Carroll (2005). Otherwise, we will be forced to assign you this: remedial hox homework. **[2]**.

Branchiopoda: An Example

Crustacea: The Usual Suspects	
Branchiopoda	*Artemia*, *Daphnia*. Arguably the most

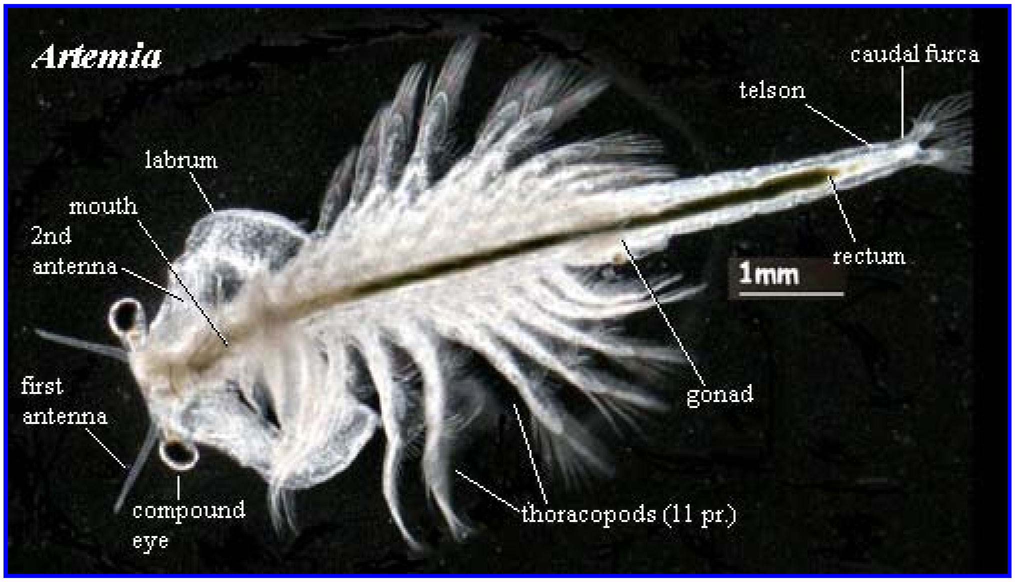
We commonly discuss diversity only after developing some vague notions concerning the sort of organism under discussion. But, Crustacea being a sort of catch-all, we need to offer an example first. If nothing else, this may help you appreciate the size and difficulty of the problem the

	basal group.
Cephalocarida	
Malacostraca	Crabs, real shrimp, lobster, etc.
Maxillopoda	
Ostracoda	
Remipedia	Blind cave-dwellers, only discovered in the 1970's

Crustacea represent. For a more rational taxon, we would start with the most basal of the major included groups. Unfortunately, there is no consensus about who the main groups of crustaceans might be, much less which one is basal. The usual suspects are noted in the table. Any one or more of them may be paraphyletic. Any one or more may be the earliest branching, except possibly Ostracoda. At least, we have never seen a paper in which the claim is made that ostracods are basal to other crustaceans.

Perhaps the most frequently mentioned candidate for basal Crustacea are the Branchiopoda. They have the advantage of possessing a rather good Furongian fossil record. In addition, the branchiopods include 800-900 species of extant fairy shrimp, sea monkeys, tadpole shrimp, water fleas, and clam shrimp. Where do people come up with these asinine names? None of the branchiopods are actually shrimp, of course. Nor do they bear the slightest resemblance to fairies, monkeys, tadpoles, fleas, clams, etc.

One of these extant genera is the "brine shrimp" or "sea monkey," *Artemia*, which, naturally, is not a shrimp, much less a monkey, and does not live in the sea. *Artemia* is probably so named because it has no conceivable connection with the goddess Artemis, either. Despite a conspicuous lack of theomorphism, *Artemia* is scientifically important. Considerable biological and genetic work has been done with *Artemia* on the theory that it is a very primitive crustacean. Whether or not *Artemia* is actually primitive for Crustacea, there seems to be general agreement that the Anostraca in general, and *Artemia* in particular, are plesiomorphic within Branchiopoda.



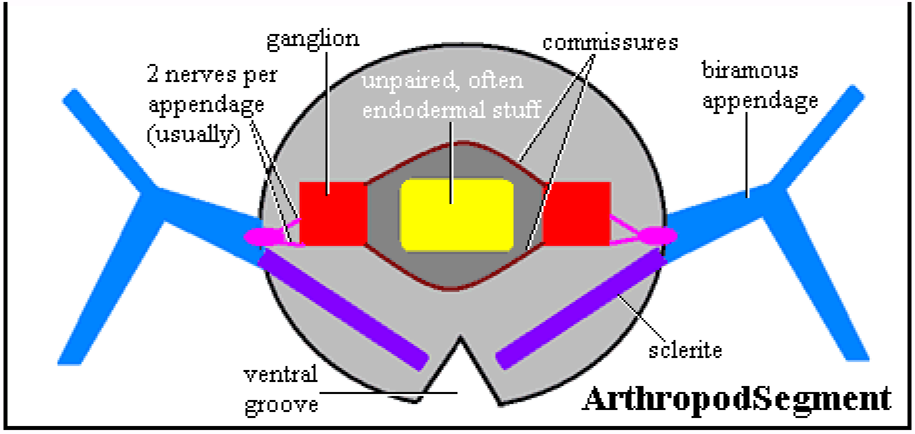
Branchiopods tend to be no larger than 2 cm in length, with the exception of a few "giant" Cladocera, which can reach 10 cm or more. Most branchiopods live in fresh or brackish water. Many, like *Artemia*, are specialists, adapted to life in temporary pools. They often have the expected suite of adaptations for that lifestyle, *e.g*. a broad tolerance for changes in salinity (are *euryhaline*), rapid development, facultative *parthenogenesis*, and a spore-like resting stage in which the fertilized egg can survive for years, if necessary, until conditions are favorable for development **[4]**.

We will refer frequently to *Artemia* -- not because it is necessarily either typical or primitive, but because so many people have thought it so. Consequently, it is much studied and relatively well-known. *Artemia* is not a "typical" crustacean, if there is such a thing. We will use the Branchiopoda, and particularly *Artemia*, simply as a point of reference, so that we don't waste too much time having to re-orient ourselves to the numerous different geometries which the Crustacea have adopted.

Anatomical System

The Arthropod Segment

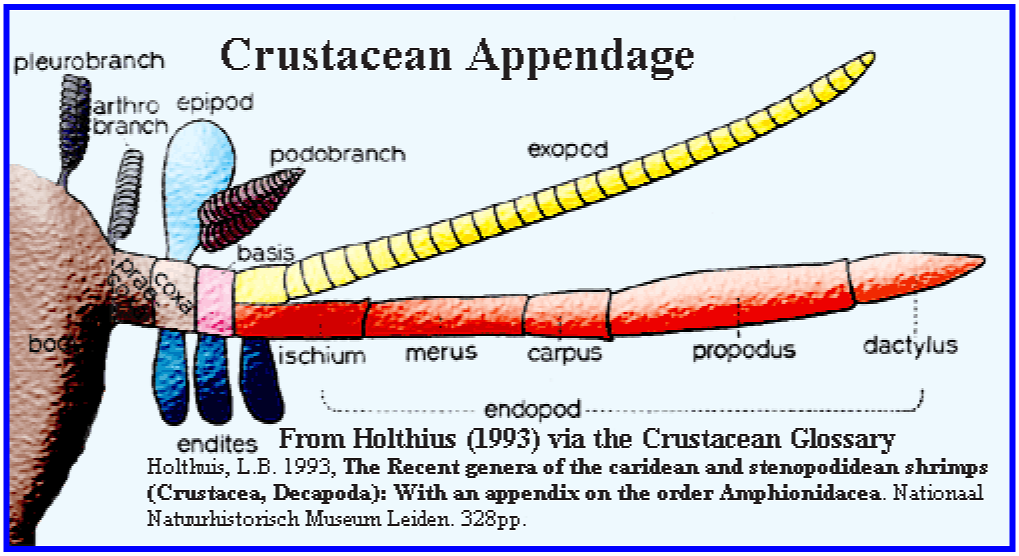
Arthropods are segmented animals, and Crustacea are no exception. Generally, the segments are organized into three groups, the head (*cephalon*), thorax (or *pereon*), and



abdomen (or *pleon*) **[1]**. These groups are referred to as *tagmata*. Generally, the Branchiopoda show little *tagmosis*. The head, thorax, and abdomen are continuous and less markedly differentiated than in most crustaceans.

But just what is a segment? For now, we will confine ourselves to the anatomical part of the answer. If one asks about segments, one is usually told about appendages, or about *engrailed* expression and the process of segmentation, or about hox expression boundaries. What one is rarely told is that the arthropod segment is essentially a neurological unit. *But see* Harszch (2006). To be more exact, the essence of the arthropod segment seems to be a pair of nerve ganglia attached (a) to each other by one or two commisures, (b) to adjacent segments by a pair of ventral nerve cords (one on each side, or a single fused nerve cord), and (c) to an appendage, if one is present, again usually by two nerves. Arthropods can do almost anything with a segment, but this basic neurological unit is remarkably constant -- from the anterior protocerebrum of primitive pycnogonids (Maxmen *et al*., 2005) to the *telson* of derived insects (Richards, 1955). Fanenbruck *et al*. (2004); Scholtz & Edgecombe (2005).

Leg Words: an Epistemological Endite



From Holthius (1993) via the Crustacean Glossary
Holthuis, L.B. 1993, **The Recent genera of the caridean and stenopodidean shrimps (Crustacea, Decapoda): With an appendix on the order Amphionidacea**. Nationaal Natuurhistorisch Museum Leiden. 328pp.

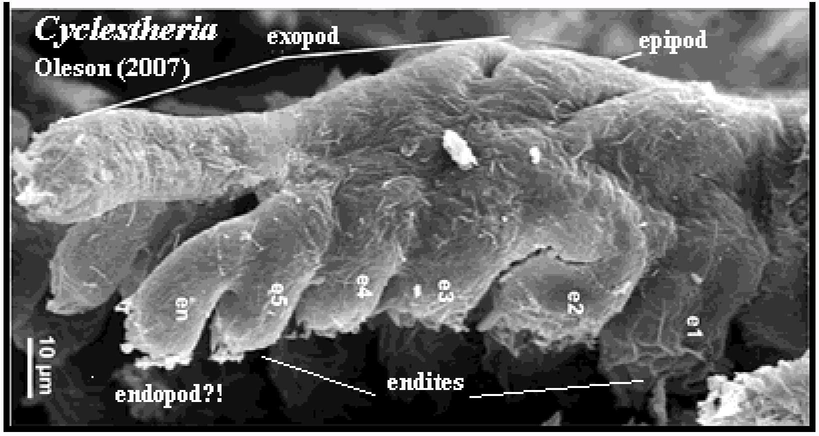
But however comforting the constancy of the arthropod nervous system may be, the appendages get most of the press and require our urgent attention. Almost anything which sticks out of a crustacean, and some things that don't, is a an appendage, and is built on a characteristic appendicular ground plan. For example, the antennae are just specialized legs. In fact, they often begin as larval swimming legs.

Crustaceans are justly famous for the diversity of their appendages, and carcinologists are just as rightly vilified for the complex, inconsistent, terminology they have associated with their legs. We are uncertain how non-carcinologists were expected to deal with the subject before Dr. Joel Martin created the on-line **Crustacea Glossary**. As a precaution, we have downloaded all 400 pages of Dr. Martin's Glossary -- just in case he should meet with an unfortunate accident after exposing these inner mysteries of carcinology to the profane gaze of the uninitiated.

The fundamental appendage rules are three:

(1) The crustacean leg may branch like a particularly aggressive shrub. However, the main axis is conceived to run through two proximal *elements* called the *basis* and *coxa* (basis + coxa = *protopod*), then through a variable number of distal elements collectively referred to as the *endopod* (see figure).

(2) The suffixes *-ite*, *-pod*, and *-podite* are all equivalent and are equally meaningless. Thus *coxa*, *coxite*, *coxapod*, and *coxapodite* all refer to the first segment of an appendage. The suffix -*cerite* is sometimes used for antennal elements (or *articles*). The only useful common suffix is



-*branch*, which tells us that the segment is a gill.

(3) The prefixes do all the real work. They are best understood as directional indicators. Thus an *epi*pod grows upward, an *exo*podite points out, and an *endite* grows down. Other industrious prefixes are positional: *arthro-* = at the "joint" (i.e., the base) of the leg and *pleuro-* = off to the side somewhere. ***Fuzzy Exception***: as stated, the endopod is the outer part of the "main" axis. However, it isn't always clear whether an element is an endopod, or simply the outermost member of a series of endites, or whether, in fact, there *is* no difference and we have once again been duped into making meaningless Latinate noises. See image adapted from Oleson (2007).

For more dark mutterings and skepticism about this entire scheme, see our glossary entry at *endopod*.

The Head

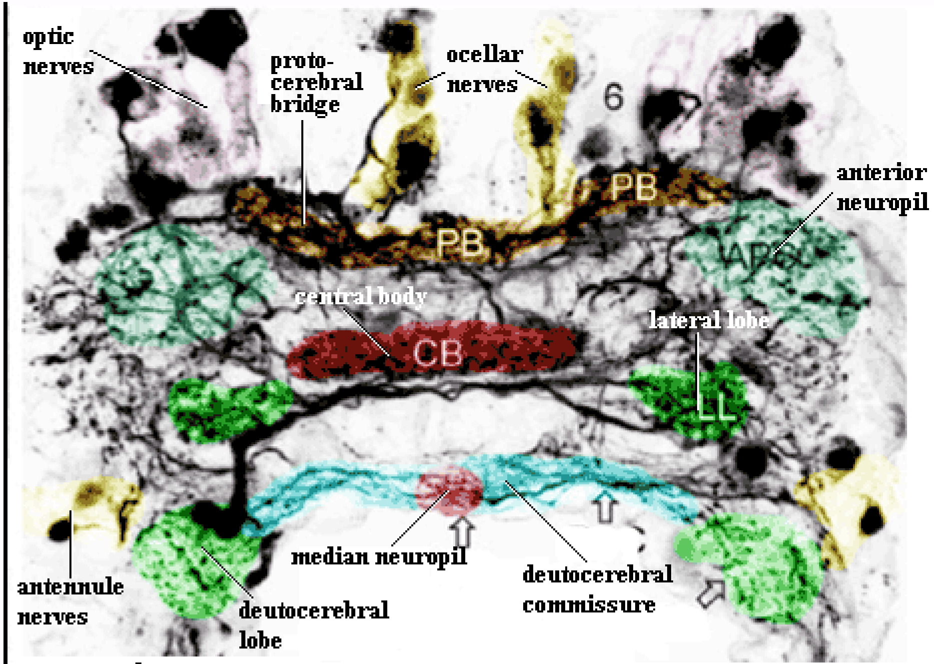
Crustacean Head				
Segment	**Neural**	**Appendage**	**Other**	**Homeobox (anterior boundary)**
0 (*Acron*)	*Protocerebrum*	None	Eyes and *ocelli*.	*engrailed*, wingless
1	*Deutocerebrum*	*Antennules*		
2 (Intercalary)	*Tritocerebrum*	*Antennae*	Hypostome/labrum & adult mouth	*lab*, *pb*
3 (1st gnathal)	paired ganglia with usual commisures & connectives	Mandibles		*dfd*, *scr*
4 (2nd gnathal))	"	Maxillules		
5 (3rd gnathal)	"	Maxillae	Labium?	
6 (1st thoracic)	"	1st thoracic limbs		*Abd-A*

The arthropod head is one of those horrendously difficult problems in homology which we encounter from time to time. On a biological scale of intellectual misery, the cephalon falls somewhere between the fungal cell wall and the vertebrate braincase. This may explain why we have not been able to locate a single, reasonably complete image of the crustacean head. Perhaps a more important reason is that no known crustacean, living or extinct, actually displays a complete set of head parts laid out in such a way that the segmental relationships are clear. In addition, the homologies are contentious. We probably ought to give a fair and balanced review of the topic, but we are not good at that sort of thing. In any case, the fighting is over the chelicerates and stem group arthropods. Budd (2002); Scholtz & Edgecombe (2005). To the extent there is disagreement, we generally follow the system of Scholtz & Edgecombe (2005). Our views have also been corrupted by the work of Prof. Dieter Waloszek **[5]** in ways which are difficult to tie down with particular citations.

But enough name-dropping. The essential correspondences are listed in the table. We'll work through the head in a generally anteroposterior fashion. This all sounds impressively organized, but no regular reader of Palaeos will be fooled. We will quickly degenerate into the usual random remarks and chaotic speculation. To minimize the inevitable disorientation and distracting nausea, please look carefully at the table *before* reading the discussion.

Acron: Eyes and Invisible Legs

For well over a century, carcinologists have debated whether the most anterior



Artemia Larval protocerebrum, immunostained for histamine, adapted from Harzsch (2006).

region of the head, the acron, is actually a segment or a pre-segmental region. In part, this is likely a meaningless question. "Segment" is a concept from gross anatomy. It may not always mean the same thing when translated into the languages of developmental genetics, evolution, neurology, etc. Here, we have framed the concept of segment by reference to neuroanatomy. In that sense, the acron is *at least* a segment, but it may be more.

The *protocerebrum* is the neuroanatomical foundation of the acron. Harszch (2006). It seems to have the usual lateral ganglia ("lateral lobes"), apparently connected in some variant of the usual arthropod fashion. However, it also has a large *central body* which is a median, unpaired *neuropil* of variable size. The central body seems to be a gigantic version of a small median neuropil, as is sometimes found on the commisures between other ganglia. Note, for example, the small median neuropil on the deutocerebral commisure in the image. In short, the posterior part of the protocerebrum is not all that different from any other segment. For convenience, we'll refer to this as the South End.

Away from the South End, things become more peculiar. Two large *anterior neuropils* lie anterolateral to the lateral lobes. North of this is the Optic Coast, with two large optic nerves northeast and northwest for the compound eyes, and two small projections medially, for the naupliar eyes. Remarkably, the same basic structure seems to hold, not only crustaceans and insects (Harszch, 2006), but also the pycnogonid (sea spider) *Anoplodactylus* (Maxmen *et al*., 2005: 1146, fig. 3b) and the millipede *Glomeris* (Prpic, 2004: fig 2). However, a fully-developed protocerebral bridge is only present in insects and crustaceans. Harszch (2006).

It is tempting to think of the Optic Coast as a sort of half-segment, making the acron a segment-and-a-half. Resist this temptation. That's typological thinking. One reason we suspect the posterior acron is essentially a segment is that the homeobox gene engrailed (en) is expressed along the South End in species which use en to make segments. En is sometimes expressed

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|     |  `--+--Remipedia
|     |     `--+--Cephalocarida
|     |        `--+--Malacostraca
|     |           `--+--Maxillopoda
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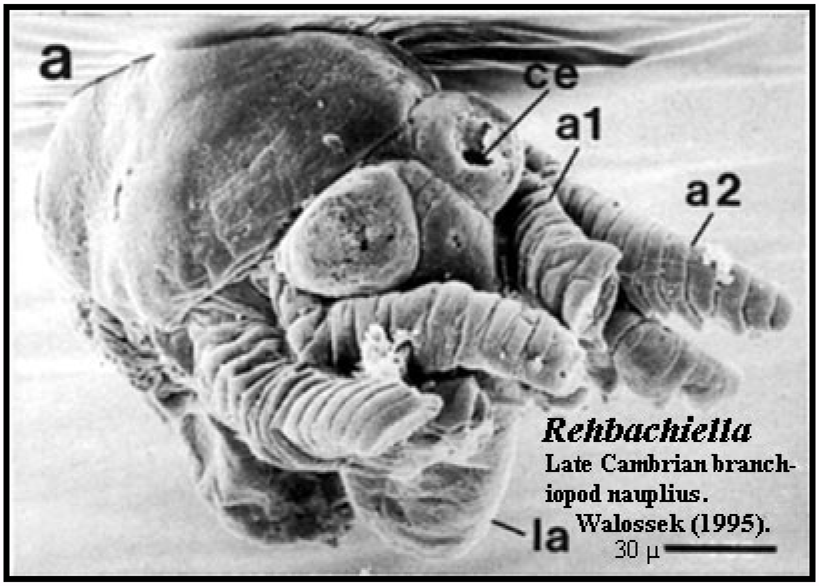
The Eyes



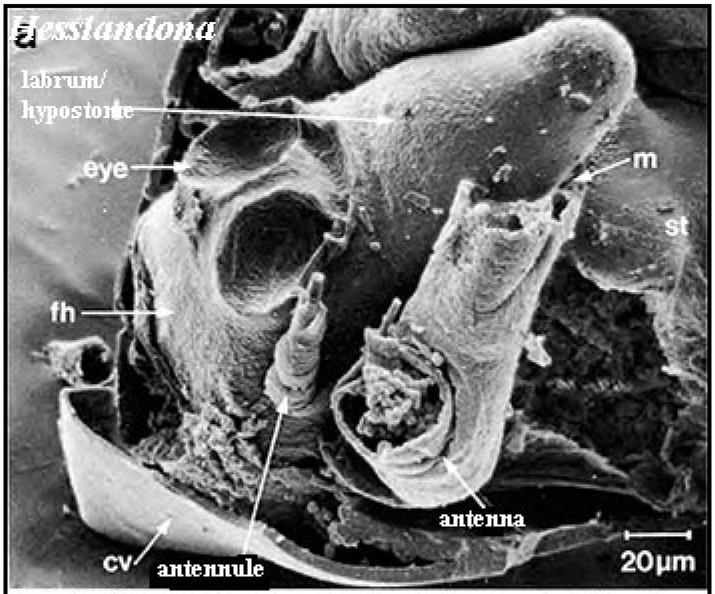
Rehbachiella Late Cambrian branchiopod nauplius. Walossek (1995).

Like most crustaceans, branchiopods have at least three eyes. In addition to the usual paired compound eyes, crustaceans have one or more central, unpaired *naupliar eyes*. The naupliar eye takes its name from the *nauplius*, the characteristic larval form of crustaceans (see image above). The nauplius is essentially a swimming head bearing three pairs of appendages which will later become the antennules, antennae and *mandibles* (anterior mouth parts.) This form of development -- starting with a free-floating head and growing backwards in stages -- has inspired considerable deep thought about animal development and evolution. See, for example, Meinhardt (2002).

While we're on the subject, we should mention that some crustaceans, particularly Malacostraca, pass through the naupliar stage in the egg. Later larval stages (with functional limbs on the thorax/pereon) are often referred to as *zoeae*. Frequently a larval crustacean will pass through several zoeal forms before graduating to juvenile and adult stages. Terms for last larval and for post-larval juvenile stages tend to be specific to particular taxa, and it would be pointless to cover them here. However, it *is* worth knowing that development tends to be more plastic in crustaceans than in most animals. That is, some larval stages may be skipped or prolonged, depending on environmental conditions. For a recent review, see Anger (2006).

But we were supposed to be discussing naupliar eyes, and we will do so. The naupliar eye is a set of simple photosensitive organs, of a sort that may well have been present in the first Bilateria. In many branchiopods, the naupliar eye is retained into adulthood **[3]**. Crustacea may have an even or odd number of naupliar eyes. The primitive number for crustaceans may be three, innervaed by a median ocellar nerve center. This may become paired in some crustaceans. Harzsch (2006). The naupliar eye develops some fairly interesting bells and whistles in some species. For example, in copepods, the median eye is not only quite large, but it develops a *tepetum*, an internal reflective layer, such as the layer which makes the eyes of cats appear to glow in the dark. Martin & Davis (2001). However, even the tapetum may be primitive character. Giribet *et al*. (2002). Some of the Orsten stem-crustaceans, or perhaps stem-arthropods, apparently bear the simple eyes on the hypostome, a structure we will discuss later. Müller & Waloszek (1985).

We will not engage in the usual discussion of compound eye structure because we think it's boring. However, the crustacean compound eye does have two ancillary points of interest. First, carcinologists have had recurring suspicions that the eyestalk might be the missing appendage of the acron.

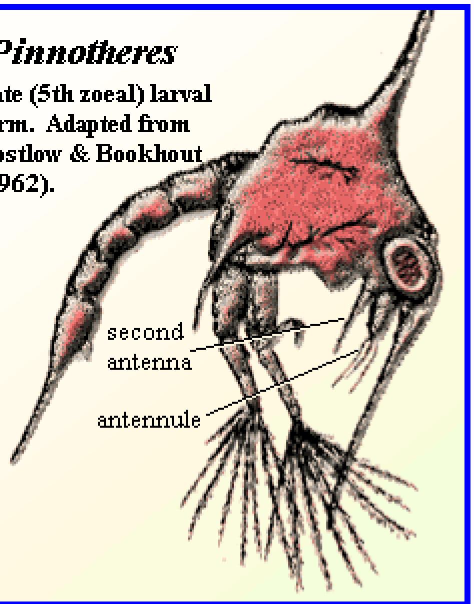


Late Cambrian of Sweden, ventral cephalon in anterolateral view. Adapted from Muller & Waloszek (1985).

There may be yet a third sort of photoreceptive organ, the so-called "frontal organ." Harzsch (2006). However, we have little information on these systems; and it appears that there is not much information to be had.

Pinnotheres

Late (5th zoeal) larval form. Adapted from Costlow & Bookhout (1962).



The mouth is a ventral slit, as in the great majority of crustaceans. Brachiopods have two pairs of maxillae in addition to the mandibles. Often, crustaceans exapt one or more pairs of thoracic limbs to become mouth parts (*maxillipeds*); but this does not occur in branchiopods. Averof & Patel (1997).

The leaf-like (*phyllopodous*) thoracic limbs of *Artemia* are perhaps typical of branchiopods. Some crustaceans have two types of trunk appendages.

All but the smallest crustaceans have a heart. Branchiopods generally have no other circulatory system, and the heart simply circulates fluid in an open *hemocoel*. Branchiopods, and several other crustacean groups, have an iron-heme oxygen carrier protein referred to as hemoglobin and distantly related to the vertebrate hemoglobin. However, branchiopods do not have a separate respiratory system and rely on diffusion for gas exchange. ATW

Links: Introduction to the Crustaceamorpha - UCMP; 'Orsten' Research and Dieter Waloszek on Arthropod and Crustacean Phylogeny; From *The Crayfish*, by T. H. Huxley, 1879; Crustacean - Wikipedia; Crustacea net - data base; Crustacea - Tree of Life Web Project; Animal Diversity Web; The Encyclopedia of Earth MAK120515

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Notes

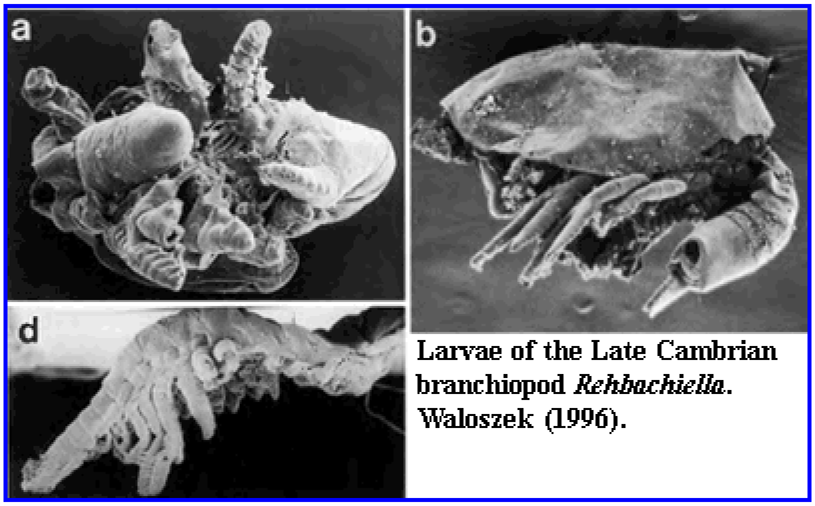
[1] We will treat *thorax* and *pereon* as synonymous. Most writers also treat *abdomen* and *pleon* as synonymous. Here, we will try to be more careful in view of the distinction suggested by Schramm & Koenemann (2004), which will be discussed later. Briefly they propose that *pleon* be used for body regions expressing Abd-B during development and generally bearing a distinctive form of appendage. *Abdomen* corresponds to a posterior hox-free zone without appendages.

[2] In any case, you should review our excuses for certain idiosyncracies of nomenclature and typography at Nomenclature.

[3] Like the median, light-sensitive pineal organ of many vertebrates, with which it may share some distant homology.

[4] For an excellent site on the biology and ecology of *Artemia*, see **ARTEMIA SALINA**.

[5] Variously spelled Waloszek, Walossek, and Waloßek. We suspect that Waloszek has also influenced many real arthropod workers (which we, of course, are not) in the same way. Waloszek began working on the Furongian Orsten arthropods in the 1980's and has published numerous, striking electron micrographs of his discoveries. Orsten exposures lack the near-perfect preservation of sites such as the Burgess Shale or Chengjiang. However, Orsten animals are often uncrushed and, critically, Waloszek eventually assembled virtually complete developmental sequences of several species. Waloszek's influence is communicated through the cumulative impact of his images, together with his clear identification of homologous larval structures. These have reshaped the way scientists perceive arthropod body plans, but in a manner not easily captured by citation to particular papers.



Larvae of the Late Cambrian branchiopod *Rehbachiella*. Waloszek (1996).

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Branchiopoda

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--BRANCHIOPODA
   |  |--Anostraca
   |  `--+--Notostraca
   |     `--+--Conchostraca
   |        `--+--Cladocera
   |?--Xenocarida
   `--+==Maxillopoda
      |--Ostracoda
      `--Malacostraca
```

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`--+--BRANCHIOPODA
   |  |--Anostraca
   |  `--+--Notostraca
   |     `--+--Conchostraca
   |        `--+--Cladocera
   |?--Xenocarida
   `--+==Maxillopoda
     |--Ostracoda
     `--Malacostraca
```

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Anostraca

Introduction

Fairy shrimp are easy to distinguish from all other branchiopods because they swim upside down with their legs extending upwards. They occur in temporary freshwater ponds from the arctic circle to southernmost Canada.

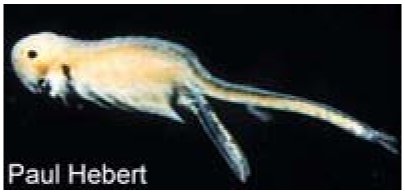
Morphology

(Source: Biodiversity Institute of Ontario)

(Source: Biodiversity Institute of Ontario)

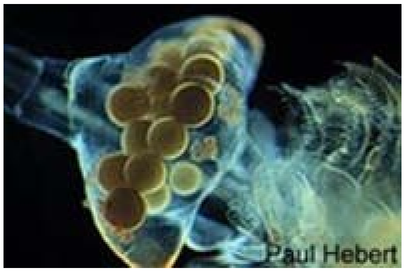
Distinguishing characteristics of fairy shrimp are the absence of a carapace, an elongate body and distinct head region. They have a pair of stalked compound eyes and 11, 17 or 19 pairs of thoracic legs. The largest fairy shrimp are 100 mm long, though most species are between 7 and 20 mm. Anostracans are sexually dimorphic; the males have a pair of ventral penes on their genital segments, while the females have a ventral, medial brood pouch to hold their eggs.

Reproduction



(Source: Biodiversity Institute of Ontario)

Anostracans usually reproduce sexually, though parthenogenetic reproduction occurs in some populations of *Artemia salina*, the brine shrimp. Mating usually occurs just after the female has moulted, so nearly mature females are often attended by several males. After mating, the female retains the eggs in her brood pouch until she dies, and the eggs settle to the bottom. The eggs are resistant to dessication, freezing, and ingestion by birds. The eggs hatch into nauplius or metanauplius larvae which undergo several moults before reaching maturity. Species that live in temporary ponds typically only have one generation per year.



(Source: Biodiversity Institute of Ontario)

Ecology

Fairy shrimp are restricted to temporary pools of freshwater during the cool months of the year. They are not usually found in habitats that contain fish. Algae, bacteria, protozoans, rotifers, and bits of detritus constitute most of their diet, but large species, such as *Branchinecta gigas*, are predators.

(Source: Biodiversity Institute of Ontario)

(Source: Biodiversity Institute of Ontario)

Many species of fairy shrimp compete intensely for mates. Since mating usually occurs just after the female moults, males often grasp her and are towed around while waiting for her to moult. Some females have a chain of these attached males, including some which have died while awaiting her moult!

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Branchiopoda

Abbreviated Dendrogram

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CRUSTACEA
|--Phosphatocopida
`--+--BRANCHIOPODA
   |  |--Anostraca
   |  `--+--Notostraca
   |     `--+--Conchostraca
   |        `--+--Cladocera
   |?--Xenocarida
   `--+==Maxillopoda
     |--Ostracoda
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|--Phosphatocopida
`--+--BRANCHIOPODA
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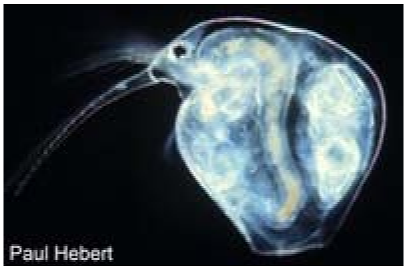
Cladocera



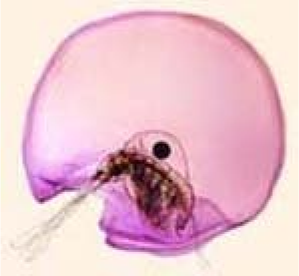
Introduction

In the early spring, the water in many lakes and ponds teems with pale specks moving through the water column. Cladocerans, or water fleas as they are commonly known, are small crustaceans (0.2-3.0 mm). They have successfully invaded a wide variety of aquatic habitats, ranging from hot springs to polar ponds, from large lakes to temporary pools. Cladocerans are an important

(Source: Biodiversity Institute of Ontario)

component of aquatic food-webs; they feed on phytoplankton and are themselves consumed by fish. Cladocerans have attracted much scientific interest, partly because they are easy to culture in the laboratory. They are often used in studies of animal behaviour, functional morphology, evolution, speciation and community ecology.

Morphology

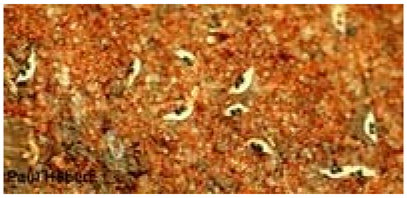

(Source: Biodiversity Institute of Ontario)

(Source: Biodiversity Institute of Ontario)

One of the most obvious features of a cladoceran is its single, large compound eye. It is especially evident in living specimens, because it is constantly rotated by three pairs of muscles. The heart lies behind the head and is a simple bag-like structure. The rostrum of cladocerans is the beak-like termination of the head. The first antennae are inconspicuous and are used in olfaction. The second antennae, which are used in swimming, are large, branched appendages powered by three pairs of muscles. Cladocerans have five or six pairs of lobed thoracic legs covered with fine projections called setae. The postabdomen bears two long abdominal setae and two terminal claws. It is used primarily for cleaning debris from the thoracic legs, but may also be used for locomotion. The brood chamber is located dorsally in the carapace and is used to hold the eggs until they hatch.

Reproduction

Most cladocerans reproduce both parthenogenetically and sexually, employing a breeding system termed cyclic parthenogenesis. For much of the year, populations consist entirely of females reproducing by parthenogenesis. The females deposit clutches of 1 to 100 eggs in the brood chamber, which undergo direct development, meaning that they develop into miniature versions of their parent before being released. Parthenogenesis occurs until adverse conditions are encountered; females then produce both males and resting eggs which cannot develop without fertilization. These resting eggs are then enclosed in a thick, protective case called an ephippium. A few species have given up sex entirely, and reproduce only parthenogenetically. In all species, the resting eggs play a key role in the colonization of new habitats, because of their resistance to freezing and drying. Eggs of some zooplankton species have remained viable for up to 300 years in the absence of water.



(Source: Biodiversity Institute of Ontario)

Ecology


(Source: Biodiversity Institute of Ontario)

Cladocerans are primarily freshwater organisms. They are abundant everywhere in these habitats except in grossly polluted or rapidly flowing water. The highest diversity of species occurs in the littoral zone of lakes where the most common inhabitants are chydorids and macrothricids. The open-water areas of the lakes are dominated by other genera such as *Bosmina*, *Daphnia*, and *Holopedium*. Rooted aquatic plants actually have a repellent effect on cladocerans.

Most cladocerans are filter feeders which consume algae, protozoans, bacteria and organic detritus. The movement of their thoracic legs creates water currents which draw food particles to them. Tiny projections on the legs filter the particles out of the water. Once transferred to the mouth, food is crushed by the mandibles. A few Cladocera are predatory. They use modified thoracic limbs to seize their prey, which include protozoans, rotifers and other small crustaceans.

Many cladocerans show dramatic changes in their body shape over the year, so individuals in midsummer look very different from those of the same species in winter. These changes are known as cyclomorphosis. *Daphnia retrocurva*, a common cladoceran in the Great Lakes of North America, has a rounded head from fall to early spring. As summer advances, the females's head becomes greatly elongated. By winter, the head returns to its original size.

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Branchiopoda: Conchostraca

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--BRANCHIOPODA
   |  |--Anostraca
   |  `--+--Notostraca
   |     `--+--Conchostraca
   |        `--+--Cladocera
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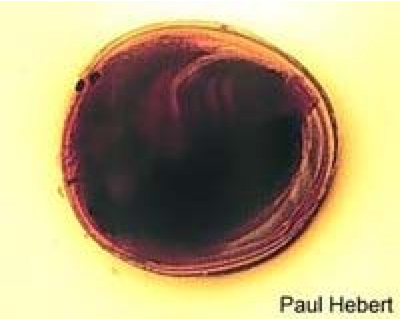
Conchostraca

Introduction

Conchostracans have the flattened leaf-like legs of branchiopods, but they are completely encased by their carapace. They can usually be found swimming along the bottom amid vegetation.

(Source: Biodiversity Institute of Ontario)

Morphology



(Source: Biodiversity Institute of Ontario)

Conchostracans are fairly small (2 to 16 mm long) animals, with a carapace that wraps around their entire body. There are two groups of conchostracans that can be divided by their shell morphology; the clam-like conchostracans (Apinicaudata) and the globular conchostracans (Laevicaudata). They can extend their second antennae out of the carapace to swim. The head has a pair of close-set compound eyes that are fused in one genus (*Cyclestheria*) and 10 to 32 pairs of thoracic legs.

Reproduction

Most conchostracans reproduce sexually, but other species reproduce parthenogenetically. Male conchostracans have specialized hooks on the first and/or second pairs of thoracic legs which grasp the female during mating. The females often swim about with the male holding onto her carapace. Conchostracans hatch from resting eggs as nauplii and don't develop a carapace until their third naupliar stage. As they moult, juveniles become more and more adult-like until they become sexually mature. Species that live in temporary ponds only have one generation per year.

Ecology

Conchostracans occur in transient ponds throughout much of Canada except the high arctic. They feed on detritus or on plankton by drawing water into the carapace and removing the food particles with their phyllopods.

Some conchostracans look remarkably like a tiny clam - until they start swimming!

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   |  `--+--Notostraca
   |     `--+--Conchostraca
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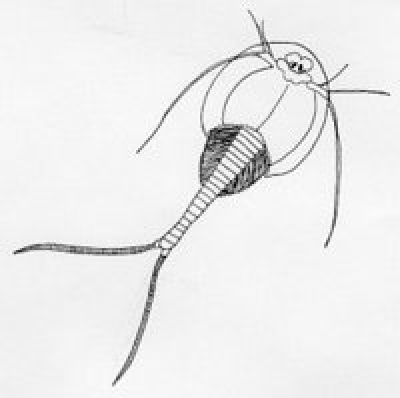
Notostraca

Introduction

Tadpole shrimp are large branchiopod crustaceans that occur in arctic Canada and on the prairies.

Morphology

Tadpole shrimp have a large, flattened carapace that covers their head and thorax. The rest of their body is elongate terminating in a pair of filamentous cercopods. Adults are from 10 to 58 mm long and have 35 to 70 pairs of thoracic legs that are often partially hidden by the carapace. The first pair of legs is used for swimming, while the rest are used for walking, digging and handling food as well as swimming.



(Source: Biodiversity Institute of Ontario)

Reproduction

Most notostracans have separate males and females (gonochoristic), but self-fertilizing hermaphrodites are not uncommon. Females have a specialized brood pouch on their eleventh pair of legs which carries their eggs. The eggs are carried in the brood pouch until they hatch into either nauplius or metanauplius larvae. These larvae undergo around 12 moults before becoming mature in 2 to 3 weeks. Adults moult throughout their life.

Ecology

Most species of notostracans occur in very temporary ponds, though one species *Lepidurus arcticus* is also found in large arctic lakes. Within Canada, notostracans occur in the north and the west. Notostracans feed on detritus and on anostracans, conchostracans and other benthic invertebrates.

Because of their resemblance to primitive arthropods, such as the trilobites, the tadpole shrimp are celebrities. Their dried eggs are sold in tiny boxes and you can grow your own!

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Maxillopoda

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |?--Xenocarida
   `--+==MAXILLOPODA
      |  |--Thecostraca
      |  |--Branchiura
      |  `--Copepoda
      |--Ostracoda
      `--Malacostraca
```

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Maxillopoda: Branchiura

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |?--Xenocarida
   `--+==MAXILLOPODA
      |  |--Thecostraca
      |  |--Branchiura
      |  |--Branchiura
      |  `--Copepoda
      |--Ostracoda
      `--Malacostraca
```

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1. Branchiura

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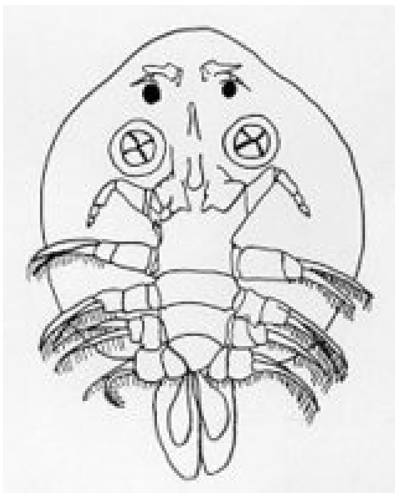
Branchiura

Introduction

Branchiurans are parasites once considered to be a group within the copepods, but recent phylogenetic studies have elevated the group to its own subclass. Their common name "fish lice" comes about because they attach themselves to the outside of fish.

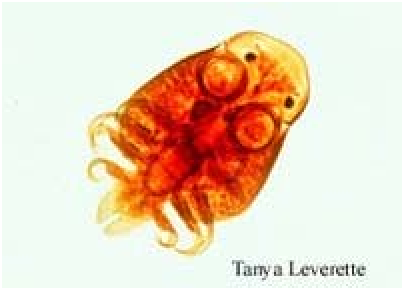
Morphology



(Source: Biodiversity Institute of Ontario)

Branchiurans are highly modified to suit their parasitic life style. They are dorsoventrally flattened and their carapace has been widened to cover most of their appendages. Two compound eyes make them easily distinguishable from parasitic copepods. Their mandibles have been modified into a proboscis used to suck food out of their prey. Large suckers are actually modified maxillules and are used to help 'stick' to their host. They have eight legs and a small tail that acts like a rudder when swimming. A hollow spine is used to pierce the skin of the host and access the nutrients inside. *Argulus* sp. can grow to 10 mm in length, but most are only 7 mm.

Reproduction



(Source: Biodiversity Institute of Ontario)

Male and females branchiurans drop off their host to look for mates. They swim (or somersault) through the water until a mate is encountered. After mating the females search for an egg-laying site where they attach their eggs in rows to rocks and other submerged objects. The free swimming larvae attach themselves in the gill chamber, mouth or on the outer surface of host fish with hooks that are modified antennae and maxillules. In 4 to 5 weeks the larvae become adults.

Ecology

Branchiurans feed on the blood or body fluids of their host. They attach to their host using modified hooks and sucker, but can also detach and swim through the water when looking for mates. They have many host species including the common carp, *Cyprinus carpio*, and the white sucker, *Catostomus commersoni*. Heavy infestations of branchiurans can cause mass mortalities in fish populations. *Argulus* sp. are also suspected to spread viruses.

Many parasites eat blood, but branchiurans also feed on the mucous of their hosts.

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Maxillopoda: Copepoda

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |?--Xenocarida
   `--+==MAXILLOPODA
      |  |--Thecostraca
      |  |--Branchiura
      |  `--Copepoda
      |--Ostracoda
      `--Malacostraca
```

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1. Copepoda

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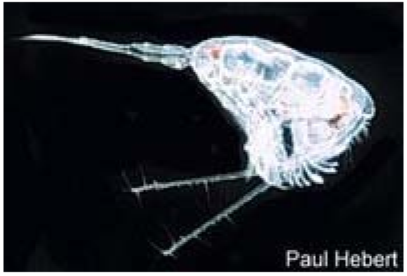
Copepoda

Introduction

The Copepoda is one of the largest groups of crustaceans. Approximately 12,000 species have been described, but this may be as little as 15% of the total number of species! Copepods are abundant in both marine and freshwater systems, but are much more diverse in marine environments.



(Source: Biodiversity Institute of Ontario)

Morphology

(Source: Biodiversity Institute of Ontario)

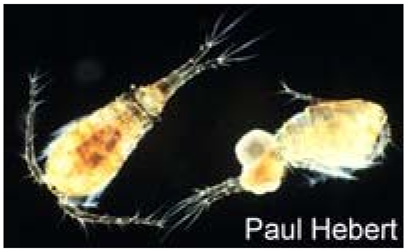
Copepods have long first antennae and a single, median eye located on the anterior (front) portion of the head. They have two pairs of antennae and biramous feeding appendages. The first pair of antennae is often sexually dimorphic and bears chemoreceptors and mechanoreceptors. Antennules (first antennae) are used for locomotion, feeding and reproduction. Each segment of the thorax bears a pair of swimming appendages. The last abdominal segment has two caudal rami which have an unknown function, but are useful in taxonomy for distinguishing between groups of copepods. The largest copepods attain lengths of 3 mm, although most species are less than 1.0 mm.

Reproduction

All species of freshwater copepods reproduce sexually. After mating, the eggs undergo brief embryonic development before they are released into the water as nauplius larvae. The nauplius undergoes five moults before it transforms into a copepodite stage that more closely resembles the adult. If unfavourable environmental conditions, such as declines in temperature, oxygen or food availability, occur, the copepodite larvae of some freshwater species can enter a diapause stage until conditions improve.

(Source: Biodiversity Institute of Ontario)

Ecology



(Source: Biodiversity Institute of Ontario)

Copepods occur in oceans, estuaries, lakes, ponds, groundwater, wet moss and even in pools of water that collect in the leaves of terrestrial plants. They are an important food source for larval fish and other invertebrates in aquatic systems. Most are omnivores, filtering algae and bacteria from the water as well as preying upon other small invertebrates. As a result they are an important link between the primary producers (algae) and the larger secondary consumers (fish larvae). Almost half of all known copepod species are either parasitic or commensal with other organisms. Parasitic copepods often cling to the outside of their host, but others are more intrusive, having invaded their gills, nostrils, or mouths of their hosts. Copepods are the intermediate hosts of other parasites, such as the nematode *Dracunculus medinensis* and the tapeworm *Diphyllobothrium latum* which can be passed on to humans.

Although copepods are extremely small and generally harmless, some species can be dangerous. Copepods carry many parasites and diseases that can cause death in humans - and all you have to do is eat or drink the copepod.

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Palaeos	Παλαιός	MAXILLOPODA
ARTHROPODA		THECOSTRACA

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Maxillopoda: Thecostraca

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |?--Xenocarida
   `--+==MAXILLOPODA
      |  |--Thecostraca
      |  |--Branchiura
      |  `--Copepoda
      |--Ostracoda
      `--Malacostraca
```

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1. Thecostraca

Chthamalus stellatus, photo Michael Maggs, Wikipedia, Creative Commons Attribution Share-Alike

The Thecostraca are the barnacles and their relatives. This is a holding page, pending something being written here

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Ostracoda

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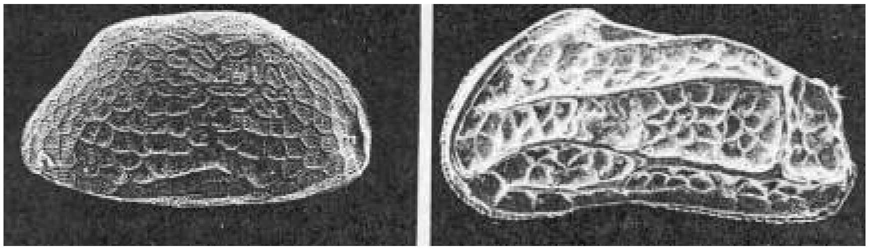
CRUSTACEA |--Phosphatocopida `--+--Branchiopoda    |?--Xenocarida    `--+==Maxillopoda |--OSTRACODA `--Malacostraca	Overview Ostracoda

---



Two species of fossil ostracods. Left: exterior view of right valve of *Microcytherura* (Pleistocene x 70). Right: exterior view of left valve of *Orionina* (Pliocene, x 58) (from Boardman et al 1987), via these study notes..

Under Construction

Ostracoda

Abbreviated Dendrogram	Contents
see below	Overview Ostracoda

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |?--Xenocarida
   `--+==Maxillopoda
      |--OSTRACODA
      `--Malacostraca
```

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1. Ostracoda

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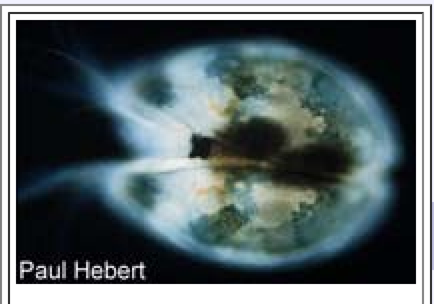
Ostracoda

Introduction

Ostracods are small crustaceans enclosed in a bivalved carapace. They are the oldest known crustaceans in the fossil record because their shells preserve well. They occur in nearly every aquatic habitat from polar lakes to tropical oceans, and they are important microfossils for dating ancient sediments.



Morphology

(Source: Biodiversity Institute of Ontario)

Ostracods are small animals, ranging in size from 0.3 to 30.0 mm, although most freshwater species range between 0.5 and 2.5 mm. Their bodies are completely enclosed in a calcified, bivalved carapace which is hinged dorsally. The surface of the shell may be smooth or pitted, punctuated, wrinkled, or reticulated. Several large muscles are directly attached to the carapace, and these points of attachment leave scars that are useful in discriminating some groups of ostracods.

(Source: Biodiversity Institute of Ontario)

Adult ostracods have 6 to 7 pairs of appendages. Although distinct segmentation is absent, the head possesses four pairs of appendages including the antennules, antennae, mandibles and maxillae, while the thorax has 3 pairs of legs.

Reproduction

(Source: Biodiversity Institute of Ontario)

Freshwater ostracods go through eight moult stages before they mature. Their life span varies from one month in temporary ponds to a year or longer in larger water basins. Reproduction may be either sexual or asexual. Some lineages are exclusively parthenogenetic , but other species reproduce sexually.

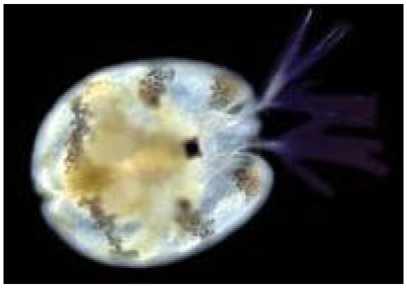
Freshwater ostracods are remarkable for their high frequency of species which have abandoned sexual reproduction. While transitions to parthenogenesis are rare in most other animal groups, about one-third of all freshwater ostracods have given up sex. The breeding system employed by any population is easily determined, as asexual populations contain only females, while sexual populations include both males and females.

Very few ostracod species incubate their eggs within their body; most lay their eggs either singly or in groups on sediment or aquatic vegetation. These eggs may hatch soon after they are laid or remain undeveloped for a year or longer. The ability of eggs, larvae, and adults to withstand freezing and desiccation is a very important biological characteristic which aids the dispersal of ostracods from one body of water to another.

Ecology

Freshwater ostracods are free-living except for members of one group which are commensal on the gills of crayfish. Most free-living forms are benthic, though pelagic forms also occur.

Ostracods possess the largest sperm in the animal kingdom in both relative and absolute terms. Ostracod sperm can be up to ten times the length of the male's body! Some male ostracodes need a special organ (Zenker's organ) to aid in sperm transport.



(Source: Biodiversity Institute of Ontario)

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Malacostraca

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              `--Eucarida
                 `--DECAPODA
```

Contents

The diversity of malacostraca, showing representatives of different orders. Not to scale.
Image by Hans Hillewaert, Wikipedia, Creative Commons Attribution Share Alike.

The malacostraca are the largest of the six classes of crustaceans, containing over 25,000 extant species, divided among 16 extant orders. Its members display a greater diversity of body forms than any other class of animals, and include crabs, lobsters, shrimp, krill, woodlice, scuds (Amphipoda), mantis shrimp and many other less familiar animals. They are abundant in all marine environments and have also colonised freshwater and terrestrial habitats. They are united by a common *bauplan* (ground plan), comprising 20 body segments (rarely 21), divided into a head, thorax and abdomen. - Wikipedia. They have a reasonable fossil record extending back to the Ordovician (Cambrian forms attributed to them are misinterpretations of other taxa, or stem Crustacea or stem athropods

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Malacostraca

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |--Remipedia
   `--+==Maxillopoda
      |--Ostracoda
      `--MALACOSTRACA
         |--Phyllocarida
         `--+--Hoplocarida
            `--Eumalacostraca
               |--Syncarida
               |--Peracarida
               `--Eucarida
                  `--DECAPODA
```

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1. Malacostraca

The diversity of malacostracan crustaceans as illustrated by a number of representative taxa: (A) The phyllocarid *Ceratiocaris* (Silurian); (B) The syncarid *Palaeocaris* (Carboniferous); (C) The eocarid *Tealliocaris* (Carboniferous); (D) The hoplocarid *Acanthosquilla* (Recent); (E) The Decapoda *Eryma* (Jurassic). From Clarkson, 1993; from Prothero, 1990), via these study notes.

The following is copied with minor modifications from William Twenhofel and Robert R. Shrock 1935, *Invertebrate Paleontology*, McGraw Hill Book Co. New York & London, posted at the Internet Archive as public domain. The content has been lightly edited MAK120518

The Malacostraca comprise a great number of diverse forms, including familiar crustaceans as crabs, crayfish, lobsters, shrimps, etc.

Ecology

The Malacostraca are also the great scavengers of the sea bottom, eating everything of organic character irrespective of the degree of decomposition. Many have a "gastric mill" in the intestinal tract in which shells that have been swallowed are broken into bits or ground into powder. Some of the larger species break open shells with their claws in order to obtain the animals inside. Under favorable conditions all organic matter on certain bottoms passes through the alimentary tracts of some of the Malacostraca and suffers both mechanical and chemical alteration during the passage.

Morphology

Living members of the subclass have 14 or 15 body segments posterior to the head. In addition to the appendages on the head, there are eight pairs of thoracic appendages and six pairs on the abdomen. Paired eyes are generally present and are frequently stalked. The newly born individual has progressed beyond the nauplius stage and is frequently quite similar in appearance to its parents except for size.

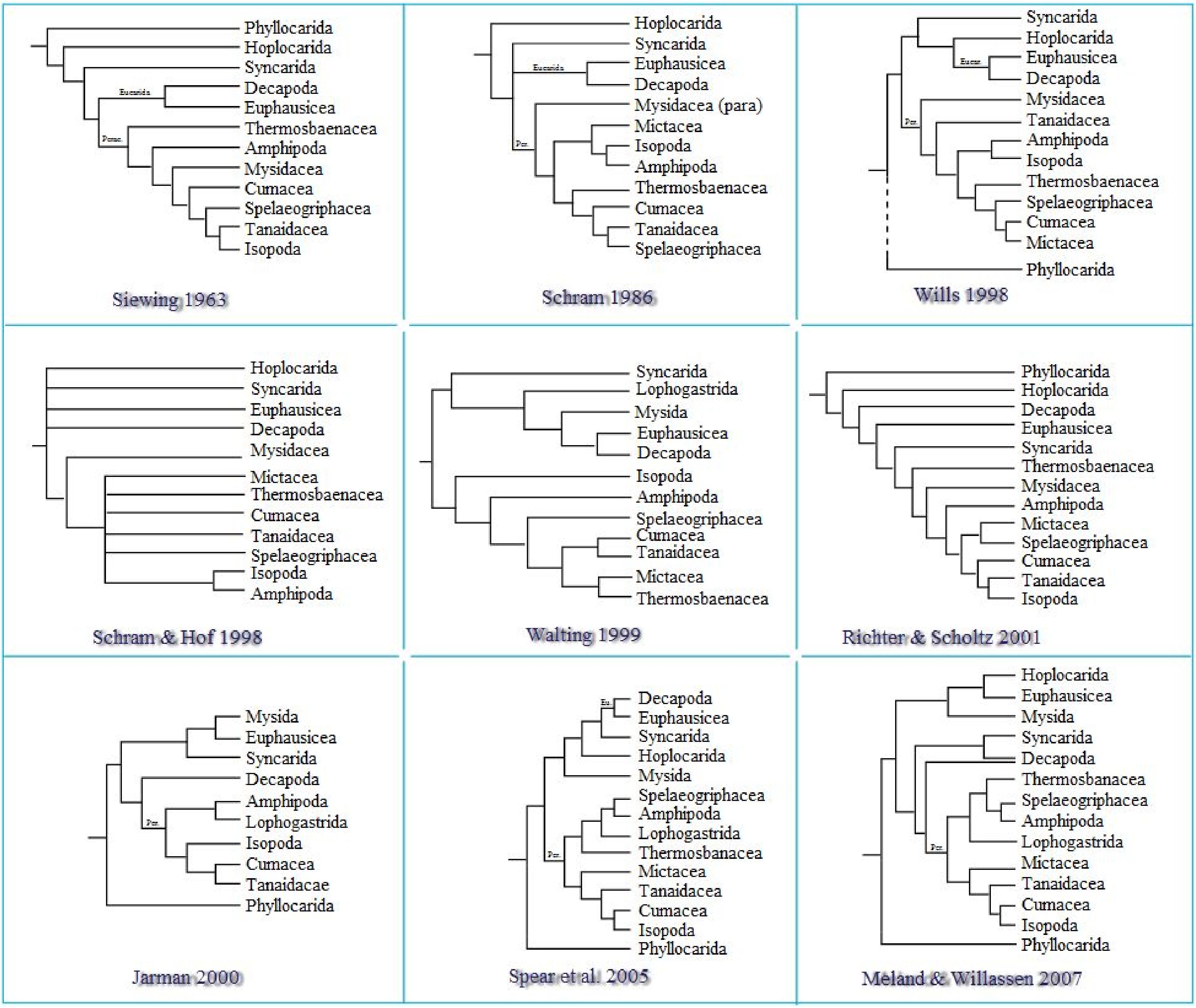
Phylogeny

The following is from Wikipedia. To save time, refernces have not been hyperlinked

The class Malacostraca is united by a number of well-defined and documented features, which were recognised a century ago by William Thomas Calman, who in 1904 ,[1] and 1909 described these common morphological features and introduced the major taxonomic subdivisions of the Malacostraca which are still in use today: he divided the Malacostraca in two subclasses the Phyllocarida and the Eumalacostraca, which is further subdivided into four superorders: Eucarida, Peracarida, Hoplocarida and Syncarida.[8]

Calman coined the term caridoid facies for the common eumalacostracan (shrimp-like) features; the most important of these is the constant number of segments in each tagma: members of this class have five segments in the cephalon, eight thoracic segments (thoracomeres) and six segments in the pleon and possess a telson, which forms a characteristic tail fan when the uropods are present. Many other characteristic features are present but their presence varies amongst lineages; one notable ancestral feature which varies is the carapace, which may be absent, reduced or well developed covering the whole cephalothorax. Monophyly has also been confirmed by molecular studies .[7] Furthermore, Richter, S., & Scholtz, G. (2001)[9] list five separate unique eumalacostracan features which taken together form a strong argument in favour of the monophyly of the main subgroup, the Eumalacostraca.

However the phylogenetic relationship (the evolutionary tree) of the orders which compose this class is unclear due to the vast diversity present in their morphology. Molecular studies have attempted to infer the phylogeny of this clade,[2][3][4] resulting in phylogenies which have a limited amount of morphological support,[5] to resolve a well-supported eumalacostracan phylogeny,it will be necessary to look beyond the most commonly utilized sources of data (nuclear ribosomal and mitochondrial sequences) to obtain a robust tree in the future.[6]



Phylogenetic trees from several published studies. The first six were obtained via morphological data whereas the last three were obtained with molecular data using a GTR+G+I model (General time reversible + gamma distribution + independent frequencies). (Adapted from Spear et al., 2005[2][4]).
Image by Squidonius, Wikipedia, Public domain.

References

To save time, pdfs have not been hyperlinked or formatted, see the Wikipedia page for links

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[9] Stefan Richter & Gerhard Scholtz (2001). "Phylogenetic analysis of the Malacostraca (Crustacea)". Journal of Zoological Systematics and Evolutionary Research 39 (3): 113–136. doi:10.1046/j.1439-0469.2001.00164.x.

- Wikipedia

Descriptions

Malacostraca

Range: Fr Ordovician (ref)

Phylogeny: Phosphatocopida + (Branchiopoda + Remipedia + (Maxillopoda + Ostracoda + * **:** Phyllocarida + (Hoplocarida + Eumalacostraca))

Characters: typically fourteen (rarely fifteen) body somites besides the telson. All the somites (except the fifteenth) bear appendages which are differentiated into two groups, a thoracic of eight and an abdominal of six pairs. - Zittel & Eastman 1913

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Malacostraca: Amphipoda

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |--Remipedia
   `--+==Maxillopoda
     |--Ostracoda
     `--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              |   |--Pygocephalomorpha
              |   |--Mysida
              |  `--+--Amphipoda
              |     `--Isopoda
              `--Eucarida
```

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Amphipoda

Introduction

Amphipods, also known as side-swimmers or scuds, are ubiquitous in marine and freshwater environments. They are small, laterally compressed crustaceans with a shrimp-like appearance, but without a carapace. Amphipods occur in vegetation, under rocks, on sand and burrowing deep in profundal sediments. Most of the 6000 known species of amphipods live in the oceans, but many are also found in freshwater and terrestrial environments. A spectacular evolutionary radiation of amphipods has occurred in Lake Baikal, in Siberia, where there are hundreds of species of amphipods and these animals.

(Source: Biodiversity Institute of Ontario)

Morphology

(Source: Biodiversity Institute of Ontario)

Amphipods are many-segmented crustaceans. The body is divided into three parts; the cephalothorax, the thorax, and the abdomen. The first thoracic leg is modified into a feeding appendage ("mouth part"), the maxilliped, while the other seven pairs of thoracic legs are used for movement. The first two pairs of thoracic legs are modified for grasping food and are also used by male amphipods to hold onto the female during copulation. The two pairs of antennae are elongate and curved ventrally. Females have a marsupium in which they brood their young until they are ready to be released into the environment.

Reproduction

The timing of reproduction varies among amphipods. Some species have an extended breeding season, and produce multiple broods, while others have a discrete breeding season and produce only a single brood. Before mating, males of some species such as *Gammarus* spp. and *Hyalella azteca* seize females with their gnathopods and hold on for up to a week, waiting for her to moult and be ready for mating. During this time, the pair is said to be in precopula. Copulation consists of the male wrapping the posterior part of his body around the female's ventral side, bringing his uropods in close proximity to her marsupium. He then releases sperm which she sweeps into her marsupium by vibrating her pleopods. After mating is complete, the female releases eggs into her marsupium where fertilization takes place. The incubation period varies with species, locality and time of year.

(Source: Biodiversity Institute of Ontario)

(Source: Biodiversity Institute of Ontario)

The newly hatched young amphipods stay in the marsupium until the female undergoes a post-copulatory moult. The total number of instars (developmental stages) undergone by most amphipod species is poorly known. Amphipods usually only live for one year, though some species, such as *Diporeia hoyi*, may live for more than two years.

Ecology

Amphipods can be found in marine and freshwater habitats from shallow, densely vegetated areas, to the deepest ocean depths, sometimes at densities of 10,000 per square metre.

Amphipods are more active at night than during the day. Because many species are scavengers and consume a wide variety of organic detritus, they form an important trophic link within both freshwater and marine ecosystems, recycling organic material which is then passed back up through the food chain. Amphipods are an extremely important food source for numerous species of fishes, as well as for the opossum shrimp *Mysis relicta*. Due to their importance in aquatic food webs, scientists use amphipods to study the effects of chemical contaminants like PCB's and DDT on aquatic ecosystems.

The swimming speciality of amphipods is a rapid escape response where the abdomen flicks the animal away after the uropods are dug into the ground. - Encyclopedia of Earth - Crustacea

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Malacostraca: Eucarida

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              `--Eucarida
                 |--Euphausiacea
                 |--Amphionidacea
                 `--DECAPODA
```

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3. Amphionidacea

Descriptions

Eucarida

Range: From the Triassic

Phylogeny: Eumalacostraca **:** Syncarida + Peracarida + * **:** Euphausiacea + Amphionidacea + Decapoda

Characters: the carapace covers the cephalothorax and the eyes are stalked. - Twenhofel & Shrock 1935

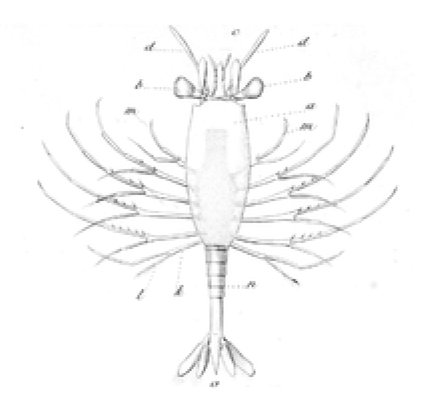
Euphausiacea

Range: No fossil record

Phylogeny: Eucarida **:** Amphionidacea + Decapoda + *

Characters: Caridoid (shrimp-like) forms in which none of the thoracic appendages are specialised as maxillipeds and the gills are in a single series attached to the bases of the thoracic limbs.- Zittel & Eastman 1913

Amphionidacea



Range: No fossil record

Phylogeny: Eucarida **:** Euphausiacea + Decapoda + *

Comments: *Amphionides reynaudii* is the sole representative of the order Amphionidacea, and is a small (less than one inch long) planktonic crustacean found throughout the world's tropical oceans, the larvae mostly in shallow waters, and the adults at greater depth. - Wkipedia

Illustration: Wkipedia

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Malacostraca: Hoplocarida

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              `--Eucarida
                 `--DECAPODA
```

Contents

Taxa on This Page

1. Eumalacostraca
2. Hoplocarida

Squilla mantis, showing the spearing appendages
Public domain, via Wikipedia.

Introduction

From Wikipedia

Close-up of the trinocular vision of *Pseudosquilla ciliata*
Photo by Shumpei Maruyama Wikipedia, Creative Commons Attribution Share Alike/ GNU Free Documentation License,.

Mantis shrimp or stomatopods are marine crustaceans, the members of the order Stomatopoda. They are neither shrimp nor mantids, but receive their name purely from the physical resemblance to both the terrestrial praying mantis and the shrimp. They may reach 30 centimetres in length, although exceptional cases of up to 38 cm have been recorded.[2] The carapace of mantis shrimp covers only the rear part of the head and the first four segments of the thorax. Mantis shrimp appear in a variety of colours, from shades of browns to bright neon colours. Although they are common animals and among the most important predators in many shallow, tropical and sub-tropical marine habitats they are poorly understood as many species spend most of their life tucked away in burrows and holes.[3]

Called "sea locusts" by ancient Assyrians, "prawn killers" in Australia and now sometimes referred to as "thumb splitters" – because of the animal's ability to inflict painful gashes if handled incautiously[4] – mantis shrimp sport powerful claws that they use to attack and kill prey by spearing, stunning or dismemberment. Although it happens rarely, some larger species of mantis shrimp are capable of breaking through aquarium glass with a single strike from this weapon.[5]

References

[2] James Gonser (February 14, 2003). "Large shrimp thriving in Ala Wai Canal muck". Honolulu Advertiser. [3] Ross Piper (2007). Extraordinary Animals: An Encyclopedia of Curious and Unusual Animals. Greenwood Press. ISBN 0-313-33922-8. [4] Gilbert L. Voss (2002). "Order Stomatopoda: Mantis shrimp or thumb splitters". Seashore Life of

Florida and the Caribbean. Dover pictorial archive series. Courier Dover Publications. pp. 120–122. ISBN 978-0-486-42068-4. [5] April Holladay (September 1, 2006). "Shrimp spring into shattering action". USA Today.

--Wikipedia

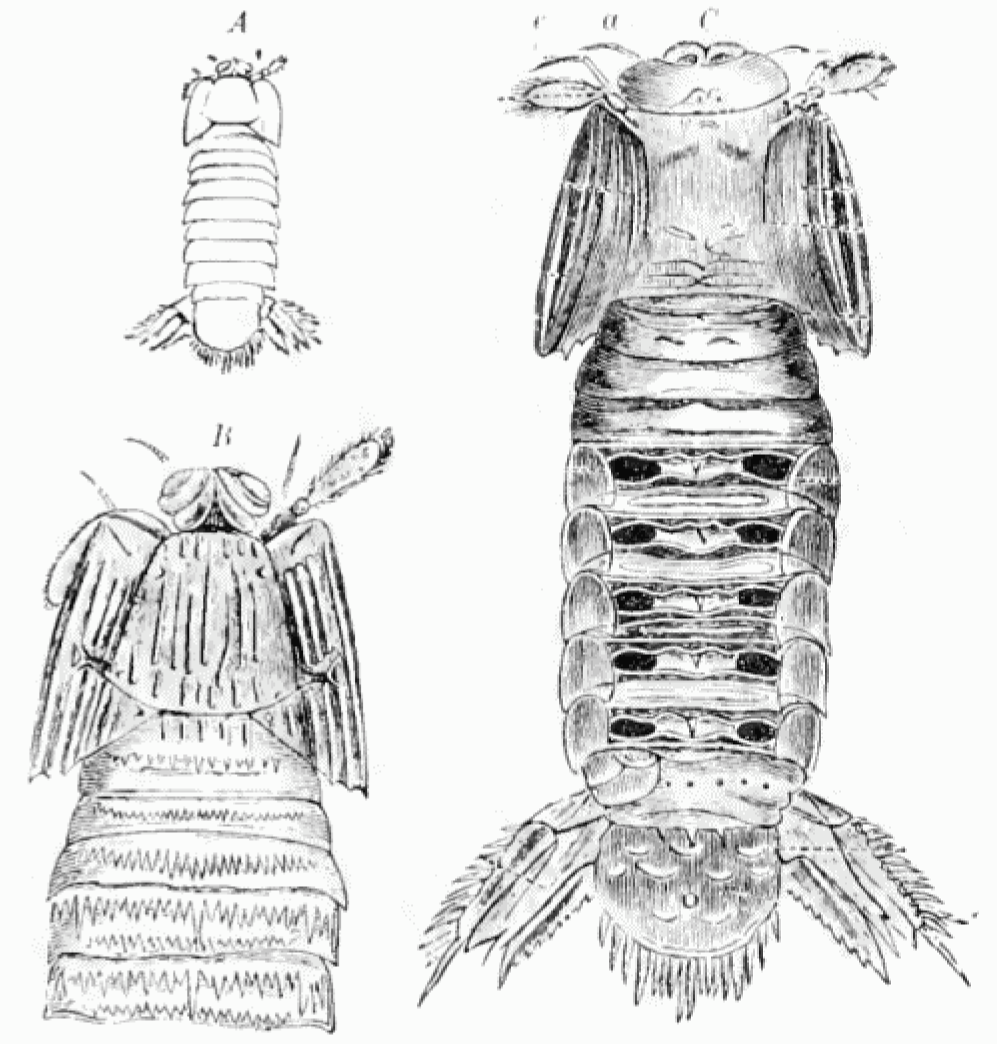
Description

The following is copied with minor modifications from William Twenhofel and Robert R. Shrock 1935, *Invertebrate Paleontology*, McGraw Hill Book Co. New York & London, posted at the Internet Archive as public domain. The content has been lightly edited MAK120518

The existing Stomatopods form a very homogeneous group. originally only one family (Squillidae) was recognised. Many of the genera are separated by comparatively slight differences. Representative forms include *Squilla*, *Lysiosquilla*, *Pseudosquilla*, *Gonodactyhis* Latreille ; and *Coronida* Brooks. Modern Stomatopods are exclusively marine, the adults generally inhabiting burrows in the sand or mud of the seabottom in shallow water, chiefly in the tropics, but extending also 50 degrees on either side of the equator. Many species seem never to wander far from their burrows, into which they retreat with great rapidity when alarmed. The larval stages, on the other hand, are exclusively pelagic, of glass-like transparency, and occur in great numbers in the plankton of the warmer seas. All the Stomatopods appear to be of active, predatory habits. They range in size approximately from 38 to 340 mm.

Fossil history

Stomatopods similar to but generally smaller than modern taxa are known from the Carboniferous. *Perimecturus rapax* (Order Palaeostomatopoda) is known from the Bear Gulch Limestone, and the genus is also known from Scotland, shows several features, such as the massiveness of the abdomen and the movable rostral plate, that suggest an affinity with the group. In the Late Kimmeridgian/Early Tithonian Solnhofen lagerstätte, undoubted Stomatopods occur, some very similar to the Eocene to Recent genus *Squilla*. Other Solnhofen forms like *Sculda* (right) and *Buria*, differ considerably from Recent forms. Larvae of Stomatopods belonging to what is known as the *Erichthus* type have been recognised in the Cretaceous of the Lebanon. - Zittel & Eastman 1913



Sculda pennata Late Jura ; Solnhofen , Bavaria, A and B, Dorsal views, C, Ventral aspect, a, e, First and second pairs of antennae, from- Zittel & Eastman 1913. See also Fossils of Solnhofen.

Descriptions

Hoplocarida

Range: From the Carboniferous

Phylogeny: Malacostraca **:** Phyllocarida + (Eumalacostraca + *)

Characters:. Small carapace and at least four free thoracic segments. The abdomen is large and ends in a tail fan. Twenhofel & Shrock 1935

Comments: There are three orders, the Paleozoic Aeschronectida Schram, 1969 and Palaeostomatopoda Brooks, 1962 and Archaeostomatopoda Schram, 1969, and the Mesozoic and extant Stomatopoda Latreille, 1817 MAK120518

Eumalacostraca

Range: From the Devonian

Phylogeny: Malacostraca **:** Phyllocarida + (Hoplocarida + * **:** Syncarida + Peracarida + Eucarida)

Comments: The most successful of the crustacean clades. The main arthropod groups are often distingusihed by different numbers of segments, and the same applies here. Eumalacostracans have 19 segments altogether, devided according to head, thorax, and abdomen; There are five cephalic (head) seqments . There are eight segments in the thorax and the same number of thoracic appendages. The appendages are rarely alike and have the appearance of legs, which are jointed and used for swimming or walking. The abdomen has six segments, all of which may bear appendages. The common ancestor is thought to have had a carapace, and most living species possess one, but it has been lost in some subgroups. The group as originally defined included the Stomatopoda (mantis shrimp), but these are now generally placed in their own subclass, Hoplocarida. Although the earliest forms appeare in teh Devonian, the group only became common in the Triassic, and has continued to flourish ever since - Twenhofel & Shrock 1935, Wikipedia MAK120518

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Malacostraca: Isopoda

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |--Remipedia
   `--+==Maxillopoda
     |--Ostracoda
     `--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              |   |--Pygocephalomorpha
              |   |--Mysida
              |  `--+--Amphipoda
              |     `--Isopoda
              `--Eucarida
```

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1. Isopoda

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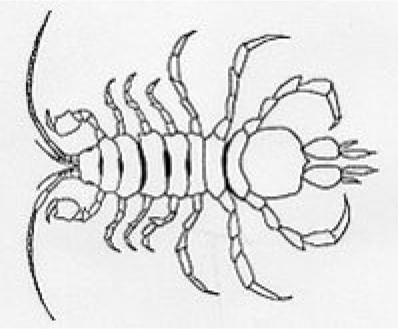
Isopoda

Introduction

(Source: Biodiversity Institute of Ontario)

With over 10,000 species, the order Isopoda is the second most diverse group of crustaceans. Isopods can be found in all types of habitats, but most species live in the sea or on land. Looking under garden rocks or rotting logs, you will often discover them. They are the small, hard-shelled creatures which resemble miniature armadillos, that roll into a tiny ball when disturbed. You might know them as rolly-pollys, or sow bugs. The most striking characteristic of isopods is their dorsoventral compression.



(Source: Biodiversity Institute of Ontario)

Morphology

(Source: Biodiversity Institute of Ontario)

The body of isopods is divided into three sections; the cephalothorax, the thorax and the abdomen. The compound eyes of isopods are dorsal and unstalked. Isopods are negatively phototactic (reathey ct to light by moving away from it), and usually remain hidden under rocks and debris. Their first antennae are short, while the second set is much longer and reach ahead of the isopod to "feel' for signs of food sources as well as potential danger. The first pair of legs are called gnathopods ("jaw-feet") because they are modified for grasping and tearing food. The other thoracic segments each bear a pair of walking legs. The last abdominal segment is a result of the fusion of the last four abdominal segments to form a posterior shield in all North American species. Uropods are the last pair of abdominal appendages that are biramous and extend beyond the end of the abdomen. Mature females have large, inwardly directed, platelike oostegites at the inner base of their anterior (front) legs. They form a shallow chamber on the ventral surface of the thorax called a marsupium. It serves to hold and protect developing eggs or young.

Reproduction

(Source: Biodiversity Institute of Ontario)

(Source: Biodiversity Institute of Ontario)

Isopods reproduce sexually and breeding occurs throughout the year. Thus, egg-bearing females may be found year-round, but most are found during the spring and summer months. During mating, males grasp females and carry them under their bodies using their periopods. They may remain attached for months. The male presses his ventral surface against the side of the female, placing his genital pores close to one of the female's genital pores. Sperm are released while the male pleopods vibrate rapidly. The male then moves to the other side of the female and repeats the process with the other genital pore. After 1 to 10 months, the eggs are fertilized and pass into the marsupium. The incubating eggs and newly hatched young remain in the marsupium for up to one month. The newly hatched first instar young look much like miniature versions of the adult. The number of instars in unknown, but there are thought to be at least 15 before maturity is reached. Most freshwater isopods have a lifespan of approximately one year.

Ecology

Freshwater isopods are primarily benthic and occur in the littoral zone of ponds, lakes, streams and springs, but they have been recorded at depths of as much as 55 m. They are the poorest swimmers of all freshwater crustaceans. In fact, they can barely swim at all and locomotion is usually restricted to a slow crawl. For this reason, they are exclusively associated with the substrate, or aquatic macrophytes where they live a somewhat secretive existence. Most species are scavengers, feeding primarily on dead and injured organisms, as well as green, decaying vegetation. As a result they form an important link in food chains by recycling dead and decaying material back into living tissue. Isopods have also been shown to be an important food item in the diet of many stream fishes.

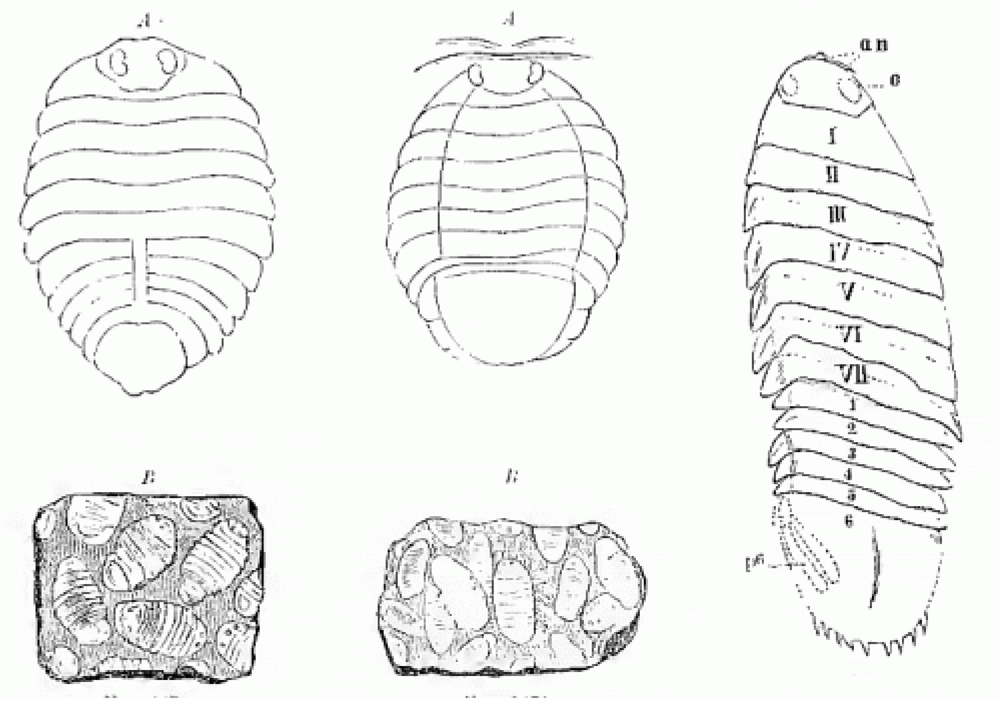
(Source: Biodiversity Institute of Ontario)

The tongue-eating isopod, *Cymothoa exigua*, lives in the mouth of the rose snapper (*Lutjanus guttatus*) and causes tongue stub and the floor of the fish's mouth and resembles the missing tongue! -- Encyclopedia of Earth - Crustacea

Fossil Record

Of the earlier fossils that have been referred to this group, *Oxyuropoda* from the Devonian of Ireland, has previously been considered the earliest Isopod. but seems to be a more primitive form; the similarity due to convergence.

Undoubted Isopods appear in Mesozoic, *Urda* from the Kimmeridgian Solenhofen lagestatte, has some peculiar characters in which it approaches the males of the Recent *Gnathia*, although differing in the large size of the eyes. *Cyclosphaeroma*, from the Jurassic (Great Oolite and Purbeck), resembles in general form some Recent members of the family SiDhaeromidae, as do also *Archaeoniscus* from the English Purbeck (Latest Jurassic/Earliest Cretaceous) and *Eosphaeroma* from the Eocene and Miocene. *Palaega* Cenomanian and Oligocene, resembles the Recent *Aega* and allied genera. *Proidotea* from the Oligocene of Romania, is closely allied to the Recent *Mesidotea* in the tribe Valvifera.. - Zittel & Eastman 1913, slightly modified MAK120517



Fossil isopods. Left, A, *Archaeoniscus brodei* Purbeck, Wiltshire. B, Fragment of matrix. Center *Eusphaeroma brougniarti*, Middle Oligocene, Butte de Chaumont, near Paris, B, Fragment of matrix, i; Right *Palaega scrobiculata*. Early Oligocene; Tyrol, Austria, Abbreviations: an. Antennae ; o, Eyes ; p^6, Uropod ; I-VII, Thoracic segments ; 1-6, Abdominal segments. Zittel & Eastman 1913.

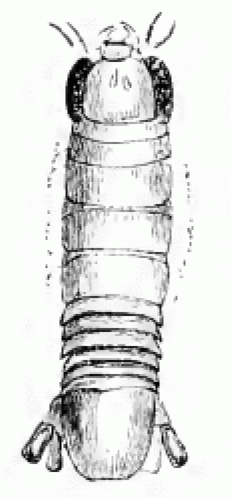
Descriptions

Isopoda

Range: From the Permian

Characters: Body usually broad and depressed. Carapace absent; first thoracic somite, rarely also the second, fused with the head. Abdomen short, the last somite almost always coalesced with the telson. Eyes sessile. Thoracic limbs without exopodites. Abdominal limbs lamellar, branchial - Zittel & Eastman 1913

Comments: Terrestrial pill bugs and their marine relatives. *Cyclosphaeroma* (Jurassic) and *Sphaeroma* (Recent) are representatives - Twenhofel & Shrock 1935



Urda rostrata Kunth, 1870, from the Lithographic Stone, Solenhofen, Bavaria (Early Tithonian). This species is distinguished by the large lateral eyes, frontally protruding mandibles, Image from Zittel & Eastman 1913

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From "Crustacea", Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment) 100219; revised 110529;

Malacostraca: Mysida

Abbreviated Dendrogram

```
CRUSTACEA
|--Phosphatocopida
`--+--Branchiopoda
   |--Remipedia
   `--+==Maxillopoda
     |--Ostracoda
     `--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              |   |--Pygocephalomorpha
              |   |--Mysida
              |  `--+--Amphipoda
              |     `--Isopoda
              `--Eucarida
```

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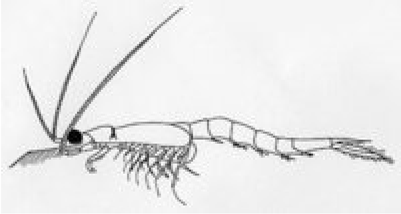
1. Mysida

Mysida

Introduction

Superficially, mysidans look much like small shrimp, and since they have a ventral marsupium, they are often called opossum shrimp. However, they are not true shrimp (order Decapoda), but belong to the order Mysida, a large, almost exclusively marine order. Mysidans are easily distinguished from decapods because they have 6 pairs of legs, while decapods have only 5. *Mysis relicta* is the most important and most abundant member of this order in North American freshwater systems, though it is seldom seen by humans except in the stomachs of fish! The name *relicta* refers to the fact that this species has a distribution which is restricted to areas of past marine inundation.



(Source: Biodiversity Institute of Ontario)

Morphology

As with many crustaceans, the first thoracic segment is fused with the head to form the cephalothorax in mysids. The head has two pairs of antennae and a pair of eyes. The eyes of *Mysis* are very large and are attached to stalks. The thorax has eight segments of which the first six are covered by carapace (segment 1 is fused with the head). The thorax of mature females bears oostegites, which project from the base of the thoracic legs. They are large and platelike, and form the marsupium, in which the eggs and developing young are protected. Because of this pouch-like structure, Mysis is sometimes called the opossum shrimp. Maxillipeds are found on the first two thoracic segments and are used to filter plankton and particulate matter from the water for food. The remaining six pairs of thoracic appendages are used for swimming, as well as for conveying water to the maxillipeds for filtering. The abdomen has 6 segments, of which the first five bear a pair of pleopods. On males, the fourth pleopod is long and specialized for mating. The last abdominal segment bears a pair of uropods that bear gravity-sensing statocysts that help the animal orient itself in the water column.

Reproduction

Mysis relicta reproduces sexually. Breeding occurs in the early autumn in Lake Ontario, but some individuals also reproduce in the spring. By contrast, studies in Michigan have identified four breeding seasons: mid-spring, late summer, mid-autumn and late winter. The difference may be due to differing water temperature in these two lakes. No one has ever observed mating, but males are thought to die shortly after copulation. Up to 40 developing embryos are carried by the female in its brood pouch, and pass through seven embryonic stages before their release after approximately five months. At this point, they are three to four millimetres long, and often migrate into shallow water. The entire life cycle of Mysis is completed in about two years.

Ecology

Mysis relicta occurs naturally in deep lakes in the glaciated regions of North America and Europe. It is usually absent from water less than 25 metres deep and its abundance increases with depth up to approximately 200 metres. During the day, *Mysis* remains very close to the lake bottom where it feeds on benthic organisms. At night, when it is closer to the surface, *Mysis* feeds on both zooplankton and phytoplankton.

(Source: Biodiversity Institute of Ontario)

Fisheries biologists have long recognised that *Mysis* forms an important part of the diet of many fishes. In an attempt to boost fish populations, *Mysis* has been introduced into many lakes in North America. However, interfering with a natural food web can be a dangerous business! In 1983, *Mysis* was stocked in Lake Tahoe. The assumption was that it would provide food for young salmon, speeding their growth. Instead, *Mysis* ate the zooplankton that all the smallest fish (too small to eat *Mysis*) had depended on. The young salmon starved! In 1970, before the introduction of *Mysis relicta*, 40,000 kokanee salmon spawned in Lake Tahoe. Afterward, the spawning population was reduced to a few hundred individuals – Encyclopedia of Earth -

Crustacea.

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From "Crustacea", Encyclopedia of Earth. Eds. Cutler J. Cleveland (Washington, D.C.: Environmental Information Coalition, National Council for Science and the Environment) 100219; revised 110529;

Malacostraca: Peracarida

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
               |--Syncarida
               |--Peracarida
               |   |--Pygocephalomorpha
               |   `--+---Mysida
               |      `--+--Amphipoda
               |         `--Isopoda
               `--Eucarida
                  `--DECAPODA
```

Contents

Taxa on This Page

1. Peracarida
2. Pygocephalomorpha X

Descriptions

Peracarida

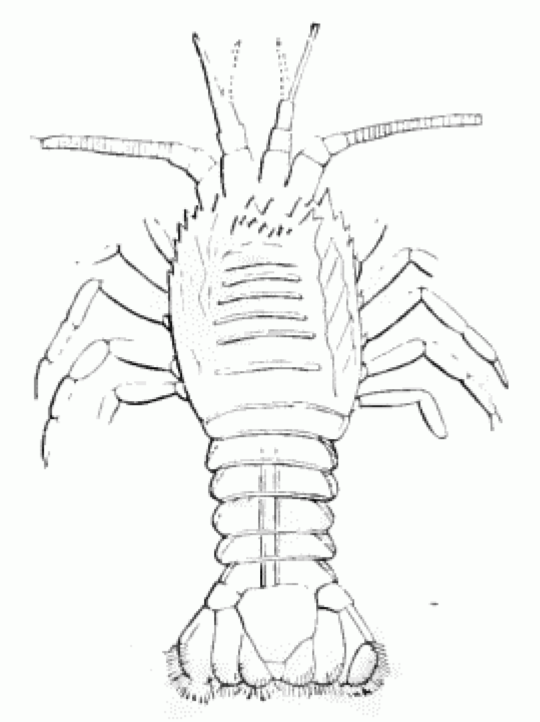
Range: From the Devonian

Phylogeny: Eumalacostraca **:** Syncarida + Eucarida + * **:** Pygocephalomorpha + Mysida + (Amphipoda + Isopoda)

Characters: Carapace, when present, leaving at least four of the thoracic somites distinct ; first thoracic somite always fused with the head. Eyes pedincidate or sessile. Oostegites attached to some or all of the thoracic limbs in the female, forming a brood pouch. - Zittel & Eastman 1913

Comments: Small, mainly marine forms in which the test, if present, consists of four free thoracic segments and a carapace - Twenhofel & Shrock 1935

Pygocephalomorpha



Range: Carboniferous to Permian.

Phylogeny: Peracarida **:** (Mysida + (Amphipoda + Isopoda)) + *

Comments: A number of Carboniferous forms, such as *Pygocephalus* (English Late Carboniferous), *Crangopsis* (Early Carboniferous of Scotland and Kentucky), *Anthrapalaemon* (illustrated) *Pseudogalathea*, *Tealliocaris*, and *Palaemysis* probably belong here. Part of the Paleozoic paraphyletic basal Eumalacostraca group Eocarida

Illustration: *Anthrapalaemon gracilis*, Carboniferous of Illinois, from Zittel & Eastman 1913

Links: life reconstruction of *Tealliocaris*

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Malacostraca: Phyllocarida

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              `--Eucarida
                 `--DECAPODA
```

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Malacostraca: Syncarida

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |  |--Anaspidacea
              |  `--Bathynellacea
              |--Peracarida
              `--Eucarida
                 `--DECAPODA
```

Contents

Taxa on This Page

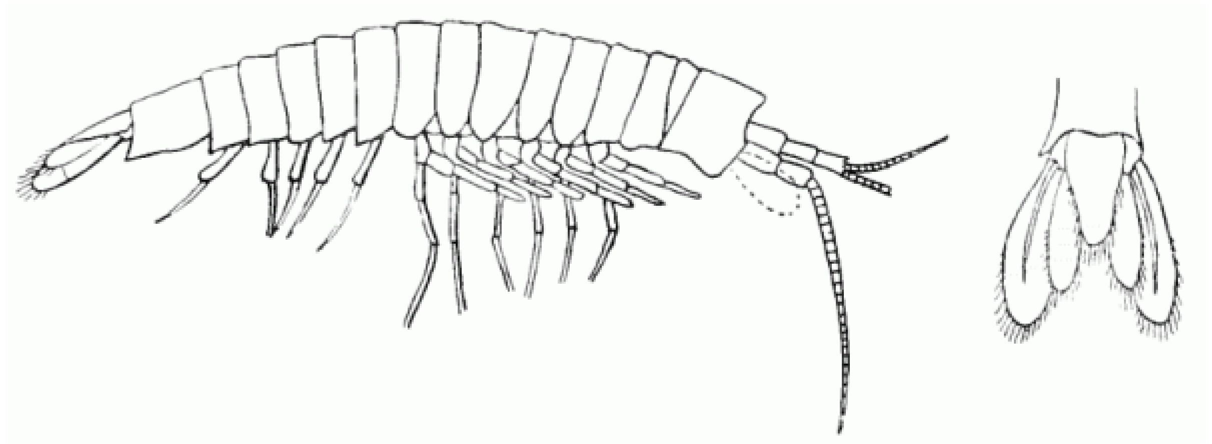
1. Syncarida
2. Anaspidacea
3. Bathynellacea

Introduction

The name Syncarida was applied by Packard to a group of Carboniferous and Permian Crustacea of obscure affinity. The discovery of living animals in South-East Australia shed new light on the subject, and reinvestigation of some of the fossils emphasised their close agreement with the Recent *Anaspides* and similar species .- Zittel & Eastman 1913

Species in the family Anaspididae vary from being strict stygobionts (only living underground) to species living in lakes, streams and moorland pools, and are found only in Tasmania. The family Koonungidae is found in Tasmania and the south-eastern part of the Australian mainland, where they live in the burrows made by crayfish and in caves. The families Psammaspididae and Stygocarididae are both restricted to caves, but Stygocarididae has a much wider distribution than the other families, with Parastygocaris having species in New Zealand and South America as well as Australia; two other genera in the family are endemic to South America, and one, Stygocarella, is endemic to New Zealand. - Wikipedia. The current geographic distribution indicates these are relics from an original pan-Gondwanan population. During the Carboniferous, these animals were common in freshwater envirnments in the northern continents. MAK120518

IFossil Record


Palaeocaris typus Meek and Worthen. Mazon Creek Lagerstätte (Westphalian D; Illinois), Moscovian age. Left, Restoration of body, omitting eyes, Right, Telson and uropods, Zittel & Eastman 1913.

Of the fossil genera, *Palaeocaris* Meek and Worthen (*Praeanaspides* Woodward) (right) from the Late Carboniferous of England and North America, is now the most completely known. It resembles *Anaspides* in general form, in the segmentation of the body, the pedunculated (stalked) eyes, the characters of antennules, antennae, and even of the minute mouth-parts, the exopodites of the thoracic legs, and the form of the tail-fan. The only important difference, apart from the delicate lamellar gills which may not be preserved in a fossil, is the presence in *Palaeocaris* of a wedge-shaped first thoracic somite, which, in *Anaspides*, is fused with the head. *Uronedes*, from the Early Permian of Saarbrücken (in Saarland in Germany), resembles *Palaeocaris* but has one of the anterior pairs of legs enlarged and armed with spines. *Acanthotelson* Meek and Worthen, and *Pleurocaris* Caiman, from the Late Carboniferous of Illinois and of England respectively, have the first thoracic somite fused with the head and may perhaps have no thoracic exopodites. These exopodites are also stated to be absent in *Gasocaris* Fritsch, from the Earliest Permian Gaskohle of Bohemia - Zittel & Eastman 1913

Descriptions

Syncarida

Range: From the Carboniferous

Phylogeny: Eumalacostraca **:** Eucarida + Peracarida + * **:** Anaspidacea + Bathynellacea

Characters: no carapace, the first thoracic segment is fused with the head. Twenhofel & Shrock 1935

Anaspidacea

Range: From the Carboniferous

Phylogeny: Syncarida **:** Bathynellacea + *

Characters: Carapace absent. First thoracic somite fused with the head, or defined therefrom by a groove. Eyes pednncidate or sessile. Thoracic legs typically toith exopodites ; no oostegites. Uropods and telson forming a tail-fan.

- Zittel & Eastman 1913

Comments: known from the Carboniferous and Permian. The only living represnetatives are a few Gondwanan fresh-water forms. *Palaeocaris* (Pennsylvanian) is representative of the fossil genera and *Anaspis* is the best known living genus. The carapace covers the cephalothorax and the eyes are stalked. - Twenhofel & Shrock 1935

Bathynellacea

Range: No fossil record

Phylogeny: Syncarida **:** Anaspidacea + *

Comments: Live interstitially in groundwater. Some species can tolerate low salt concentrations, and at least one African species is a thermophile, living in hot springs and tolerating temperatures up to 55 °CBathynellaceans are minute, blind, worm-like animals with short, weak legs, reaching a maximum size of 3.4 millimetres. They are found on every continent except Antarctica, although they are missing from some islands, including Fiji, New Caledonia and the Caribbean islands. There are two families, Bathynellidae and Parabathynellidae; a third family, "Leptobathynellidae", is considered a synonym of Parabathynellidae. - Wikipedia

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Malacostraca: Classification

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              `--Eucarida
                 `--DECAPODA
```

Contents

The following very provisional classification is copied from Wikipedia, and does not include many extinct taxa

---

Superclass Crustacea
  Class Malacostraca Latreille, 1802
    Subclass Phyllocarida Packard, 1879
        Order † Archaeostraca Claus 1888
        Order † Hoplostraca Schram, 1973
        Order Leptostraca Claus, 1880
    Subclass Hoplocarida Calman, 1904
        Order † Aeschronectida Schram, 1969
        Order † Archaeostomatopoda Schram, 1969
        Order Stomatopoda Latreille, 1817
    Subclass Eumalacostraca Grobben, 1892
      Superorder Syncarida Packard, 1885
        Order † Palaeocaridacea Brooks, 1979
        Order Bathynellacea Chappuis, 1915
        Order Anaspidacea Calman, 1904

Superorder Peracarida Calman, 1904
  - Order Pygocephalomorpha (shrimp-like basal eumalacastruca - Carboniferous to Permian)
  - Order Spelaeogriphacea Gordon, 1957
  - Order Thermosbaenacea Monod, 1927
  - Order Lophogastrida Sars, 1870
  - Order Mysida Haworth, 1825 (= Mysidacea)
  - Order Mictacea Bowman et al., 1985
  - Order Amphipoda Latreille, 1816 (sand hoppers and sand fleas. Tertiary to Recent.)
  - Order Isopoda Latreille, 1817 (Terrestrial wood lice and pill bugs and their marine relatives; Carboniferous - Recent.)
  - Order Tanaidacea Dana, 1849
  - Order Cumacea Krøyer, 1846

Superorder Eucarida Calman, 1904
  - Order Euphausiacea Dana, 1852
  - Order Amphionidacea Williamson, 1973
  - Order Decapoda Latreille, 1802 (see next unit)

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Malacostraca: Dendrogram

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              `--Eucarida
                 `--DECAPODA
```

Contents

This is a very rough holding page

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |  |--Anaspidacea
              |  `--Bathynellacea
              |--Peracarida
              |   |--Pygocephalomorpha
              |   |--Mysida
              |   `--+--Amphipoda
              |      `--Isopoda
              `--Eucarida
                 |--Euphausiacea
                 |--Amphionidacea
                 `--DECAPODA
```

Malacostraca: References

Abbreviated Dendrogram

```
CRUSTACEA
|
`--MALACOSTRACA
        |--Phyllocarida
        `--+--Hoplocarida
           `--Eumalacostraca
              |--Syncarida
              |--Peracarida
              `--Eucarida
                 `--DECAPODA
```

Contents

Eastman C. R. *Text Book of Paleontology* edited by C. R. Eastman adapted from German of K. A. von Zittel, 2nd edition revised and enlarged by the editor in collaboration with the following named specialists: R.S. Bassler, W. H. Dall, C. D. Walcott. Volume 1. MacMillan & Co., London. xii + 839 pp. Internet Archive

William Twenhofel and Robert R. Shrock 1935, *Invertebrate Paleontology*, McGraw Hill Book Co. New York & London, posted at the Internet Archive as public domain.

Palaeos | DECAPODA
ARTHROPODA | DECAPODA

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Unit Back: Malacostraca | Clade Down: None | Dendrogram | References | Unit Next: Hexapoda

Decapoda

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinura
           `--+--Anomura
              `--Brachyura
```

Contents

The Atlantic Ghost Crab, *Ocypode quadrata* (Decapoda: Pleocyemata: Reptantia: Eureptantia: Meiura: Brachyura: Eubrachyura: Thoracotremata: Ocypodidae) on Martinique, Antilles
Photo by Patrick Verdier, via Wikipedia.

The most successful of all the malacostraca, the Decapoda ("ten-footed") appeared during the Devonian but remained insignificant until the start of the Mesozoic, when they underwent a tremendous evolutionary radiation, perhaps in response to the extinction of the Palaeozoic shrimp-like malacostractans at the end of the Permian.

The group includes all the most familiar animals we ordinarily think of as crustaceans - prawns, shrimp, crayfish, lobsters, and crabs, There are thought to be around 15,000 extant species in some 2,700 genera. Nearly half of these species are crabs, with the prawns or shrimp (Dendrobranchiata) and a group called the Anomura (including hermit crabs, porcelain crabs, squat lobsters, and others), making up the bulk of the remainder. While some decapods are tiny, others such as ordinary lobsters, the cocconut crab, and the Japanese spider crabs are easily the largest living arthropods, although still exceeded in size by Paleozoic eurypterids and arthropleurids. Approximately 3,300 fossil decapod species are know, although this obviously would only be a tiny fraction of all those that ever lived. - modified from Wikipedia, MAK120530

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Decapoda

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
         |--Eryonoidea
         `--Eureptantia
            |--Astacidea
            |--Palinuroidea
            `--+--Anomura
               `--Brachyura
```

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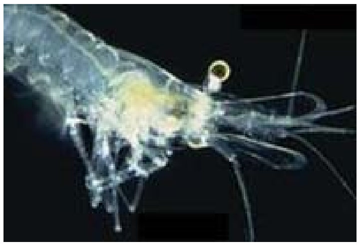
1. Decapoda

Southern rock lobster, *Jasus edwardsii*, (Decapoda: Pleocyemata: Reptantia:

Eureptantia: Palinuroidea: Palinuridae) at Southern Encounter Aquarium, Christchurch, New Zealand
Photo by Stemonitis, Creative Commons Attribution Share Alike, GNU Free Documentation License, via Wikipedia.

Introduction


(Source: Biodiversity Institute of Ontario)

The Decapoda are one of the most familiar groups of crustaceans, as well as the most succesful and diverse of all the extant orders. They include such well-known marine species as lobsters, crabs, and shrimp. While most are marine, the crayfish are a characteristic freshwater group. Several groups of mostly tropical shrimp have also entered freshwater. Some species of crab have addapted to an almost terrestrial existence.

The Order Decapods has traditionally been divided into two suborders.

The **Natantia** ("swimmers") or shrimps are a paraphyletic assemblage defined by abdominal appendages well developed for swimming. In other words, all deacpods were originally shrimp like forms

In the **Reptantia** ("walkers") include crabs, lobsters and crayfish. Here the abdominal appendages are small, whilst the first pair of legs are usually enlarged and provided with pincers.

Current classifications however are cladistically based and so the paraphyletic Natantia is rejected in favour of a stepwise series of taxa leading to the monophyletic Reptantia. On this basis, taxonomic classifications now divide the Order Decapoda into the two Suborders Dendrobranchiata for the largest shrimp clade, and Pleocyemata for all other decapods. The Pleocyemata are in turn divided into half a dozen infra-orders.. MAK120523

Morphology

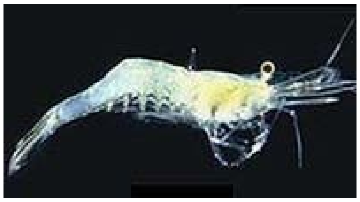
Decapod morphology may be illustrated by that of the crayfish. The cephalothorax has a pair of stalked eyes and 12 pairs of appendages. The first and second pairs of antennae are used as sense organs to probe the substrate. The base of the first antennae houses a statocyst which is used for balance. The next five pairs of appendages on the cephalothorax are used in food handling, while the last five pairs of appendages are the walking legs. The first 2 or 3 pairs of these legs are clawed and are used for food handling, defence and digging into the substrate. Their abdomen bears pleopods (swimming legs) on the first five segments. Decapods are sexually dimorphic. The first two pleopods of males are modified to transfer sperm to the female, while females have a calcified area between the fourth pair of periopods used to receive the male's spermatophore during copulation. The typical tail fan is composed of expanded uropods on the end of the abdomen.


(Source: Biodiversity Institute of Ontario)

Decapods have a breaking point at the base of each leg. If they are grabbed or agitated, the muscles contract, severing the leg at this point. If the leg is broken at this point, it can be regenerated later. - Encyclopedia of Earth - Crustacea - Creative Commons

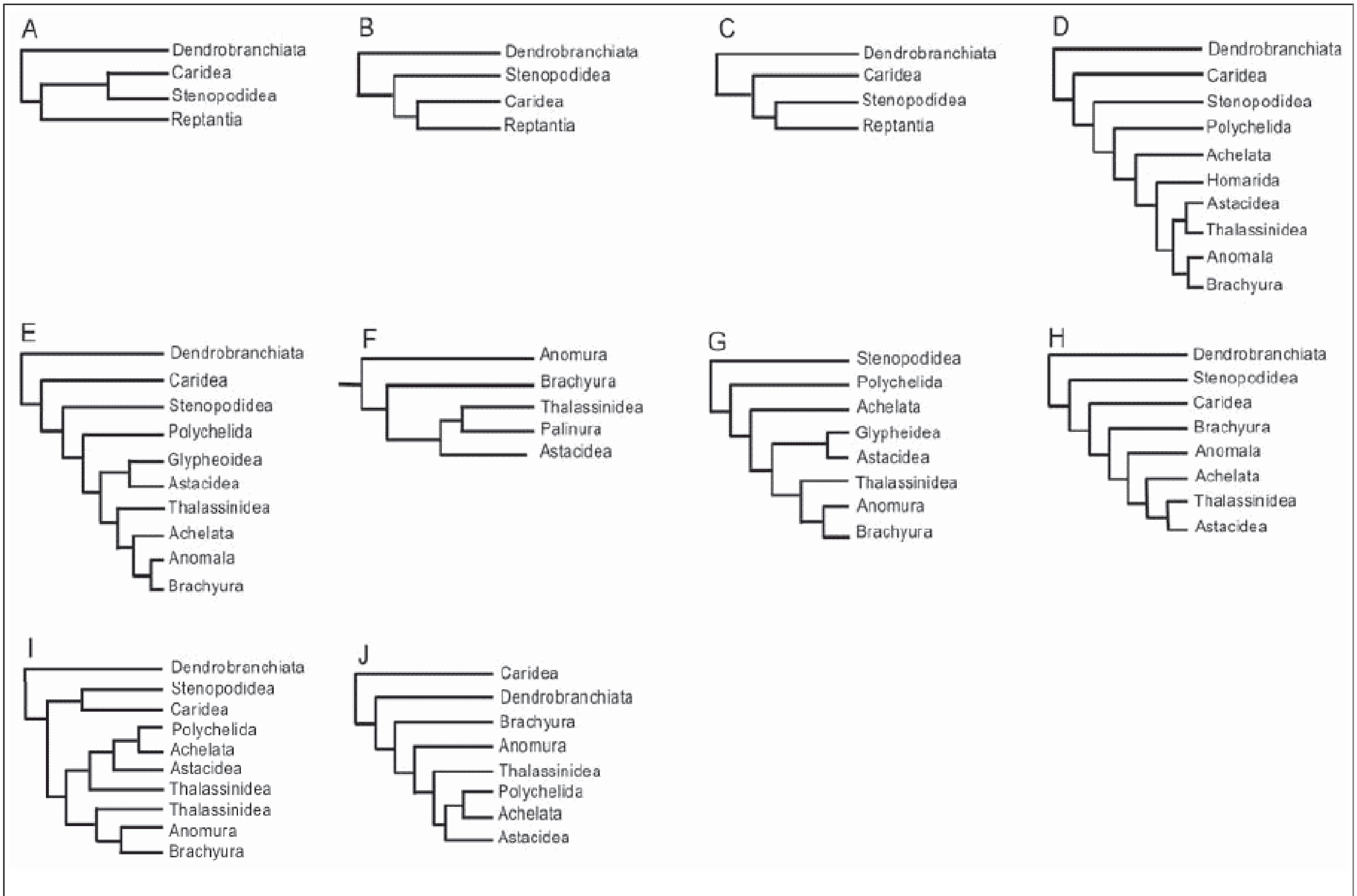
Ecology

Decapods are enormously diverse ecologically, occuring throughout the world's oceans and freshwaters, from surface plankron to abyssal depths. Some species even live on land, including various terrestrial crabs. The decapods include a wide variety of herbivores, omnivores, scavengers, and predators. In temperate freshwaters, decapods are most commonly encountered along rocky or weedy shorelines of quiet bays in water less than 2 m deep, though they occur in water up to 30 m deep. Crayfish can be burrowers, benthic or semi-pelagic. They are mainly nocturnal foragers; their diet consists mainly of macrophytes and debris, but they also eat small insects and crustaceans as well as dead animal matter. Decapods are important prey items for many fish, waterfowl, and aquatic mammals. - Encyclopedia of Earth - Crustacea - Creative Commons


(Source: Biodiversity Institute of Ontario)

Phylogenetic conundrums

As with the Malacostraca as a whole, there is no agreement on decapod phylogenetic relationships (the same could be said for the various groups of decapods, such as Brachyura and Anomura). The following diagram, from Bracken et al 2009 illustrates this by comparing various phylogenies:



Hypotheses of higher-level decapod relationships, using different methodologies.
Morphological similarity: **A**: Burkenroad (1963, 1981); **B**: Christoffersen (1988); **C**: Abele & Felgenhauer 1986.
Morphological cladistic analyses **D**: Scholtz & Richter 1995; E: Dixon et al 2003
Molecular phylogenetic analyses: **F**: Crandall et al. (2000); **H**, Porter et al 2005; **I**: Tsang et al. 2008; **J**: Toon et al. (2009).
Total evidence method that combines cladistic morphology and molecules:).;**G**: Ahyong & O'Meally 2004; -
Diagram and caption from Bracken et al 2009 fig 1

Even just considering the two morphological-cladistic analyses, the only clades that are agreed upon are Pleocyemata, Reptantia (the lobster-like forms and the crabs) , Eureptantia , and Meiura (the crabs and crab-like forms, which here form a monophyletic clade). The molecular analyses are for the most part too variable to be of any use in forming any consenus, apart from the Pleocyemata (hence Dendrobranchiata as a basal taxon (or near basal in one analysis) and Reptantia. Only two molecular analyses out of six (the five in the above diagram plus Bracken et al 2009) recognise the Meiura and only one the Eureptantia (perhaps because the authors also incorporate morphological data in a total evidence approach).

Methodological considerations and false signal artifacts (such as long branch attraction) aside, lack of resolution among molecular analyses might reasonably be the result of a sudden adaptive radiation. This is why it may be impossible to ever determine the exact sequence of cladogensis of the major phyla from the Cambrian explosion, or groups of Placental mammals at the start of the Cenozoic. If decapods underwent a dramatic evolutionary radsiation at the start of the Triassic, we would expect the same situation here regarding the Reptantia. While convergences and reversals - a phenomenon common in the animal kingdom - may explain the lack of agreement between the two morphological studies. For this reason, we have adopted a low resolation phylogeny, at least until future studies verify their results - MAK120528

Descriptions

Decapoda Latreille, 1802

Range: From the Devonian

Phylogeny: Eucarida **:** Euphausiacea + Amphionidacea + * **:** Dendrobranchiata + Pleocyemata

Characters:. Synapomorphies (from Ax 2000): Body divided into cephalothorax and pleon: carapace covering and fused dorsally with first eight thoracomeres, reaching laterally down to leg bases and enclosing gill cavity; thoracopods with four gills and extra epipodite for gill cleaning; thoracopods 1 and 2 transformed into maxillipeds; scaphognathite (large lobe-shaped exopodite of second maxilla) present, used for pumping water through gill cavity. - CKT.

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Decapoda: Anomura

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--+--Eureptantia
           |--Palinuroidea
           `--Meiura
              |--Anomura
              |  |--Hippoidea
              |  `--Aeglidae
              |      |--Galatheoidea
              |      |--Kiwa
              |      |--Lomis
              |      `--+--Paguroidea
              |         `--Lithodoidea
              `--Brachyura
```

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1. Aeglidae
2. Anomura
3. Galatheoidea
4. Hippoidea
5. *Kiwa*
6. Lithodoidea
7. *Lomis*
8. Paguroidea

Hermit crab
Photo by Stephen Gibson, Creative Commons Attribution.

The Anomura is a group that includes various organisms commonly called crabs, such as hermit crabs, stone crabs, mole crabs, and half crabs, that are not actually true crabs (Brachyura) . After the tryue crabs, they are the most speciose decapod group.

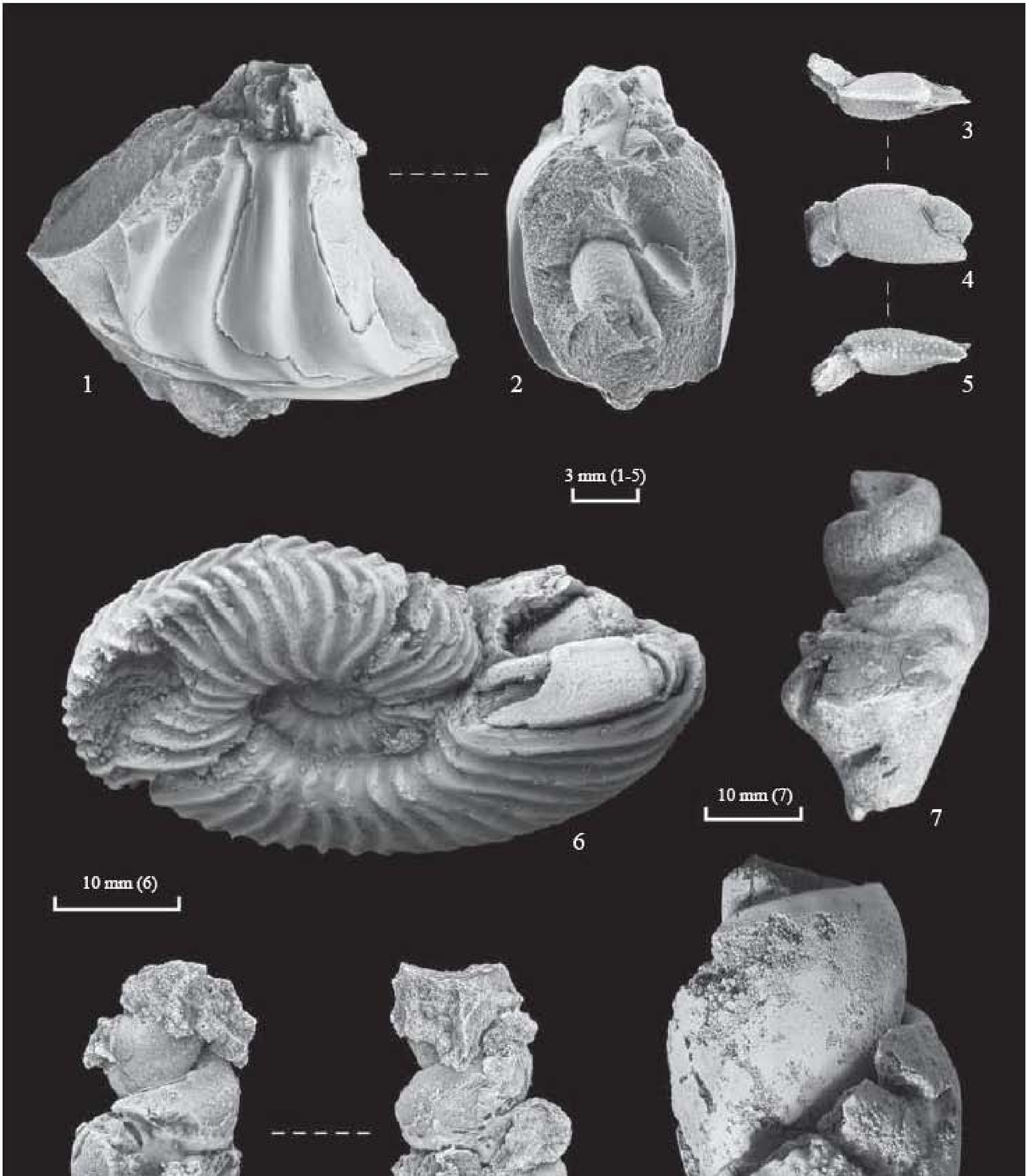
A morphologically diverse group, some anomurans are little different from lobsters, whereas others are very crab like in appearance. The various lineages independently evolved crab-like charcetristics. The differ from true crabs in that the abdomen is not as small. In true crabs the abdomen is tiny and folded under the thorax, to shift the center of gravity forward and improive mobility. In crab-like anomurans the abdomen may be soft or bent upon itself with reduced side-plates and tail-fan (Zittel & Eastman 1913) but it is still reasonably large, and hence anomurans are slower moving than their fast side-scuttling cousins.

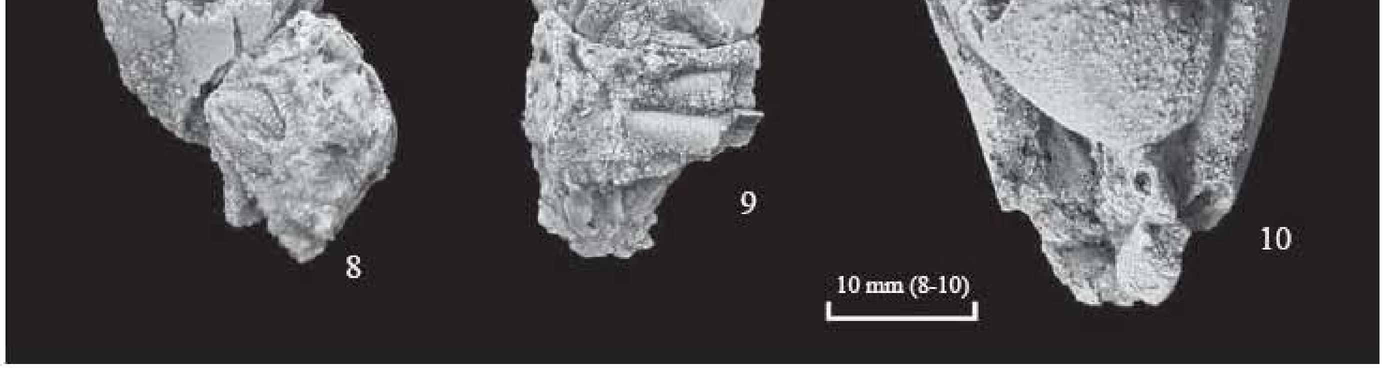
The only two comprehensive cladistic analyses of the decapoda (Scholtz & Richter 1995 and Dixon et al 2003) both place anomurans as the sister group to the true crabs, the two together being known as the Meiura. Molecular analysis doesn't support this, and instead have the two groups popping up all over the Reptantian family tree without rhyme or reason (see comparison of cladograms). It seems likely that the anomura and the brachyura diverged very soon after evolving from a lobster-like ancestor; in too short a time scale to be picked up by molecular phylogeny.

As for the relations of the Anomuran subgroups (which themselves diverged somewhat later as they are not jumbled in molecular phylogeny with other decapod clades) there is no real consensus. There isn't even agreement over what the group as a whole should be called. Cladists tend to prefer Anomala, because the original definition of Anomura is parphyletic or polyphykletic as it includes the Thalassinida (which may or may not still be related). The majority of zoologists still use the Anomura, which has taxonomic priority as the older term. We have already given our opinion why excluding groups from a taxon is no reason to change the taxon's name, if the original type species is still included or the original definition still stands. For this reason the older and more widely used name of Anomura is here retained. MAK120529

Fossil Record

The Anomura are rare as fossils, although that is now changing. The **Galatheidea** (porcellan crabs) have generally been represented only by chelae (originally known only from the late Cretaceous of Denmark, and referred to the Recent *Galathea*). However four genera in each of the superfamilies Galatheoidea and Paguroidea were cited by Glaessner 1969 (*Treatise on Invertebrate Palaeontology*) as occurring as early as the Jurassic, while a review by Schweitzer & Feldmann (2000) has eight galatheoid genera with fossil records dating back to the Middle or Late Jurassic. The freshwater **Aeglidae**, is now known from Late Cretaceous marine rocks in New Zealand, suggesting that its freshwater adaption might be a recent development, and then discovered in the Early Cretaceous of Mexico, implying much greater distribution during the Mesozoic than at present. The **Hippidea**, which previously lacked a fossil record, have been reported from the Middle and Late Eocene. The **Paguroidea**, including the Hermit-crabs and their allies, was at first very doubtfully represented in the Eocene of Hungary by chelae referred to the Recent *Pagurus*. For a long time they were known in the fossil record primarily from isolated claws (chelipeds), which is not sufficent for them to be placed phylogenetically. A few descriptions of *in situ* gastropod shell-inhabiting hermit crabs are known from the Late Cretaceous, Oligocene, and Miocene. But a perfectly preserved Early Cretaceous hermit crab found occupying the shell of an ammonite cephalopod Fraaije (2003), apparently a diogenid from the larger left cheliped. might explain the rarity or absence of hermit crabs in gastropod shells of Jurassic and Early Cretaceous ages, if paleontologists have focused their attentions on the wrong class of molluscs. Since then, more discoveries of hermit crabs occupying ammonite and gastropod shells have been made (Jagt et al 2006, and see graphic, below). Even though hermit crabs occupied Mesozoic gastropod shells, the shift in prefernce from ammonites to gastropod shells was the logical conseque of the former's extinction at the end Mesozoic. Bakel et al. (2008) reported the discovery of a series of Jurassic age paguroid carapaces, including two that appear assignable to families of the Pylochelidae. - (Zittel & Eastman 1913, Lemaitre & McLaughlin 2009 MAK120528





Figures 1-10. *In situ* hermit crabs (Paguroidea) from the Lower Jurassic, Upper Cretaceous, Eocene and Miocene of northwest Europe and Russia. All specimens were whitened with ammonium chloride prior to photography. Figures 1-5: '*Palaeopagurus*' sp. (MB.A 1113), in fragmentary body chamber of *Pleuroceras solare* from the lower *spinatum* Zone (*apyrenum* Subzone; Lias δ_{2a}, upper Pliensbachian) of Banz (Franken, southern Germany); 1, 2. specimen prior to preparation; note imprint of left cheliped in upper right-hand corner; 3-5: right cheliped in various views (compare with Figure 6). Figure 6: *Palaeopagurus vandenengeli* Fraaije, 2003, holotype (MAB k.0012), from the middle Hauterivian, Speeton Clay Bed C4, at Speeton (Yorkshire, England); oblique view of simbirskitine ammonite conch to illustrate the large left cheliped (compare with Figures 2-5). Figure 7: Indeterminate paguroid (IRScNB, Ubaghs Colln, IG 6521) within last whorl of a ?volutid gastropod (internal mould), from the Kunrade Limestone facies (Maastricht Formation, upper Maastrichtian) of Kunrade (southern Limburg, the Netherlands), revealing shield and some appendages; the chelipeds are just visible to the left of the shield. Figures 8, 9: *Pagurus* sp. (aff. *bernhardus* Linné, 1758) (MAB k.2400), in an indeterminate (?volutid) gastropod (internal mould), consisting of right cheliped and fragmentary pereiopods, from the Miocene of Liessel (Noord-Brabant, the Netherlands). Figure 10: Indeterminate paguroid (= *Pagurus damesii* Noetling, 1885, *nomen dubium*) (MB.A 1114), from the Middle Eocene (Bernsteinformation, Zone A1) of the Kaliningrad area (Samland Peninsula, Russia; formerly Palmnicken, East Prussia). Note the stout and heavily tuberculate chelipeds, with associated remains of pereiopods.

Fossil hermit crabs, Jagt et al 2006 - original url of graphic

Carcinisation

The following text and image is copied verbatim from Wikipedia. Owing to limitations of time, the content has not yet been formatted or hyperlinked MAK120528

In evolutionary biology, carcinisation (or carcinization) is a hypothesised process whereby a crustacean evolves into a crab-like form from a non-crab-like form. The term was introduced by L. A. Borradaile, who described it as "one of the many attempts of Nature to evolve a crab".[1]

Carcinisation is believed to have occurred independently in at least five groups of decapod crustaceans, most notably king crabs, which most scientists believe evolved from hermit crab ancestors. The other examples are the family Porcellanidae, or porcelain crabs (these are closely related to squat lobsters), the hairy stone crab *Lomis hirta*, the coconut crab *Birgus latro*, and true crabs.[2] The example of king crabs (family Lithodidae) evolving from hermit crabs has been particularly well studied and, although some doubt this theory, there is considerable evidence in its favour. For example: most hermit crabs are asymmetrical, so that they fit well into spiral snail shells; the abdomens of king crabs, even though they do not use snail shells for shelter, are also asymmetrical.[3][4][5][6]

An exceptional form of carcinisation, termed "hypercarcinisation", is seen in the porcelain crab *Allopetrolisthes spinifrons*.[7] In addition to the shortened body form, A. spinifrons also shows similar sexual dimorphism to that seen in true crabs, where males have a reduced pleon compared to females.[7]

Image: The porcelain crab *Neopetrolisthes* resembles a crab, but is more closely related to squat lobsters and hermit crabs.

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Phylogeny

While there is now agreement that the Anomura, minus the Thalassinidea, constitute a monophyletic group, composition and relationships of the various lineages within this clade remain highly controversy. Several phylogenetic studies based on molecular data are particularily contradictory. (Lemaitre & McLaughlin 2009) implying either that the various groups evolved during a short period, but some time after the initial early Triassic radiation of the repantian decapods, or that the various taxa are insufficiently studied, artifacts haven't been corrected, and so on.

The following dendrogram is modified and updated (Lemaitre & McLaughlin 2009), from Christopher Taylor - Variety of LIfe. Not all groups are included MAK120530

```
    Anomura (= Anomala, Anomalia, Anomaux)
    |--Hippoidea B02
    |  |--Albuneidae B02
    |  |  |--Lepidopinae B02
    |  |  `--Albuneinae B02
    |  |--Hippidae B02
    |  |  |--Hippa Fabricius 1787 [incl. Remipes Latreille 1806] B01
    |  |  `--Emerita Scopoli 1777 B02
    |  `--Blepharipodidae B02
    |     |--Lophomastix Benedict 1904 [=Lophmastix (l. c.), Lophomastrix (l. c.), Lophopmastrix (l.
c.)] B02
    |     `--Blepharipoda Randall 1840  B02
    `--+--Paguridea ML01
       |  |--Paguroidea ML01
       |  `--Coenobitoidea ML01
       |--Galatheoidea CA04
       |  |--Chirostylidae MD01
       |  |--Porcellanidae MD01
       |  `--Galatheidae CA04
       `--+--Aegla Leach 1821 H86 [Aeglidae MD01]
          `--Lomis [Lomidae, Lomisidae, Lomisoidea, Lomoidea] DAS03
```

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Descriptions

Anomura MacLeay, 1838.

Synonym: Anomala De Haan, 1839

Range: From the Jurassic

Phylogeny: *Either* (if (if *Platykotta* and *Eocarcinus* are basal or stem Anomura not related to crabs, in which case the present taxon becomes Crown Anomura)

Stem Anomura **:** *Platykotta* + (*Eocarcinus* + * **:** Hippoidea + (Aeglidae + Galatheoidea + *Kiwa* + *Lomis* + (Paguroidea + Lithodoidea))))
or (if *Platykotta* and *Eocarcinus* are basal Meiura rather than basal Anomura) Meiura **:** *Platykotta* + (*Eocarcinus* + (Brachyura + * **:** Hippoidea + (Aeglidae + Galatheoidea + *Kiwa* + *Lomis* + (Paguroidea + Lithodoidea)))

Characters:. Synapomorphies (from Dixon et al. 2003): Basal articles of second antenna fitting into a notch in the carapace; coxosternal joints of thoracopods reversed; cheliped rotated so that dactylus is horizontal; first pleopod of female absent. - CKT.

Comments: [1] from the Greek, *anomoios* unlike, different and *oura*, tail, referring to the fact taht these animals have a different tail (more properly abdomen) to the true crabs.

[2] In terms of priority, Anomura just pips Anomala at the post (1938 to 1839) (ref)

[3] Alternative phylogenies are used here owing to uncertainty over status of the two basal forms *Platykotta* and *Eocarcinus*. See Förster, 1985 and Krobicki & Zaton 2008 for the thesis that they are transitional between Triassic Pemphicidae and Jurassic Prosopid and Homolodromioid crabs (the most primitive crab lineages). See Feldmann & Schweitzer 2010 and Chablais et al 2011 for the thesis that they are basal Anomura and not in any way related to true crabs.

Thumbnail images for the following taxa are from the Wikipedia Anomura page MAK120530

Hippoidea Latreille, 1825

Range: From the Late Cretaceous; ghost lineage suggests at least a Jurassic origin

Phylogeny: Anomura **:** (Aeglidae + Galatheoidea + *Kiwa* + *Lomis* + (Paguroidea + Lithodoidea)) + *)

Comments: sand crabs or mole crabs, remarkably convergent with raninid true crabs. In some recent phylogenetic analyses (Ahyong & O'Meally 2004; Porter et al 2005; Tsang et al. 2008) they are the most basal extant anomuran taxon

Image and link; Wikipedia

Galatheoidea Samouelle, 1819

Range: From the Jurassic

Phylogeny: Anomura **:** Hippoidea + (Aeglidae + *Kiwa* + *Lomis* + (Paguroidea + Lithodoidea) + *)

Comments: The porcelain crabs, squat lobsters, and their relatives

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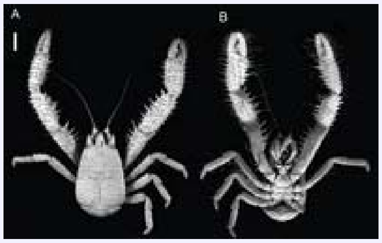

Kiwa

Range: No known fossils

Phylogeny: Anomura **:** Hippoidea + (Aeglidae + Galatheoidea + *Lomis* + (Paguroidea + Lithodoidea) + *)

Comments: a small but higher specialised group of marine decapods living at deep-sea hydrothermal vents and cold seeps. The animals are commonly referred to as "yeti lobsters" or "yeti crabs" (Wikipedia). Several species of the single genus are placed in the monotypal family Kiwaidae. This was originally placed in the Galatheoidea, but then elevated to its own superfamily rank (Kiwaoidea), although not all accepted this (Lemaitre & McLaughlin 2009)

Aeglidae

Range: From the Cretaceous; Recent restricted to of South America

Phylogeny: Anomura **:** Hippoidea + (Galatheoidea + *Kiwa* + *Lomis* + (Paguroidea + Lithodoidea) + *)

Comments: secondarily freshwater lobster-like forms currently restricted to South America, in the Cretaceous they may have had a Gondwana-wide distribution as fossils are known also from New Zealand and as far north as Mexico. Relations with other anomuran groups are uncertain; they have previously been included under the Galatheoidea but are now placed in their own superfamily. Several studies (e.g. Ahyong & O'Meally 2004, Porter et al 2005) place them as sister group to the monophyletic Lomisidae.

Lomis hirta (Lamarck, 1818)

Range: Recent of southern Australia

Phylogeny: Anomura **:** Hippoidea + (Aeglidae + Galatheoidea + *Kiwa* + (Paguroidea + Lithodoidea) + *)

Comments: The hairy stone crab, *Lomis hirta* (monotypal family Lomisidae and superfamily Lomisoidea Bouvier, 1895; the name Lomidae is incorrect), is a slow-moving crab-like animal covered in brown hair. Its relations to other anomuran groups are unclear, but represents a separate case of carcinisation - Wikipedia.

Paguroidea Latreille, 1802

Range: From the Jurassic

Phylogeny: Anomura **:** Hippoidea + (Aeglidae + Galatheoidea + *Kiwa* + *Lomis* + (Lithodoidea + *)

Comments: The hermit crabs, a familiar group of decapod crustaceans, with over a thousand extant species. They occupy empty gastropod shells which protect the sSoft, coiled, asymmetrical abdomen. Mesozoic forms seem to have preferred ammonites, which have a planospiral shell, and so they would have had symmetrical abdomens.

Lithodoidea

Range: From the Jurassic

Phylogeny: Anomura **:** Hippoidea + (Aeglidae + Galatheoidea + *Kiwa* + *Lomis* + (Paguroidea + *))

Comments: King crabs, somewhat spider-crab-like anomurans thought to have evolved from hermit crabs, and previously included with them, but now placed in a separate superfamily, Lithodoidea

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Decapoda: Astacidea

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           `--+--Anomura
              `--Brachyura
```

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1. Astacidea

Astacidea is a group of decapod crustaceans including lobsters, crayfish and their close relatives. It comprises five extant superfamilies, two of crayfish (Astacoidea and Parastacoidea), one of true lobsters (Nephropoidea), one of reef lobsters (the genus Enoplometopus), and a number of fossil taxa (De Grave et al 2009). As of 2009, the group contains 782 recognised species, over 400 of which are in the family Cambaridae. - Wikipedia

Taxonomy

```
Enoplometopoidea (reef lobsters)
        Enoplometopidae
        Uncinidae †
Nephropoidea (true lobsters)
        Chilenophoberidae †
        Nephropidae
        Protastacidae †
        Stenochiridae †
Astacoidea (freshwater crayfish)
        Astacidae
```

```
        Cambaridae
        Cricoidoscelosidae †
Parastacoidea (freshwater crayfish)
        Parastacidae
```

Introduction

Freshwater crayfishes are taxonomically distributed among three families; two Northern Hemisphere families, Astacidae and Cambaridae and one Southern Hemisphere family, Parastacidae. There are two centers of species diversity for freshwater crayfishes. The first is located in the Southeastern United States where some 80% of the cambarid species can be found. The second center of diversity is in Victoria, Australia; housing a large proportion of the parastacid species. Freshwater crayfishes naturally occur on all of the continents except Africa (Figure 1). The Astacidae are distributed West of the Rocky Mountains in the Northwest United States into British Columbia, Canada and in Europe. The Cambaridae are found in the Eastern United States and south through Mexico. The Parastacidae are distributed in Australia, New Zealand, South America, and Madagascar.- KAC & JWF, ToL CC

Development

Hatching in Canadian crayfish occurs in two to twenty weeks. After they hatch, the larvae cling to the stalk still attached to their mother. In a few days they moult and lose the stalked connection with their mother, but they remain attached to her swimming legs with their chelae for up to two weeks. Third instar larvae begin to make excursions away from their mother and eventually leave permanently. Maturity is reached in six to ten moults. After their last juvenile moult, males enter their sexual form with larger chela, increased length, sharper spines and increased sclerotization. This form seeks out females and is ready to do battle with other males. At the end of the mating season, males moult back to a form that resembles the juvenile stage. - EoE - CC

Discussion of Phylogenetic Relationships

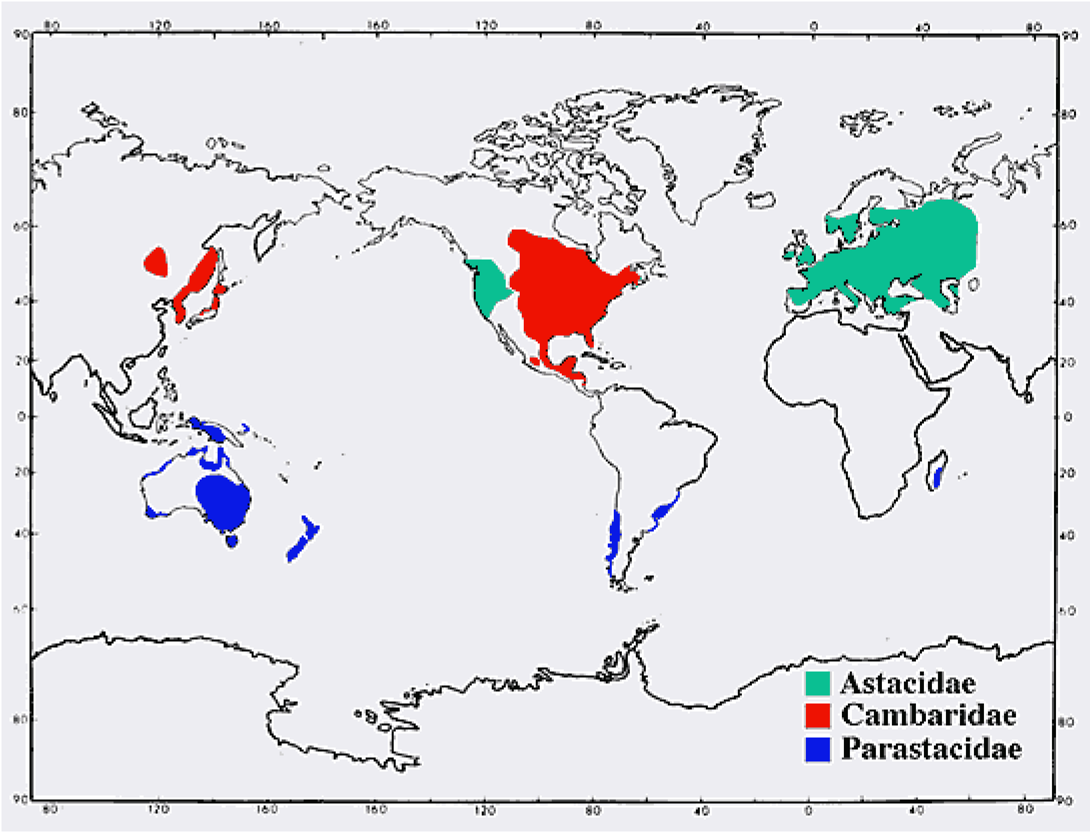

Figure 1. World distributions of the three crayfish families. - KAC & JWF, ToL CC

The phylogenetic relationships among the freshwater crayfish families and their relationships to lobster-like ancestors has been of considerable debate for at least 100 years. Two alternative hypotheses have been proposed for the origins of crayfishes. The first supposes a diphyletic origin of astacoids and parastacoids suggesting independent invasion of the freshwater habitat (Huxley, 1880). This idea is supported by the two centers of diversity in the northern and southern hemispheres and by a number of morphological features (Hobbs, 1974). However, Ortmann (1902) argued for a monophyletic origin of the crayfishes. This position has recently been supported by sperm ultrastructure characteristics (Jamieson, 1991) and by embryonic characters (Scholtz, 1993). Because of this ongoing debate, the positioning of Parastacidae is shown as unresolved.- KAC & JWF, ToL CC

Quoting Schram & Dixon 2004: "The monophyly of the freshwater crayfish, though previously doubted, is now universally accepted (Dixon et al 2003). If there was a single origin for the crayfish and they cannot survive in salt water, then they must have diverged before the continents they now inhabit had separated....The last time in which these continents were conjoined was in the Triassic, before Fenno-Scandia (Eurasia) separated from Greenland (North America) with the opening of the Atlantic Ocean (Scotese, 1997).". A Triassic origin also fits in witha post-Paleozoic evolutionary radiation, as evidenced in the fossil record. This means that the rare Paleozoic decapods are more likely to be either stem taxa or represent a simple Devonian bifurcation of a few early lineages such as Dendrobranchiata, Pleocyemata, and Reptantia MAK120527

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- KAC & JWF, ToL CC

Descriptions

Range: From the Jurassic

Phylogeny: Astacura **:** Glypheoidea + *

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Page MAK120531

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KAC & JWF = Keith A. Crandall and James W. Fetzner, Jr.. , 2010. Astacidea. Freshwater crayfish. Version 11 March 2010; Tree of Life. Creative Commons Attribution-NonCommercial-ShareAlike License - Version 3.0.

Decapoda: Brachyura

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--+==Glypheoidea
           |--Astacidea
           |--Thalassinidea
           |--Palinuroidea
           `--+--Anomura
              `--Brachyura
                 |--Prosopidae
                 `--+--Dromiacea
                    |--Raninoida
                    |  |--Dakoticancroidea
                    |  |--Cyclodorippoidea
                    |  `--Raninidae
                    `--Eubrachyura
```

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1. Brachyura
2. Cyclodorippoidea
3. Dakoticancroidea X
4. Dromiacea
5. Prosopidae X
6. Raninidae
7. Raninoida

The harbour crab or sandy swimming crab, *Liocarcinus depurator*, (Brachyura: Eubrachyura: Heterotremata: Portunoidea: Portunidae
Photo © the National Museums Northern Ireland and its licensors, via Encyclopedia of Life, Creative Commons Attribution Non-Commercial Share-Alike.

The crabs need no introduction, as they are such familiar inhabitants of the sea shore. They are also the most advanced, specialised, and succesful of the Crustacea; there are more species of crabs than all other malacostraca combined. First appearing in the Jurassic, crabs, or *Brachyura* to give them their scientific name, had become abundant by the early Tertiary, a success they still hold. Most Mesozoic crabs belonged to groups such as the Dromiacea and Raninoida. Although these groups still continue today, they have been mostly replaced by the more specialised crabs of the Eubrachyura group, which include by far the greatest number of extant species. MAK120523

Classification

The infraorder Brachyura contains 6,793 species in 93 families,[17] as many as the remainder of the Decapoda.[28] The evolution of crabs is characterised by an increasingly robust body, and a reduction in the abdomen. Although many other groups have undergone similar processes, carcinisation is most advanced in crabs. The telson is no longer functional in crabs, and the uropods are absent, having probably evolved into small devices for holding the reduced abdomen tight against the sternum.

In most decapods, the gonopores (sexual openings) are found on the legs. However, since crabs use the first two pairs of pleopods (abdominal appendages) for sperm transfer, this arrangement has changed. As the male abdomen evolved into a narrower shape, the gonopores have moved towards the midline, away from the legs, and onto the sternum.[29] A similar change occurred, independently, with the female gonopores. The movement of the female gonopore to the sternum defines the clade Eubrachyura, and the later change in the position of the male gonopore defines the Thoracotremata. It is still a subject of debate whether those crabs where the female, but not male, gonopores are situated on the sternum, form a monophyletic group.[28] - Wikipedia

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Phylogeny

The following provisional phylogeny is from Christopher Taylor - Variety of LIfe Brachyura and Heterotremata

```
Eocarcinus praecursor Withers 1932 [Eocarcinidae] GT01 (basal anumara or basal meiura)
Brachyura [Brachyuri]  (Podotremata GT01 paraphyletic or polyphyletic  - De Grave et al 2009)
|--Prosopidae
`--+--Homolodromioidea MD01
   `--+--Dromiacea GT01
      |  |--Dromioidea MD01
      |  |  |--Dynomenidae MD01
      |  |  |  |--Acanthodromia erinacea Milne Edwards 1880 GT01
      |  |  |   `--Metadynomene crosnieri McLay 1999 GT01
      |  |  `--Dromiidae MD01
      |  |     |--Stimdromia GT01
      |  |     |--Dromidia spongiosa (Stimpson 1858) GT01
      |  |     |--Dromia W01
      |  |     |--Hypoconcha W01
      |  |     |--Petalomera GT01
      |  |     |--Dromilites GT01
      |  |     `--Dromidiopsis australiensis (Haswell 1882) TSH09
      |  `--Homoloidea MD01
      `--+--Raninoida GT01 [Archaeobrachyura, Gymnopleura]
         |   i. s.: Etyidae GT01
         |   |--Dakoticancridae [Dakoticancroidea] GT01
         |   |--Cyclodorippoidea [Tymoloidea] MD01
         |   |   |--Cymonomidae MD01
         |   |    `--Cyclodorippidae MD01
         |    `--Raninoidea MD01
         |        |--Symethis [Symethidae, Symethinae] MD01
         |        `--Raninidae CF06
         |           |--Ranina Lamarck 1801 B02 R. ranina (Linnaeus 1758)
         |           |--Notopus de Haan 1841 B02
         |           `--Raninella Milne Edwards 1862 CF06
         `--Eubrachyura [Brachyrhyncha] GT01
            |--Heterotremata GT01
            |  |  i. s.: Secretanella Guinot & Tavares 2001 GT01  S. arcuata (Secretan 1964)
[=Xanthosia arcuata] GT01
            |  |--Hapalocarcinus TSH09 [Cryptochiridae MD01, Cryptochiroidea, Hapalocarcinidae]
            |  |--Hymenosomatidae [Hymenosomatoidea] MD01
            |  |--Retropluma B68 [Retroplumidae, Retroplumoidea MD01]
            |  |--Bythograeidae [Bythograeoidea] MD01
            |  |--Belliidae [Bellioidea] MD01
            |  |--Dorippoidea SL03
            |  |    |--Dorippidae SL03
            |  |    `--Orithyiidae MD01
            |  |--Leucosioidea MD01
            |  |    |--Leucosiidae MD01
            |  |    `--Matutidae MD01
            |  |--Parthenopoidea MD01
            |  |    |--Parthenopidae GS79
            |  |    |--Aethra TSH09 [Aethridae MD01]
            |  |    `--Daira TSH09 [Dairidae MD01]
            |  |--Portunoidea CA04
            |  |    |--Portunidae CA04
            |  |    |--Trichodactylidae MD01
            |  |    `--Geryon H15 [Geryonidae MD01]
            |  |--Calappoidea SL03
            |  |    |--Hepatus BF07 [Hepatidae MD01]
            |  |    `--Necrocarcinidae [Necrocarcininae] SL03
            |  |         |--Cenomanocarcinus Van Straelen 1936 CF06
            |  |         |--Orithopsis Carter 1872 SL03
            |  |         `--Necrocarcinus Bell 1863 CF06
            |  |--Xanthoidea CA04
            |  |    |  i. s.: Planopilumnus Balss 1933 NT85  P. spongiosus (Nobili 1905)
[=Pilumnus spongiosus] NT85
            |  |    |         Homalaspis MD01
            |  |    |--Xanthidae MD01
            |  |    |--Menippidae NT85
            |  |    |--Pilumnidae CA04
            |  |    |--Carpilius TSH09 [Carpiliidae MD01]
            |  |    |--Hexapodidae [Hexapodinae] MD01
            |  |    |--Platyxanthidae MD01
            |  |    |--Pseudorhombilidae MD01
            |  |    |--Trapeziidae MD01
            |  |    |--Goneplacidae MD01
            |  |    |--Eriphia Latreille 1817 B55 [Eriphiidae TSH09]
            |  |    |--Domeciidae TSH09
            |  |    `--Tetralidae TSH09
            |  |--Cancroidea CA04
            |  |    |--Cancridae MD01
            |  |    |--Corystes B02 [Corystidae MD01]
            |  |    |--Cheiragonidae MD01
            |  |    |--Thia B02 [Thiidae MD01]
```

```
            |  |    `--Atelecyclidae CA04
            |  |--Gecarcinucidae [Gecarcinucoidea, Potamonidae] MD01
            |  |    |  i. s.: Thelphusula Bott 1969 H86
            |  |    |         Adeleana Bott 1969 H86
            |  |    |--Barytelphusa Alcock 1909 DC06, BS05 [incl. Maydelliathelphusa Bott 1969
BS05]
            |  |    `--+--Sartoriana Bott 1969 DC06, BS05
            |  |       `--+--+--Gecarcinucus jaquemonti DC06
            |  |          |  `--+--Gubernatoriana gubernatorus DC06
            |  |          |     `--Parathelphusidae DC06
            |  |          `--+--Phricothelphusa limula DC06
            |  |             `--+--Pseudothelphusidae DC06
            |  |                `--Potamoidea DC06
            |  `--Majoidea MD01
            |     |--Pyromaia HJ08 [Inachoididae MD01]
            |     |--Tychidae MD01
            |     |--Inachidae TSH09
            |     |--Epialtidae TF08
            |     `--Majidae MD01
            `--Thoracotremata MD01
                |--Pinnotheridae MD01
                |--Grapsoidea MD01
                `--Ocypodoidea MD01
                    |--Camptandriidae [Camptandriinae] MD01
                    |--Palicidae MD01
                    |--Mictyris T03 [Mictyridae MD01]
                    |--Macropthalmidae TSH09 [Macrophthalminae MD01]
                    |    |--Australoplax B68
                    |    |--Cleistostoma B68
                    |    `--Macrophthalmus HS01
                    `--Ocypodidae MD01
                        |--Dotillinae MD01
                        |--Heloecius B68 [Heloeciinae MD01]
                        |--Scopimerinae B68
                        `--Ocypodinae
```

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Descriptions

Brachyura Latreille, 1802

Range: From the Jurassic

Phylogeny: Meiura **:** Anomura + * **:** Dromiacea + Raninoida + Eubrachyura)))

Characters:. Synapomorphies (from Dixon et al. 2003): Orbito-antennularis fossa present, formed by carapace and one or more antennae; third maxillipedes operculiform; uropods absent; telson without any specialization for escape or digging. Posterior edge of carapace straight, second pleomere not expanded. First and second male pleopods arranged so that the second pleopod passes through the first, the two collectively forming a single gonopod. - CKT.

Comments The true crabs, a group of decapods in which the reduced abdomen is held to the underside of the sternum. - CKT.

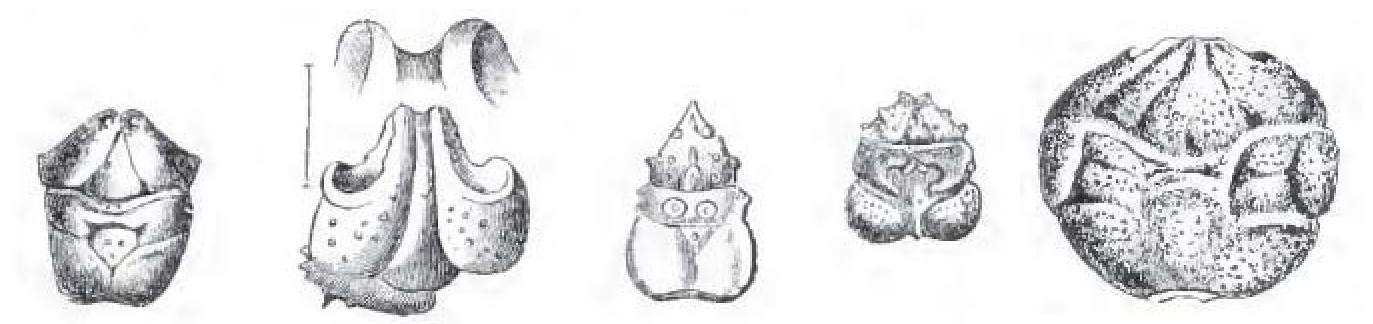
Image: Spanner crab *Ranina ranina* (Brachyura: Raninoida: Raninoidea:Raninidae), a represnetative of group that was very succesful during the Cretaceous and Tertiary. Photographed by Massimo Boyer.

Dromiacea

Range: From the Jurassic

Phylogeny: Brachyura **:** Dromiacea + Raninoida + Eubrachyura

Comments: The Dromiacea are known from 240 extant and nearly 300 extinct species. If the number of fossil species are only a fraction of the total that ever lived, that means that the extent species are merely the remnants of a much more diverse, Mesozoic and early Tertiary group MAK120523. They differ from the more specialised Brachyura in retaining many primitive characters. Thus, the last somite of the abdomen often retains vestiges of uropods, the first abdominal somite of the female has a pair of appendages, the fossettes for the reception of the antennules are less clearly defined, and the gills are more numerous. - Zittel & Eastman 1913. The larvae of Dromiacea also resemble those of the Anomura more closely than those of other crabs, reflecting their basal position in the crab phylogeny. - from Wikipedia



Mesozoic Dromiacea, fossilised carapaces, from left to right: *Prosopon marginatum*, v. Meyer. Late Jurassic, Oerlinger Valley, near Ulm, Baden-Württemberg, Germany; *P. personatum*. Late Jurassic; Weissingen, Wurtemberg. Rostrum enlarged. *P. aculeutum* v. Meyer .Same locality as *P. marginatum*; *P. pustulatum* Quenstedt, ditto; *Dromiopsis rugosa* (Schlotheim). Latest Cretaceous, Faxoe, Denmark. - Zittel & Eastman 1913, figs 1484-5.

Among the Recent Dromiacea, again, the family Homolodromiidae is the most primitive, its members, which inhabit the deep sea, presenting many features which link them with the Lobsters of the tribe Nephropsidea. The earliest fossil Brachyura, forming the extinct family Prosoponidae, are allied, by the form of the carapace and its grooves, to the existing Homolodromiidae. In the majority of cases the carapace alone is preserved, but portions of the abdomen and limbs are known in *Protocarcinus* (*Palaemachus*) Woodward, from the Forest Marble (Bathonian) of England. The genns *Prosopon* von Meyer is even earlier, appearing in the Bajocian and persisting to the Neocomian. Later forms approach more specialised Recent types, such as *Homolopsis* Bell from the Gault, leading towards the Homolidae; and *Dromiopsis* Reuss, leading towards the Dromiidae. The Tertiary *Dromilites* Milne Edwards, is scarcely different from the Recent *Dromia*.- Zittel & Eastman 1913 (public domain, slightly edited,) - needs updating

Image: above right, The sponge crab *Dromidiopsis dormia* (Dromioidea: Dromiidae) eating a sea urchin off the coast of Maui, Hawaii. Photo by Sasquatch, Creative Commons Attribution Share Alike, GNU Free Documentation License, via Wikipedia

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Raninoida

Range: From the Cretaceous

Phylogeny: Brachyura **:** Dromiacea + Eubrachyura + * **:** Cyclodorippoidea + Dakoticancroidea + Raninidae

Characters: Complete loss of the uropods, without even a modified remnant (Guinot & Tavares 2001) - CKT

Comments: Also called Archaeobrachyura. Unlike other crabs, the abdomen is not folded under the thorax.

Dakoticancridae

Range: Late Cretaceous of North Amerixca and Spain

Phylogeny: Raninoida **:** Cyclodorippoidea + Raninidae + *

Cyclodorippoidea

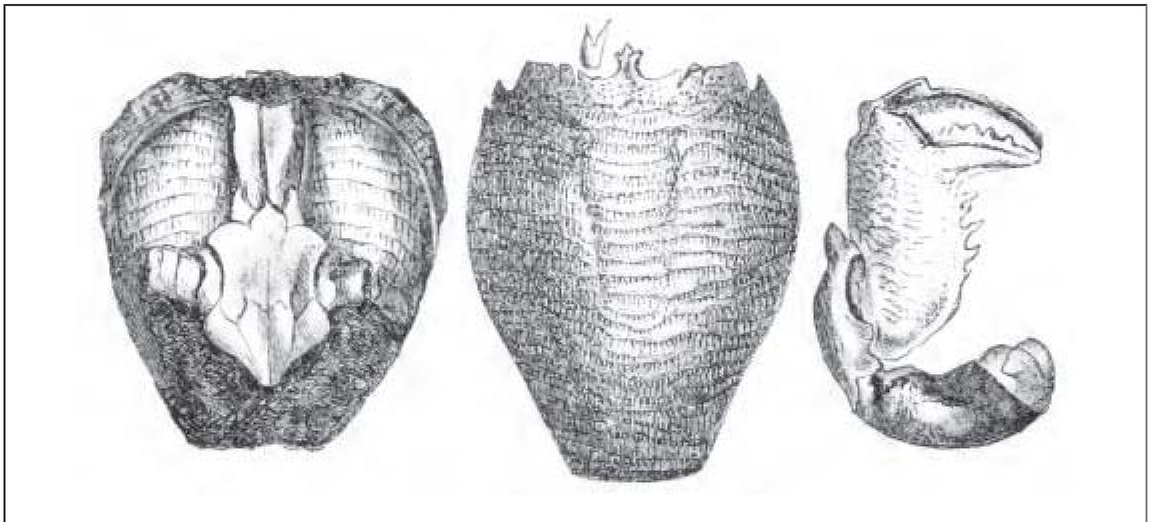
Phylogeny: Raninoida **:** Dakoticancroidea + Raninidae + *

Raninidae

Range: From the Cretaceous (Albian age)

Phylogeny: Raninoida **:** Cyclodorippoidea + Dakoticancroidea + *

Characters: Complete loss of the uropods, without even a modified remnant (Guinot & Tavares 2001) - CKT and by the unusual form of the chelae and by the elongate carapace,which is broader in front than behind Zittel & Eastman 1913



Tertiary fossils of the family Raninidae. *Ranina (Lophoranina) marestiana* König, 1825, Eocene; Kressenberg, Bavaria. Ventral and dorsal views (this species is also known from Monte Baldo, Italy). Chela (claw) of *R.bouilleana* A. Milne Edwards, 1872; Early Oligicene of Biarritz, Prance. - Zittel & Eastman 1913, figs 1488.

Comments: The Raninidae are a strange group of crabs that resemble frogs, hence the name (*Rana* - frog). These animals closely resemble the unrelated mole crabs (Anomura: Hippoidea) , due to convergent evolution. In both groups, the claws are modified into tools for digging, and the body is a rounded shape that is easy to bury in sand. Only 46 extant species, but nearly 200 fossil species are known (Wikipedia) showing that modern species are the remnants of a previously much more abundant and diverse group. They appear during the Middle Cretaceous (Albian and Cenomanian) , and are common during the early Tertiary. *Raniella* and *Raninoides* Milne Edwards, are Cretaceous genera. Of the few Recent genera, *Ranina* Lamarck is also known from the Eocene.- Wikipedia, Zittel & Eastman 1913 (public domain)

Image: *Lyreidus bairdii* Smith dorsal view. Scale: 3 cm. This elongate species has a particularily frog-like appearance, other raninids with wider carapaces are more typically crab-like in appearance. All share the nonfolded abdomen (left in this image). Image © Smithsonian Institution, National Museum of Natural History, Department of Invertebrate Zoology, via Encyclopedia of Life, Creative Commons Attribution Non-Commercial Share-Alike

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Decapoda: Caridea

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--Pleocyemata
      |--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           `--+--Anomura
              `--Brachyura
```

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1. Caridea
2. Pleocyemata

A number of individuals of *Nautilocaris saintlaurentae* Komai & Segonzac (Decapoda: Caridea: Bresilioidea: Alvinocarididae) on the sulphide wall of a hydrothermal vent, North Fiji Basin, at a depth of 2,000 meters. Distinct species and genera of Alvinocaridids are found clustered around different hypdrotherma;l vents, and illustrate the great dicersity and adaptability of the malacostraca. Among the most abundant arthropods in the sea, Malacostracans are found everywhere from the littoral zone to the pelagic water column to the bottom of the ocean, and, in the other direction, freshwater and even dry land. Photographer: T. Komai, Publisher Chris Allen, via Encyclopedia of Life, Creative Commons Non-Commercial Attribution.

The Caridea are one of the main groups of true shrimps. They were previously included under the Natantia, but as that is a paraphyletic assemblagfe the term is no longer used. Of the two main shrimp groups, the Caridea are considered to be closer to the crabs and lobsters (Reptantia) than the Dendrobranchiata (sometyimes called prawns, although generally terms like "prawns" and "shimps" are confused). MAK120530

Fossil Record

The fossil record is sparse, with only 57 fossil species known. The earliest of these cannot be assigned to any family, but date from the Early Jurassic and Cretaceous - Wikipedia. In the Solnhofen numerous genera occur, some of which, such as *Udora* Munster, and *Udorell*a Oppel have exopodites on the thoracic legs, a primitive character suggesting affinity with the Recent family Acanthephyridae. Other Solnhofen genera, in which these exopodites appear to be wanting, are Blaculla,Hefriga and Elder Miinster. The Recent deep-sea genus *Oplophorus* Milne Edwards (Acanthephyridae) has been identified in the Upper Cretaceous of Westphalia. Some Caridea are found in frosh-water Tertiary deposits, as for example *Homelys* von Meyer, from the Miocene of Oeningen; but it is impossible to say what relation they bear to recent fresh-water Caridea - Zittel & Eastman 1913 (public domain) - needs revision

Phylogeny

Dendrogram, from Christopher Taylor - Variety of LIfe.

```
Caridea
 |   i. s.: Acanthephyra M85 [Oplophoridae, Oplophoroidea MD01]
 |          Galatheacaris [Galatheacarididae, Galatheacaridoidea] MD01
 |          Bresilioidea MD01
 |            |--Agostocarididae MD01
```

```
    |           |--Alvinocarididae MD01
    |           |--Bresiliidae MD01
    |           |--Disciadidae MD01
    |           `--Mirocaris fortunata (Martin & Christiansen 1995) [Mirocarididae] [=Chorocaris fortunata] MD01
    |         Campylonotoidea MD01
    |           |--Bathypalaemonella [Bathypalaemonellidae] MD01
    |           `--Campylonotidae MD01
    |         Pasiphaea B26 [Pasiphaeidae MD01, Pasiphaeoidea MD01]
    |         Atyidae MD01
    |         Nematocarcinoidea MD01
    |           |--Eugonatonotidae MD01
    |           |--Lipkius C85 [Rhynchocinetidae MD01]
    |           |--Nematocarcinus M85 [Nematocarcinidae MD01]
    |           `--Xiphocaris H86 [Xiphocarididae MD01]
    |         Psalidopodidae [Psalidopodoidea] MD01
    |         Stylodactylidae [Stylodactyloidea] MD01
    |         Physetocarididae [Physetocaridoidea] MD01
    |         Lebbeus polaris (Sabine 1824) FZA07
    |         Processidae [Processoidea] MD01
    |           |--Ambidexter symmetricus M85
    |           `--Processa M85
    |--+--Procaris Chace & Manning 1972 DAS03, H86 [Procarididae, Procaridoidea]
    |  `--+--Alpheoidea DAS03
    |     |   |--Ogyrides Stebbing 1914 [=Ogyris Stimpson 1860 (preoc.); Ogyridae, Ogyrididae] MD01
    |     |   |--Nauticaris [Nauticarididae] MD01
    |     |   |--Bythocarididae MD01
    |     |   |--Barbouriidae MD01
    |     |   |--Alpheidae MD01
    |     |   `--Hippolytidae [Alopidae] MD01
    |     `--Crangonoidea DAS03
    |         |--Glyphocrangon M85 [Glyphocrangonidae MD01]
    |         `--Crangonidae DH83
    `--+--Atyoida pilipes (Newport 1847) DAS03
       `--+--Pandaloidea MD01
          |    |--Pandalidae MD01
          |    `--Thalassocarididae [Thalassocaridae] MD01
          |         |--Chlorotocoides Kemp 1925 C85
          |         `--Thalassocaris Stimpson 1860 DAS03, C85
          `--+--Leander tenuicornis (Say 1818) DAS03
             `--Palaemonoidea MD01
                  |--Palaemonidae DAS03
                  |--Anchistioididae MD01
                  |--Desmocarididae MD01
                  |--Hymenoceridae MD01
                  |--Kakaducarididae MD01
                  |--Gnathophyllum M85 [Gnathophyllidae MD01]
                  |--Euryrhynchus H86 [Euryrhynchidae MD01, Euryrhynchinae]
                  `--Typhlocaris Calman 1909 H86 [Typhlocarididae MD01, Typhlocaridinae]
```

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Descriptions

Pleocyemata Burkenroad 1963

Range: From the Devonian

Phylogeny: Decapoda **:** Dendrobranchiata + * **:** Caridea + (Stenopodidea + Reptantia)

Comments: Crustacean taxonomy has replaced the earlier sub-orders of Natantia and Reptantia with the monophyletic Dendrobranchiata and Pleocyemata. The latter are united by a number of features, including the fertilised eggs are incubated by the female, and remain stuck to the pleopods (swimming legs) until they are ready to hatch (hence the name) - from Wikipedia

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Caridea

Range: Fossil record only from the Triassic; ghost lineage suggests Devonian origin

Phylogeny: Pleocyemata **:** Dendrobranchiata + (Reptantia + *)

Characters: phyllobranchiate gills and chelate first and (usually) second pereiopods, but lack chelae on the third pereiopods (Dixon et al. 2003). - CKT.

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Decapoda: Dendrobranchiata

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--Pleocyemata
      |--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           `--+--Anomura
              `--Brachyura
```

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1. Dendrobranchiata

Under construction

The Dendrobranchiata are prawns as oposed to the shrimps (Caridea). Pending a more complete coverage, this rather bland holding page will have to do MAK120526

Phylogeny

As shown in the following dendrogram, from adapted from Christopher Taylor's blog, Variety of LIfe (see also Mikko's phylogeny for an earelier version), the Decapoda are divided into two two clades, the Pleocyemata and the Dendrobrachiata. This dendrogram does not include the several known fossil lineages

```
Decapoda
  |--Pleocyemata DAS03
  |    |-- Caridea DAS03
  |    `--+--Reptantia DAS03
  |       `--Stenopodidea DAS03
  |           |--Spongicolidae MD01
  |           `--Stenopus Latreille 1819 BR05 [Stenopodidae MD01]
  `--Dendrobranchiata [Penaeidea] MD01
       |  i. s.: Parapenaeopsis KW70
       |--Sergestoidea MD01
       |    |--Sergestes CH97 [Sergestidae HC79]
       |    `--Lucifer Thompson 1829 HC79 [Luciferidae MD01]
       `--Penaeoidea HC79
            |--Solenoceridae HC79
            |--Penaeidae DAS03
            |--Benthesicymidae MD01
            |--Aristeus BRP03 [Aristeidae HC79]
            `--Sicyonia Milne Edwards 1830 [Sicyoniidae] HC79
```

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Descriptions

Dendrobranchiata Bate, 1888

Range: From the Devonian

Phylogeny: Decapoda **:** Pleocyemata + *

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Decapoda: Eryonoidea

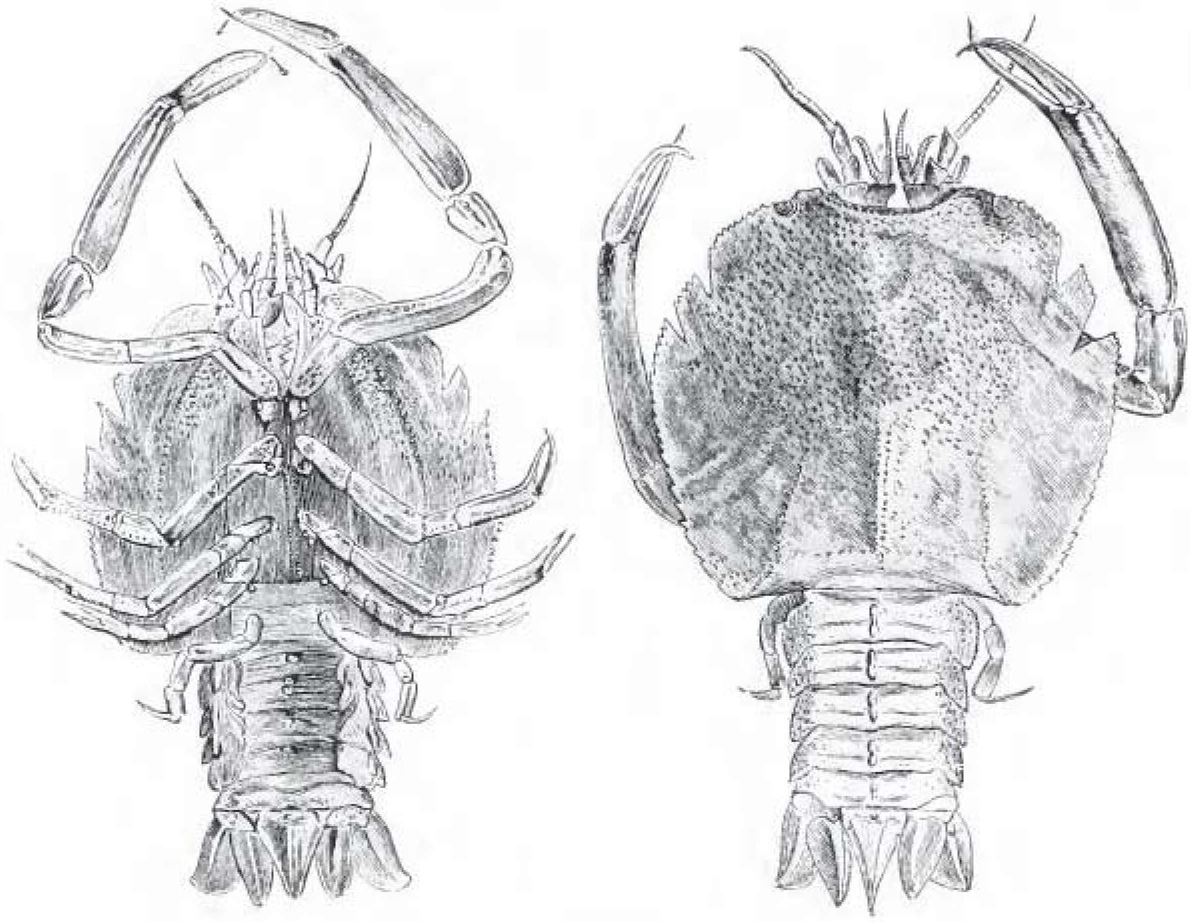
Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
         |--Eryonoidea
         |  |--Tetrachela
         |  `--+--Eryonidae
         |     `--+--Palaeopentacheles
         |        `--+--Coleiidae
         |           `--Polychelidae
         `--Eureptantia
            |--Astacidea
            |--Palinuroidea
            `--+--Anomura
               `--Brachyura
```

Contents

Taxa on This Page

1. Coleiidae
2. Eryonidae
3. Eryonoidea
4. *Palaeopentacheles*
5. Polychelidae
6. *Tetrachela*



Eryon (Cycleryon) propinquus, Solnhofen; from Zittel & Eastman 1913

When the present writer (MAK) was a kid, filling his suggestable mind with images from aleontology textbooks, among those creatures that stood out was a bizarre crustacean described as a lobster, but looking nothing like one. Instead it had a flat, discoidal body and elongate and delicate, tong-like pincers. Yet this strange creature, called *Eryon* (see image above) lived not during the Paleozoic, when the oceans were populated by such iconic prehistoric arthropods as trilobites, eurypterids, phyllocarids, and horseshoe crabs, but in the late Jurassic, at a time when invertebrates (apart from the abundant ammonites and belemnites), looked pretty much like those around today. Even the name is prehistoric sounding, recalling *Eryops*, the famous Permian amphibian who is often portyayed alongside the finback Dimetrodon (although the two probably occupied very different environments).

As it turns out, *Eryon* is not ancient Greek for "weird crab -like creature with long thin claws" but means "red" (Wikipedia) , no doubt recalling the colour of the fossils in the Solnhofen lithographic limitestone where it is found. And the commonly portrayed *Eryon propinquus* is now called *Cycleryon propinquus* (Round *Eryon*), although whether it deserves a distinct genus name (and whether it is any rounder) is debatable considering the similarity between the respective type species. In any case, these animals clearly constituted a paraphyletic assemblage or evolutionary gradation

.

And rather than call *Eryon* a lobster (or a crab), it is better referred to as a member of the walking clade of decapods, Reptantia.

Eryon arctiformis, Solnhofen
Photo by Didier Descouens, via Wikipedia, Creative Commons Attribution Share Alike/GNU Free Documentation License.

Cladistic analysis (Scholtz & Richter in 1995 and Dixon et al in 2003) shows that it belongs to the most basal (primitive, ancestral) lineage of reptants. Once common, they are today a relict group. Extant forms constitute a small number of genera, such as *Polycheles* and *Willemoesia* which have chelae on the first four or on all five pairs of legs. All are blind or with greatly reduced eyes, and inhabit deep water. Fossil genera however include forms that lived in shallow water, and all possessed well-developed eyes. The earliest is *Tetrachela* from the Late Triassic. Eryonoids reach their greatest diervisty during the Jurassic, with a number of species known from the Solnhofen lagerstatte alone (Late Kimmeridgian/Early Tithonian) (Zittel & Eastman 1913, Ahyong 2009). By the late Cretaceous and early Tertiary they were in decline, Today only a single family (Polychelidae) remains, perhaps due to absense of rivals in its deepwater environment. These have a narrower and hence more conventionally lobster-like body shape. All eryonoids are distinguished by claws not only on the elongate first pair of limbs (the pincers), but on at least three pairs of walkng legs, hence their alternative (and currently widely used) name, Polychelida (many claws). This distinguishes them from the distantly related Palinuroidea, who have no claws at all, not even pincers, Why some lobster-like animals should have delicate and lightly built claws, others (the classic lobsters and crabs) powerfully built cutting and crushing claws, and others no claws at all, shows how functionally and ecomorpghcllay diverse life can be, even among closely related types. MAK120531

Evolutionary trends

The Eryonoidea form a distinct and fairly orthogenetic evolutionary series, evolving along a single direction. From the abstract by Ahyong 2009 - "Phylogenetic trends include a general narrowing of the carapace and abdomen; shortening of the carapace front with respect to the anterolateral margins, leading to a shift in eye orientation from anterior to transverse; dorsal exposure of the base of the antennules and development of a stylocerite; and a shift in the form of the major chelipeds from relatively robust with short, triangular carpi to elongated and slender, with slender carpi. These trends within Polychelida appear to correspond to a shift from a shallow-water, epibenthic habit to the deep-water, fossorial lifestyle" These trends can be seen in the illustrations accompanying ecah taxon, below. The earliest and most primitive forms are squat and broad, the later types have a more conventional appearance. However, this was not simply like the old pictures of the evolution of the horse, because the various types evolved in parallel alongside each other. MAK120531

Eryonoidea or Polychelida?

The superfamily Eryonoidea, containing the two families Polychelidae and Eryonidea, has until recently been included as one of the three superfamilies of the infraorder Palinura, alongside the mostly fossil Glypheoidea, and the Palinuroidea, which include the spiny lobsters and slipper lobsters (e.g. Barnes 1980, Holthuis 1991). In 1995, Gerhard Scholtz and Stefan Richter of the Freie Universität Berlin the first proper cladistic study of the decapoda and specifically the Reptantia (Scholtz & Richter 1995). They found that the "Palinura" as defined up until then was paraphyletic. They therefore abandoned that taxon and replaced the Eryonoidea with the new non-rank clade Polychelida, and the Palinuroidea with the non-rank Achelata.

Due to the influence of Scholtz & Richter's important paper, the earlier terms Eryonoidea and Palinuroidea are noew very rarely used. Since however Polychelida is identical in every respect to the earlier-named taxon Eryonoidea, and Achelata likewise identical to the earlier-named Palinuroidea, there seems little justification to support a change here. Eryonoidea goes back to De Haan, 1841, and is the superfamily adjusted rank of the original family Eryonoidae. The oldest authorship for Polychelida would be the infraorder adjusted rank Polychelida Wood-Mason, 1874. Since Eryonoidea is the only superfamily within the infraorder Polychelida, the two names are only of use when listing Linnaean ranks and taxa (which cladistics does not do). Although it is not compulsory with supra-generic taxa to use the earliest name, we have tried to follow this convention, as it is so rigorously applied to species and genus names, and hence where the definitions are identical we have adopted the earliest name. For this reason, the more cladistically familiar names Polychelida and Achelata are not used. Also, a paraphyletic Infraorder Palinura is still valid under linnaean and evolutionary systematic rules, so there is no reason it should be discarded for purely taxonomic purposes. If however the Palinura were to turn out to be polyphyletic (as for example in the case of Dixon et al 2003) then the name should be discarded. MAK120530

Descriptions

Eryonoidea De Haan, 1841

Synonym: Polychelida Wood-Mason, 1874 sensu Scholtz & Richter 1995

Range: From the Late Triassic

Phylogeny: Reptantia **:** *Palaeopalaemon* + (Eureptantia+ * **:** *Tetrachela* + (Eryonidae + (*Palaeopentacheles* + (Coleiidae + Polychelidae)

Characters: Carapace dorsoventrally flattened (a fancy way of saying that it's flat); lateral margins cristate (i.e. they have a zig-zag-like outline). Antennal segments free. Pereopods (thorcic walking legs) 1-4 chelate (having chelae (pincers). Pereopod 5 chelate in one or both sexes - Ahyong 2009

Comments: The only superfamily of the infraorder Polychelida. A mostly Mesozoic group. See above comments for more.

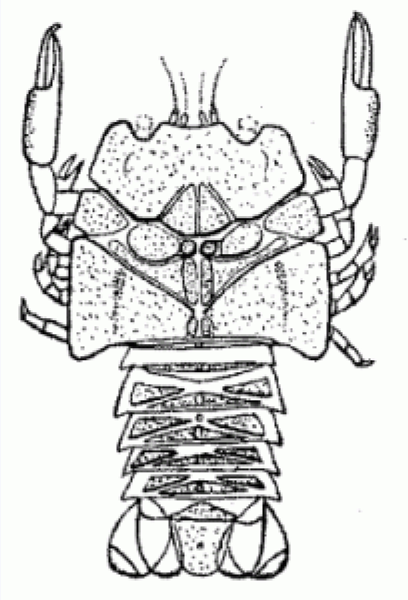
Tetrachela

Range: Late Triassic

Phylogeny: Eryonoidea **:** (Eryonidae + (*Palaeopentacheles* + (Coleiidae + Polychelidae))) + *

Comments: *Tetrachela raiblana* is the most basal Eryonoid and the only species in the monotypal family Tetrachelidae. It is distinguished from most other eryonoids by the retention of the diaeresis of the uropodal exopods. (Wikipedia, Ahyong 2009). This flattened, wide-bodied type, like its successors, was a shallow water epifaunal form

Image credits *Tetrachela raiblana* (Bronn, 1858), from the *Treatise* (Glaessner 1969 fig 272) via Ahyong 2009 fig 1 A



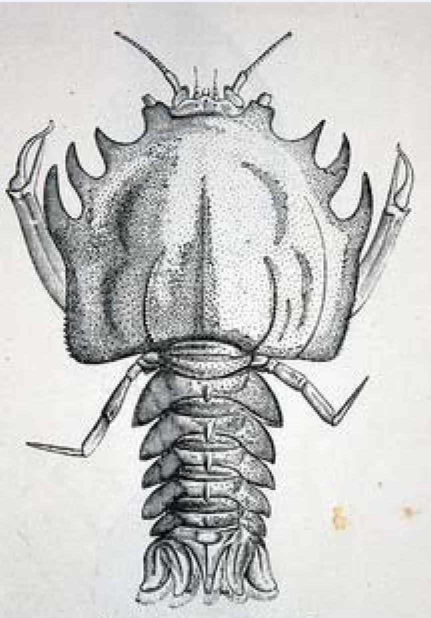


Fig. 149. Eryon arctiformis.

Eryonidae De Haan, 1841

Range: Late Triassic to Early Cretaceous

Phylogeny: Eryonoidea **:** *Tetrachela* + ((*Palaeopentacheles* + (Coleiidae + Polychelidae)) + *)

Comments: - The "classic" eryonoids with the distinctive discoidal carapace. In the analysis of Ahyong 2009, *Eryon* Desmarest, 1822 and *Cycleryon* Glaessner, 1965 are closely related and form a crown group, *Knebelia* Van Straelen, 1922 is more basal MAK120531

Image credits *Eryon arctiformis* Image from Louis Figuier, *La Terre avant le déluge* Paris : Librairie de L. Hachette, 1863. - 2e éd., courtesy El Bibliomata, Creative Commons Attribution

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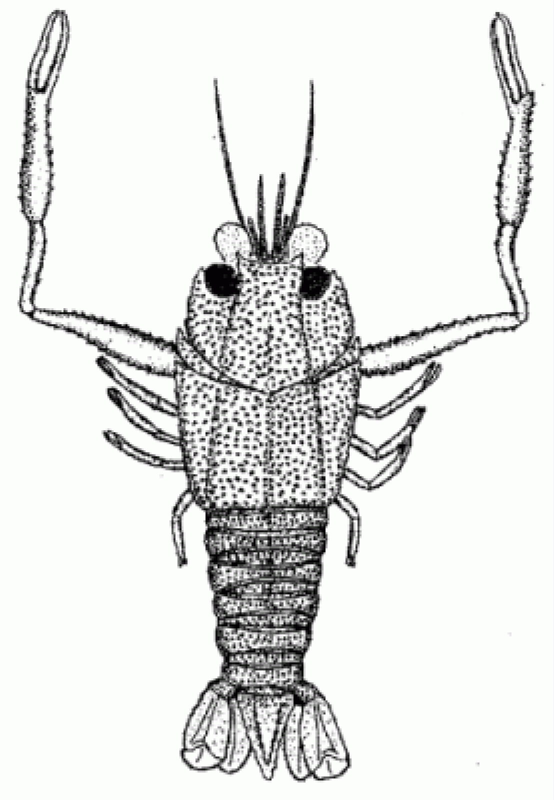
Palaeopentacheles

Range: late Jurassic to ?Oligocene

Phylogeny: Eryonoidea **:** *Tetrachela* + (Eryonidae + ((Coleiidae + Polychelidae) + *))

Comments: - *Palaeopentacheles*, formerly placed in Polychelidae, is demonstrated above to lie outside a Polychelidae + Coleiidae clade and has been placed in a monotypal family Palaeopentachelidae. Palaeopentacheles is presently known only from its type species, *P. roettenbacheri* from the Late Jurassic of Germany, illustrated here), and *P. starri* Schweitzer & Feldmann, 2001 from the Oligocene of North America. The holotype of the latter is in poor condition, and its assignment to *Palaeopentacheles* was tentative Ahyong 2009.

Image credits *Palaeopentacheles roettenbacheri* from Garassino & Schweigert 2006 via Ahyong 2009. Compare with photo of fossil in the Jura Museum Eichstaett and this reconstruction



Coleiidae Van Straelen, 1924

Range: Late Triassic to late Jurassic

Phylogeny: Eryonoidea **:** *Tetrachela* + (Eryonidae + (*Palaeopentacheles* + (Polychelidae + *)

Comments: Includes a number of genera. Intermediate between the flat-bodied Mesozoic types and the extant Polychelidae. The Late Triassic to the Late Jurassic *Coleia* Broderip, 1835 is the best known and includes a large number of species. *Willemoesiocaris* Van Straelen, 1925, from the mid-Jurassic of France, previously considered a polychelid (Glaessner 1969), is more likely a Coleiid (Ahyong 2009), although it is also possible that it could be a very primitive form transitional between the two groups MAK120531

Image credits *Coleia longipes* Fraas, 1855, from Schweigert & Died 1999 via Ahyong 2009 fig 1 E

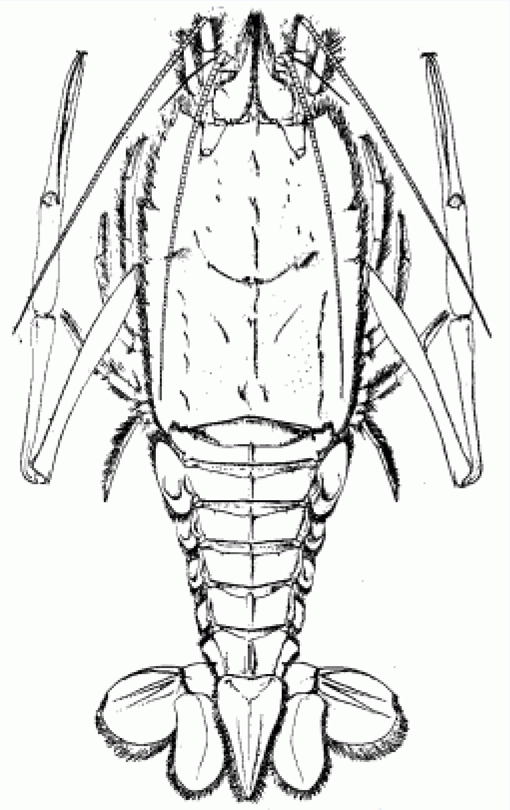
Polychelidae Wood-Mason, 1875

Range: late Jurassic to Recent

Phylogeny: Eryonoidea **:** *Tetrachela* + (Eryonidae + (*Palaeopentacheles* + (Coleiidae + *)))

Comments: the only surviving Eryonoidae, represented by several genera and 38 extant species. All recent species are restricted to deep water. The eyes are vestigial, the body narrow in relation to earlier forms, the chelae have become less robust. Among extant taxa, the most primitive genus is *Willemoesia*, the most advanced *Stereomastis* and *Polycheles* Ahyong 2009, Wikipedia. The Jurassic *Antarcticheles* Aguirre-Urreta, et al. 1990, the only fossil genus included here, may be a Polychelidaen on features of the carapace, although the pereopods and tailfan are not known and carapace morphology may simply be convergent. Regardless, the close resemblanxce to contemporary taxa shows that the 'polychelid form' was already well established by the late Jurassic. Ahyong 2009.

Image credits The advanced Polychelid *Stereomastis sculpta* (from S.I. Smith, 1882) from Holthuis 1991, © FAO 1991, reproduced under permitted terms (noncommercial/educational)



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| Unit Back: Malacostraca | Clade Down: None | Dendrogram | References | Unit Next: Hexapoda |

Decapoda: Eubrachyura

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           `--+--Anomura
               `--Brachyura
                   |--Dromiacea
                   |--Raninoida
                   `--Eubrachyura
                       |--Heterotremata
                       `--Thoracotremata
```

Contents

Taxa on This Page

1. Eubrachyura
2. Heterotremata
3. Thoracotremata

The Eubrachyura include the "higher" crabs. This group is divided into two subsections, based on the position of the genital openings in the two sexes. In the Heterotremata, the openings are on the legs in the males, but on the sternum in females, while in the Thoracotremata, the openings are on the sternum in both sexes. This contrasts with the situation in other decapods, in which the genital openings are always on the legs. - Wikipedia.

Descriptions

Eubrachyura

Range: From the Bathonian (Middle Jurassic)

Phylogeny: Brachyura **:** Dromiacea + Raninoida + * **:** Heterotremata + Thoracotremata

---

Heterotremata

Phylogeny: Eubrachyura **:** Thoracotremata + *

Comments The Heterotremata are a diverse group of crabs, characterised by having the male gonopores coxal and the female gonopores sternal. Whether the Heterotremata are a monophyletic group, or paraphyletic with regard to the Thoracotremata (in which both sexes have sternal gonopores), remains an open question. CKT. This is the larger of the two eubrachyuran groups, containing the species rich superfamilies Xanthoidea and Pilumnoidea and all the freshwater crabs (Gecarcinucoidea, Potamoidea). - Wikipedia

---

Thoracotremata

Phylogeny: Eubrachyura **:** Heterotremata + *

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Decapoda: Eureptantia

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
       `--Reptantia
         |--Eryonoidea
         `--Eureptantia
                |--Astacura
                |  |--Glypheoidea
                |  `--Astacidea
                |--Palinuroidea
                `--+--Anomura
                   `--Brachyura
```

Contents

Taxa on This Page

1. Eureptantia
2. Astacura
3. Glypheoidea

Under construction

Descriptions

Eureptantia

Range: From the Triassic

Phylogeny: Reptantia **:** *Palaeopalaemon* + (Eryonoidea + * **:** Astacura + Palinuroidea + Thalassinidea + Meiura)

Astacura

Range: From the Triassic

Phylogeny: Eureptantia **:** Palinuroidea + Thalassinidea + Meiura + * **:** Glypheoidea + Astacidea

---

Glypheoidea

Range: From the Triassic

Phylogeny: Astacura **:** Astacidea + *

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Unit Back: Malacostraca	Clade Down: None	Dendrogram	References	Unit Next: Hexapoda

Decapoda: Anomura

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
         |--Eryonoidea
         `--+--Eureptantia
            |--Palinuroidea
            `--Meiura
               |--Platykotta
               `--+--Eocarcinus
                  `--+--Crown Anomura
                     `--Brachyura
```

Contents

Taxa on This Page

1. Stem Anomura
2. *Eocarcinus*
3. Meiura
4. *Platykotta*

Meiura is one of only two new decapod clades agreed on by the only two comprehensivemorphological cladistic analyses of the group to date (Scholtz & Richter 1995 and Dixon et al 2003), the other being Eureptantia. The Meiura is the cade that includses both the anomurans or crab-like decapods and the true crabs. Molecular analysis doesn't support this, which shows that the anomura and the brachyura diverged very soon after evolving from a lobster-like ancestor; in too short a time to be resolved by molecular sequencing phylogeny.

Two taxa are currently known which together span the Triassic-Jurassic boundary and are very close to the Meiuran origin. These are *Platykotta* the *Eocarcinus*. Depending on your choice of hypotheses, they are either stem crabs, stem anomura, or (no-one seems to have suggested this so we are admittedly being rather presumptious here, but being editor of a huge paleo website does confer certain privelages) represnetives of an early meiuran lineage or lineages that don't belong to either, but continued alongside them, at least to the early Jurassic. If this latter is the case, than Triassic and early Jurassic decapods were far more diverse than existing forms, with many transitional types existing alongside the more specialised or derived taxa that continued to the present. This owuld be a somewhat smaller repat of teh Cambrian and even the early to mid Paleozoic, when there wrere many transitional ecdysozoans around that were intermediate between the extant phyla. MAK120529

Descriptions

Meiura Scholtz & Richter, 1995

Range: From the Triassic

Phylogeny: *Either* Eureptantia **:** Astacura + Palinuroidea + Thalassinidea + * **:** Stem Anomura + Brachyura
or Eureptantia **:** Astacura + Palinuroidea + Thalassinidea + * **:** *Platykotta* + (*Eocarcinus* + (Brachyura + Anomura))

Comments:. The first alternative phylogeny implies a stem and crown Anomura, the second a stem and crown Meiura MAK120529.

Stem Anomura

Range: From the Triassic

Phylogeny: Meiura **:** Brachyura + * **:** *Platykotta* + (*Eocarcinus* + Crown Anomura)

Comments:. The extra taxon is to accommodate stem taxa *Platykotta* and *Eocarcinus*, assuming these taxa are basal Anomura (Feldmann & Schweitzer 2010). Of course they could equally turn out to be basal Meiura . Hence a few of these entries have a choice of phylogenies MAK120528.

Platykotta

Horizon: Late Norian to Rhaetian from the Ghalilah Formation on the Musandam Peninsula, United Arab Emirates (Latest Triassic)

Phylogeny: *Either* Stem Anomura **:** (*Eocarcinus* + Crown Anomura) + *
or Meiura **:** (*Eocarcinus* + (Brachyura + Anomura)) + *

Comments: broad, triangular sternum, unlike the narrow sternum of Astacidea and Glypheoidea, but similar to that of Palinuroidea (which would support Dixon et al 2003's hypothesis of Achelata as stem Meiura (clade Eurysternalia)), and to lobster-like Anomura. Unlike other anomurans the carapace is considerably longer than wide (Wikipedia). Somewhat more "lobster-like" (hence more basal?) than *Eocarcinus*, but otherwise very similar to it, and placed with it in the Superfamily Eocarcinoidea (Chablais et al 2011). If however one taxon is more basal than another, than the Eocarcinoidea becomes a paraphyletic assemblage of basal Anomura (or even basal Meiura) defined by various mosaic traits. MAK120528.

Eocarcinus praecursor Withers, 1932

Range: Early Jurassic (Pliensbachian) of England

Phylogeny: *Either* Stem Anomura **:** *Platykotta* + (Crown Anomura + *)
or Meiura **:** *Platykotta* + ((Brachyura + Anomura) + *)

Comments: Depending on your preferred hypothesis, this is either the oldest true crab (e.g. Förster, 1985, Guinot & Tavares 2001, De Grave et al 2009), transitional between the Glypheoidea (specifically the Middle Triassic *Pseudopemphix*) and the Middle Jurassic crabs in the Homolodromioidea, especially the earliest known species, *Eoprosopon klugi* of the Late Pliensbachian (Krobicki & Zaton 2008), or else it is not be a crab at all, but an early member of the Anomura (Feldmann & Schweitzer 2010; Chablais et al 2011). Is one right and one wrong, or is it a matter of inputting different data resulting in different results. Or are they in a sense both right, and *Eocarcinus* (and hence also *Platykotta*) is a basal Meiuran rather than an early Anomuran or Brachyuran. MAK120529

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Decapoda: Palinuroidea

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           |  |--Palinuridae
           |  `--Scyllaridae
           `--+--Anomura
              `--Brachyura
```

Contents

Taxa on This Page

1. Palinuroidea
2. Palinuridae
3. Scyllaridae

Palinurus elephas (Fabricius, 1787), the European Spiny Lobster. This large, armoured and spiny species grows up to 60 cm in total length. Reptantia: Palinuroidea: Palinuridae
Photo © the National Museums Northern Ireland and its licensors, via Encyclopedia of Life, Creative Commons Attribution Non-Commercial Share-Alike.

The Palinuroidea are a small but unique group of decapods that include such evocatively named forms as spiny lobsters, slipper lobsters, and furry lobsters, as well as several fossil lineages.

Exactly where they belong is a mystery. According to some morphological cladistic (Scholtz & Richter 1995) and molecular and morphology (e.g. Ahyong & O'Meally 2004) analyses occupy a fairly basal position, whereas according to other cladistic (Dixon et al 2003) and molecular (e.g. Porter et al 2005, Bracken et al 2009) analyses are more related to crabs, or anywhere in between. Since no one seems to agree where they should belong (which is nothing new in the world of decapod phylogeny, we have left them in the middle for now. Should decapod phylogenetic studies ever reach any sort of consenus (which seems unlikely in the forseeable future) these pages can be adjusted accordingly.

Palinura or Achelata?

It has been argued that it is incorreect to use Palinura, as that name that more properly pertains to a paraphyletic or polyphyletic assemblage of lobster-like forms. An alternative name is Achelata (Scholtz & Richter 1995, Dixon et al 2003, Schram & Dixon 2004). The name "Achelata" derives from the fact that, unlike other decapods, the members of this group lack claws (chelae), and this synapomorphy-based designation is therefore more appropriate.

Strictly speaking there would be nothing wrong with retaining the name Palinura. Palinura still refers back to the representative genus *Palinurus*, named by German entomologist Friedrich Weber in 1795, *Palinurus* became the type genus for the family Palinuridae (the spiny lobsters), from tribe Palinurini, named by French zoologist Pierre André Latreille in 1802. Just because there are less lobster-like crustaceans included in the taxon Palinura now than there were a century ago doesn't mean the name itself is invalid. For example, the dinosaurian family Megalosauridae is still considered valid, even though it only contains a fraction of the species that were previously allocated to (or a decent percentage, depending on your choice of phylogeny). Also, we still say Insecta, even though it now refers to a single class of arthropods, rather than being, as coined by Linnaeaus, a name for the Arthropoda as a whole (hence Weber, as an entomologist, could rightly study Crustaceans).

In this instance, *Palinurus elephas* (Fabricius, 1787) the common spiny lobster, remains the type species for the genus, and hence by implication the clade as a whole (Johan Christian Fabricius, a Danish entomologist who likewise studied all types of arthropods), originally named the species *Astacus elephas* (the elphant lobster?), from the Greek *astacos* - lobster or crayfish. According to nomenclatural convention, as a species he named was reassigned its own genus, his name appears in brackets)

Nevertheless to avoid confusion, we have gone instead with the Superfamily nomen **Palinuroidea**, as this is (apart from the addition of Linnaean rank) exactly he same taxon as Achelata and moreover has nomenclatural priority (not so important admittedly with supra-generic taxa as with genus and species, but still useful, especially for consistency purposes (otherwise why care so much about the genus but not the family, as both, being supra-specoific names, are "artificial??),

Fossil Record

Palinurina Munster, from the Lower Lias and the Solnhofen Lagestatte, appears to be a member of the Palinuridae, a family which has the rostrum suppressed and the antennae very stout. *Podocrate*s Geinitz, from the Late Cretaceous and Eocene is hardly to be distinguished from the Early Cretaceous to Recent *Linuparus* Gray. *Cancrinos* Munster from Solenhofen, has short and very broad antennae. It may represent either an ancestor or the sister group to the family Scyllaridae (slipper lobsters), in which the antennae form broad flattened plates. Scyllaridia Bell is found in the Gault (MIddle Cretaceous) and London Clay (Eocene) while the Recent *Scyllarus* first appears in the Late Cretaceous. Zittel & Eastman 1913 (public domain) + Wikipedia

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Descriptions

Palinuroidea Latreille 1802

Synomym: Achelata Scholtz & Richter, 1995

Range: From the Jurassic

Phylogeny:

Phylogeny: Eureptantia **:** Astacura + Thalassinidea + Meiura + * **:** Palinuridae + Scyllaridae

Characters: absence of chelae (claws), great enlargement of the first antennae, "phyllosoma" form of the larva, and by a number of other characters (Scholtz & Richter 1995, via Wikipedia)

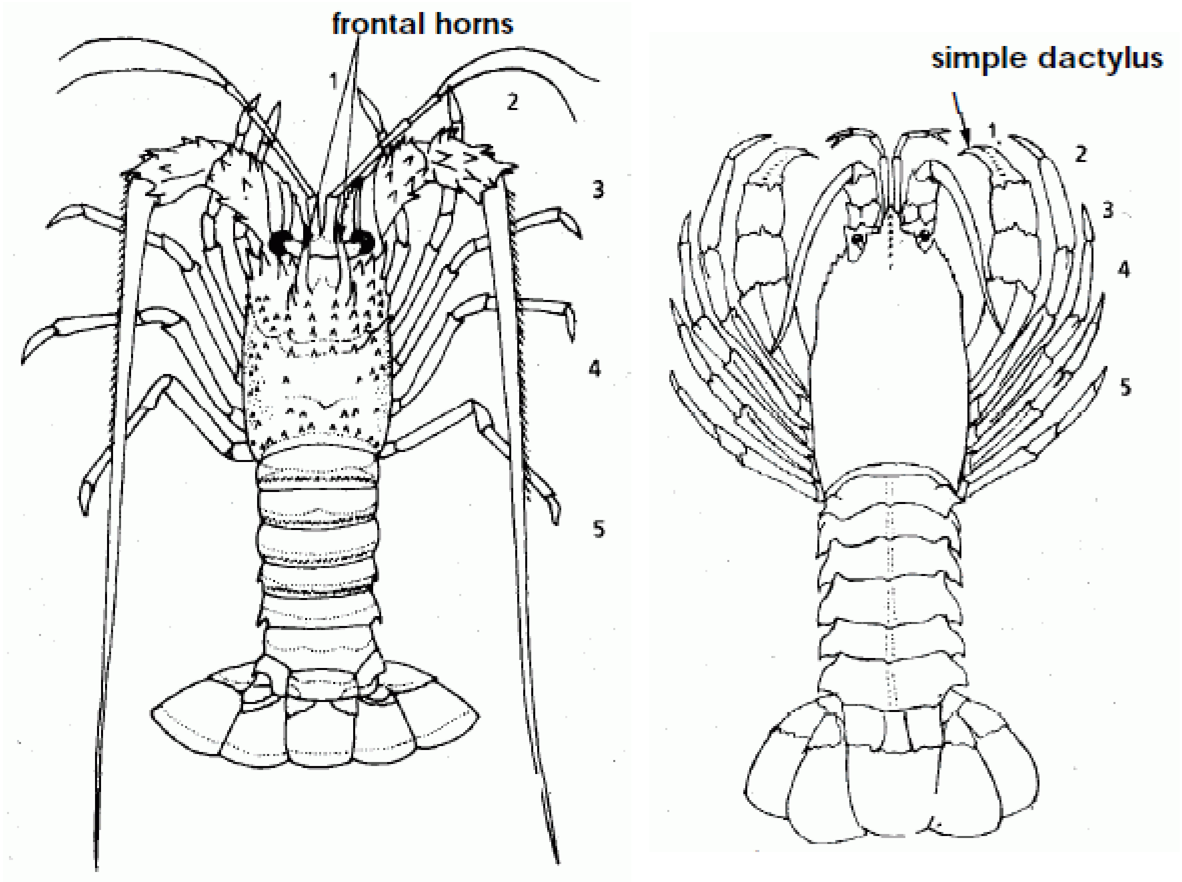
Comments: phylogenetic position in the decapod family tree very uncertain, about all that can be said is that they are more derived than the Eryonoidea MAK120527

Palinuridae Latreille 1802

Synonym: Synaxidae Bate, 1881 (Furry Lobsters)

Range: From the Jurassic

Phylogeny: Palinuroidea **:** Scyllaridae + *



Diversity of Palinuridae, showing the spiny lobster or classic Palinuridae on the left, and the highly derived furry lobster, formerly the family Synaxidae, on the right.
Images from Holthuis 1991, © FAO 1991, reproduced under permitted terms (noncommercial/educational)

Comments:. Spiny lobsters and Furry lobsters. These are quite distinct in appearance. Spiny lobsters have a carapace with numerous strong and less strong spines and two frontal horns over the eyes, and a rostrum absent or reduced to a single spine. Furry lobsters have a carapace with at most a few spines; no frontal horns, and a rostrum. Holthuis 1991 The antennae are not as enlarged as in spiny and slipper lobsters, and the body is covered in short hairs, hence the name furry lobster Wikipedia. Although the two have traditionally been placed in seperate famoilies, molecular phylogeny has shown that furry lobsters are a polyphyletic group within the family Palinuridae (Palero et al 2009)

Link: Encyclopedia of Life

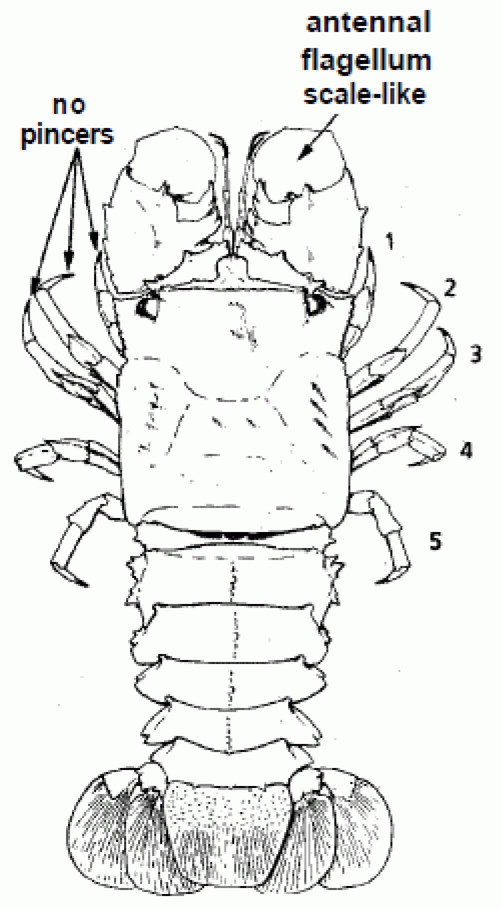
Scyllaridae Latreille, 1825

Range: From the Mid Cretaceous (or Late Jurassic if the stem species *Cancrinos claviger* is included)

Phylogeny: Palinuroidea : Palinuridae + *

Comments: cosmopolitan, found in all warm oceans and seas. Distinguished (like other Palinuroidea) by lack of chelae (claws), and instantly recognisable by their enlarged antennal flagellum reduced to a single broad and flat segment, similar to the other antennal segments, and projecting forward from the head as wide plates (see identification guide above right). Holthuis 1991, Wikipedia

Image credits above left, Peters underwater photos, via Wikipedia, Creative



Commons; above right (identification drawing) from Holthuis 1991, © FAO 1991, reproduced under permitted terms (noncommercial/educational)

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Decapoda: Reptantia

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--+--Stenopodidea
         `--Reptantia
            |--Palaeopalaemon
            |--Eryonoidea
            `--+==Glypheoidea
               |--Astacidea
               |--Thalassinidea
               |--Palinuroidea
               `--+--Anomura
                   `--Brachyura
```

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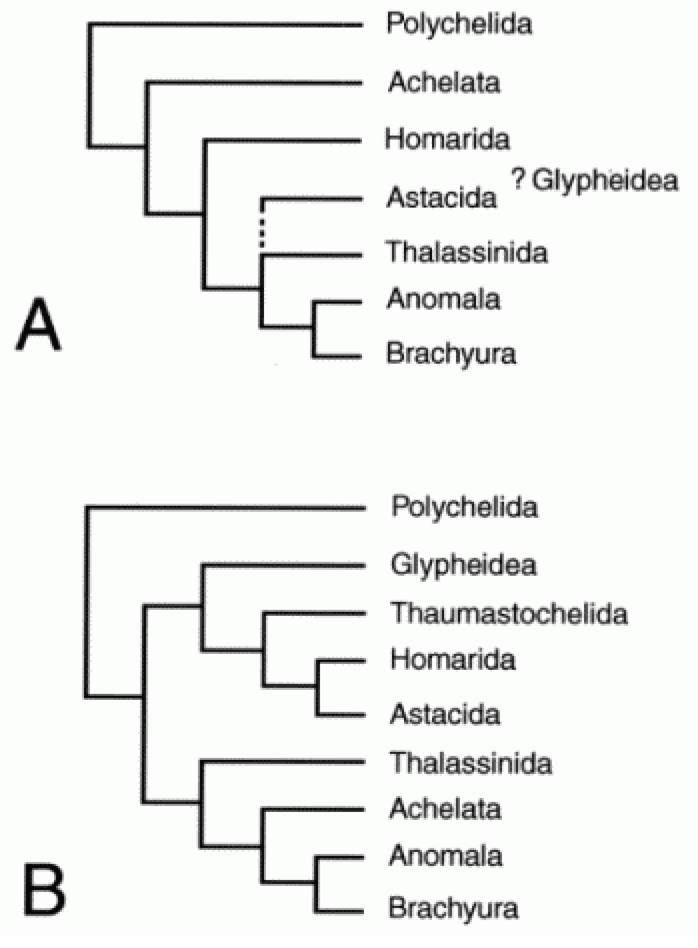
1. *Palaeopalaemon* X
2. Reptantia
3. Stenopodidea

The Reptantia or "walkers" (reptants for short) are the clade of crustaceans containing all decapods apart from the Natantia or "swimmers" , the shrimps and prawns, (presumably these would be called natants for short, but no-one uses the term Natantia anymore). Reptantia includes crabs and crab-like forms, lobsters and lobster-like animals, and freshwater crayfish (which are related to the lobsters proper) . Reptants are larger and more heavily built, with stronger and more robust legs, than natants, as a result of the shift in ecomorph from swimming and nektonic types to bottom dwellers. They are also much more morphologically diverse, featuring seemingly every possible morphotype within the basic bauplan - large claws, small claws, no claws, one set of claws, multiple pairs of claws, both main claws of the same size, one claw much bigger than the other, antennae shorter, antennae very long, body and thorax long, body ooval shaped, body short and broad, eyes stalked, eyes not stalked, and so on. The most successful of all the reptants are the short bodied Brachyura or true crabs, which invaded the littoral zone, and account for almost half of decapod biodiversity MAK120530

Phylogeny



Cladistic relationships of major reptant clades based on cladistic morphology-only analyses: A, Scholtz & Richter 1995, and B, Dixon et al 2003. There is agreement at the base and top of the tree but not the middle. From Ahyong & O'Meally 2004 fig 1

The uncertainity regarding reptant phylogeny is nothing unexpected; it is simply representative of the uncertainty regarding Crustacean phylogeny as a whole. There have to date been only two independent morphology-based cladistic analyses of the decapoda as a whole, those of Scholtz & Richter in 1995 and Dixon et al in 2003 (right). All agree regarding the basal (bottom of the tree) position of the Polychelida (in these pages we have used the more traditional term Eryonoidea, although Polychelidae can be applied to relict extant taxa), the polyphyly of the traditional Palinura (lobsters and lobster like forms, we use the term in a more specific context to refer to the spiny lobster *Palinurus* and related lineages) and a monophyletic crown clade Meiura (Anomura (crab-like forms) + Brachyura (true crabs)) as the most derived taxon (at the top of the decapod tree). Beyond that, there is no agreement. Both papers introduce a number of new clades, most of which are invalidated by the findings of the other paper; only Reptantia, Eureptantia and Meiura are recognised by both. For example the Achelata or spiny lobster group (= Palinura *sensu stricto*, or Palinuroidea) are either the second most basal group or the sister group of the highest clade (Meiura). There is a vague sort of consensus with the Thalassinidea, a small group previously placed in the Anomura, which is here either a possible sister group of the Meiura, or of Meiura + Achelata. A "total evidence" analysis by Ahyong & O'Meally 2004 incorporates aspects of both papers but again only the base and crown of the tree are in common with both of the other two. The problem with cladistics, despite its early promise, is that it faces the same homology vs homoplasy problem that defeated its fellow methodology phenetics. But pure molecular sequencing is no help here either. Unlike the mammals, where a quite stable consensus has emerged, with the decapods every study gives totally different results. Nor do even one of these studies match any of the rival morphology studies. For example the recent paper by Bracken et al 2009 replaces the Polychelidae with the Thalassinidea as the most he basal group. This is simply be due to anthropocentric bias - furry cuddly mammals are more like us than lobsters are - and hence there is more work done on, are more papers written about, mammals than there are about crusty crustaceans. And certainly there is more molecular consensus regarding arthropods as a whole than there is with particular groups. The problem remains though, as it does with mammals, or turtles, or any other sampled group, of the incompatability between molecules and morphology, and the morphological absurdities that a molecules-only phylogeny demands. The current tendency in phylogeny in general is certainly very much away from morphology and in favour of molecules, which seem far less suited to mapping deep phylogeny in groups that emerged through a sudden adaptive radiation over a short span of time, there now seems to be a counter movement back to very obscure neontological morpohological details and to paleontology to supplement the molecular sequencing and hopefully provoide a better picture.

The following syncretic dendrogram is abbreviated and slightly modified from the one byChristopher Taylor - Variety of LIfe and is mostly inspired by the more recent of the two cladistic studies mentioned earlier; Dixon et al 2003 ([DAS03] in the square brackets). It is provisionally included here to make it look like we know the details of the evolutionary tree, which we most patently do not. But don't use that last phrase as an excuse forcreationism. Evolution is a fact, like heliocentricism, electromagnetism, and gravity. And while it can also be said with equal certainty that God, or the devil (dependng on your theology), didn't put fossils in the ground to make the Earth look old, he certainly is in the details. So, on with the show (or just skip the following if it's too boring). MAK120529

```
Reptantia [Palinura, Palinuridea]
 |  i. s.: Acanthacaris DAS03
 |         Palaeopalaemon Whitefield 1880 B95, S77
 |         Chaeraps preissii [incl. C. preissii var. angustus] N24
 |         Halicarcinus HS01
 |         Leptograpsus variegatus HS01
 |         Liocarcinus corrugatus HS01
 |         Notomithrax HS01
 |         Fredius MT08
 |         Neosarmatium trispinosum W08
 |--Polychelidae [Eryonoidea, Polychelida] DAS03
 |    |--Cardus crucifer (Thomson 1873) [incl. Eryoneicus inermis Bernard 1953] B06
 |    |--Pentacheles B06
 |    `--Polycheles [incl. Eryoneicus Bate 1882 (nom. rej.)] B06
 `--Eureptantia DAS03
      |--Astacura DAS03
      `--Sterropoda [Anomura] DAS03
           |  i. s.: Paralithodes PH03
           |--Eurysternalia DAS03
           |    |--Achelata DAS03
           |    `--Meiura DAS03
           |         |--Anomala DAS03
           |         `--Brachyura DAS03
           `--Thalassinida [Callianassoidea, Thalassinidea] DAS03
```

References

[B95] Bousfield, E. L. 1995. A contribution to the natural classification of Lower and Middle Cambrian arthropods: Food-gathering and feeding mechanisms. Amphipacifica 2: 3-34.

[B06] Boyko, C. B. 2006. New and historical records of polychelid lobsters (Crustacea: Decapoda: Polychelidae) from the Yale Peabody Museum collections. Bulletin of the Peabody Museum of Natural History 47 (1-2): 37-46.

[DAS03] Dixon, C. J., S. T. Ahyong & F. R. Schram. 2003. A new hypothesis of decapod phylogeny. Crustaceana 76: 935-975.

[G75] Grant, E. M. 1975. Guide to Fishes. The Co-ordinator-General's Department: Brisbane (Australia).

[H47] Hatch, M. H. 1947. The Chelifera and Isopoda of Washington and adjacent regions. University of Washington Publications in Biology 10 (5): 155-274.

[HS01] Hayward, B. W., A. B. Stephenson, M. S. Morley, W. M. Blom, H. R. Grenfell, F. J. Brook, J. L. Riley, F. Thompson & J. J. Hayward. 2001. Marine biota of Parengarenga Harbour, Northland, New Zealand. Records of the Auckland Museum 37: 45-80.

[MT08] Magalhães, C., & M. Türkay. 2008. A new species of Kingsleya from the Yanomami Indians area in the upper Rio Orinoco, Venezuela (Crustacea, Decapoda, Brachyura, Pseudothelphusidae). Senckenbergiana Biologica 88 (2): 231-237.

[N24] Nicholls, G. E. 1924. Neoniphargus branchialis, a new freshwater amphipod from south-western Australia. Journal of the Royal Society of Western Australia 10 (14): 105-111.

[PH03] Pinheiro, M. A. A., & G. Y. Hattori. 2003. Embryology of the mangrove crab Ucides cordatus (Brachyura: Ocypodidae). Journal of Crustacean Biology 23 (3): 729-737.

[S77] Schram, F. R. 1977. Paleozoogeography of Late Paleozoic and Triassic Malacostraca. Systematic Zoology 26 (4): 367-379.

[W08] Wilson, B. 2008. Background information on Faure Island, Shark Bay, Western Australia. Records of the Western Australian Museum Supplement 75: 1-9.

Descriptions

Stenopodidea

Range: Fossil record only from the Mid Cretaceous; ghost lineage suggests Devonian origin

Phylogeny: Pleocyemata **:** Caridea + (Reptantia + *)

Comments: Stenopodidea (which contains the so-called "boxer shrimp" or "barber-pole shrimp") MAK120518

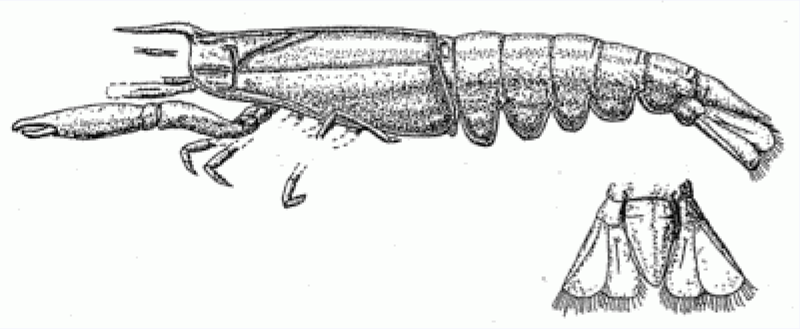
Reptantia

Range: From the Devonian

Phylogeny: Pleocyemata **:** Caridea + (Stenopodidea + * **:** *Palaeopalaemon* + (Eryonoidea + Eureptantia)

Characters:. Synapomorphies (from Dixon et al. 2003): Pereiopods articulating in a medio-lateral manner (enabling walking); first two segments of PI fused together. Carapace is calcified and flattened, telson lacking spines. Mandible with long articulation along anterior edge. Third maxilliped shortened relative to other thoracopods; first pereiopod enlarged.. - CKT.

Palaeopalaemon



Range: Devonian

Phylogeny: Reptantia **:** (Eryonoidea + Eureptantia) + *

Comments: this species has been widely assigned to various repantian taxa, but about all that can be said odf it for certain is that it is the earliest known decapod. It shows that as early as the Devonnian, the decapods had already diverged into shrimp- and lobster-like lineages. Although *Palaeopalaemon* shares a characteristic of the Thalassinidea and the Meiura, we propose a new name, Lineata, carapace lineae, which suggests it may be related to these taxa. However this would require a number of long ghost lineages to explain the anbsense of Paleozoic fossils (Schram & Dixon, 2003). It also does not explain the poor molecular resolution of the Reptantia as a whole, which only makes sense if all the major clades in the group diverged in a short period. . We believe it is more parsimonious therefore to assume that this feature is teh result of convrgence, and appeared independently in at least three groups, and that the the Reptantia was arather insignificant and not very diverse group for the first third of its history. It was only in surviving the great P-T extinction event that *Palaeopalaemon*'s descendants would initate perhaps the most dramatic and important event in crustacean evolution since the Cambrian explosion, the sudden and radical adaptive radiation of "crawlers" (Repantia) to replace the mass extinction of almost all other large aquatic arthropods at the end of the Paleozoic. MAK120528

Image: *Palaeopalaemon newberryi*, from Schram 2009

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Decapoda: Thalassinidea

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
         |--Eryonoidea
         `--Eureptantia
            |--Thalassinidea
            |--Palinuroidea
            `--+--Anomura
               `--Brachyura
```

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1. Thalassinidea

Under construction

Thalassinidea is an infraorder of decapod crustaceans that live in burrows. Recent molecular analyses have shown this group to be most closely related to Brachyura (crabs) and Anomura (hermit crabs and their allies). The monophyly of the group is not certain; recent studies have suggested dividing the group into two infraorders, Gebiidea and Axiidea.[3].

There are believed to be 556 extant species of thalassinideans in 96 genera,[4] with the greatest diversity in the tropics, although with some species reaching latitudes above 60° north. About 95% of species live in shallow water, with only three taxa living below 2,000 metres.[5] - Wikipedia

[3] Sammy De Grave, N. Dean Pentcheff, Shane T. Ahyong et al. (2009). "A classification of living and fossil genera of decapod crustaceans". Raffles Bulletin of Zoology Suppl. 21: 1–109.
[4] Peter C. Dworschak (2005). "Global diversity in the Thalassinidea (Decapoda): an update (1998-2004)". Nauplius 13 (1): 57–63.
[5] Peter C Dworschak (2000). "Global diversity in the Thalassinidea (Decapoda)". Journal of Crustacean Biology 20: 238–243.

Fossil Record

The Recent genus *Callianassa* Leach is known from the Kimmeridgian, as well as from the Cretaceous and Tertiary. *Thalssian* Latreille is Tertiary and Recent.Zittel & Eastman 1913 (public domain) - needs updating

Phylogeny

The following dendrogram is abbreviated from the one by Christopher Taylor - Variety of LIfe MAK120522

```
`--Thalassinida [Callianassoidea, Thalassinidea] DAS03
     |  i. s.: Ctenochelidae CA04
     |           |--Anacalliax MD01
     |           `--Callianopsis de Saint Laurent 1973 CA04
     |         Thomassiniidae MD01
     |--Jaxea [Laomediidae] DAS03
     `--+--+--Thalassina [Thalassinidae, Thalassinidea] DAS03
        |  `--+--Eiconaxius acutifrons Bate 1888 DAS03
        |     `--Axioidea MD01
        |          |--Micheleidae MD01
        |          |--Strahlaxiidae MD01
        |          `--Calocaris DAS03 [Calocarididae MD01]
         `--+--Upogebia Leach 1813 DAS03, B55 [Upogebiidae MD01]
           `--+--Callianidea [Callianideidae] DAS03
              `--Callianassidae MD01
                   |--Callichirus Stimpson 1866 [Callichirinae] CF06
                   `--Callianassa Leach 1814 DAS03, B55
```

References

[B55] Bott, R. 1955. Dekapoden (Crustacea) aus El Salvador. 2. Litorale Dekapoden, außer Uca. Senckenbergiana Biologica 36: 45-70.
[CA04] Casadío, S., A. de Angeli, R. M. Feldmann, A. Garassino, J. L. Hetler, A. Parras & C. E. Schweitzer. 2004. New decapod crustaceans (Thalassinidea, Galatheoidea, Brachyura) from the Middle Oligocene of Patagonia, Argentina. Annals of Carnegie Museum 73 (2): 25-47.
[CF06] Crawford, R. S., R. F. Feldmann, D. A. Waugh, B. M. Kelley & J. G. Allen. 2006. Decapod crustaceans from the Maastrichtian Fox Hills formation. Bulletin of the Peabody Museum of Natural History 47 (1-2): 3-28.
[DAS03] Dixon, C. J., S. T. Ahyong & F. R. Schram. 2003. A new hypothesis of decapod phylogeny. Crustaceana 76: 935-975.
[MD01] Martin, J. W., & G. E. Davis. 2001. An updated classification of the Recent Crustacea. Natural History Museum Los Angeles County, Science Series 39: 1-124.

Descriptions

Thalassinidea Latreille, 1831

Range: From the Jurassic

Phylogeny: Eureptantia **:** Astacura + Palinuroidea + Meiura + *

Comments: The position of the Thalassinidea, and whether they are even monophyletic, is controversial. In some phylogenies, they are basal Reptantia, in others, intermediate between lobsters and crabs and crab-like forms. MAK120531

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Decapoda: Classification

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
         |--Eryonoidea
         `--Eureptantia
            |--Astacidea
            |--Palinuroidea
            `--+--Anomura
               `--Brachyura
```

Contents

The following very provisional classification is copied from Wikipedia, and does not include many extinct taxa

---

Superclass Crustacea
  Class Malacostraca Latreille, 1802
    Subclass Eumalacostraca Grobben, 1892
      Superorder Eucarida Calman, 1904
        Order Decapoda Latreille, 1802 (Most extant crustaceans, crabs, lobsters, prawns, etc, Devonian - Rec)
          Suborder Dendrobranchiata Bate, 1888
                  Superfamily Penaeoidea Rafinesque, 1815
                  Superfamily Sergestoidea Dana, 1852
          Suborder Pleocyemata Burkenroad, 1963
            Infraorder Stenopodidea Bate, 1888
            Infraorder Caridea Dana, 1852

Superfamily Procaridoidea Chace & Manning, 1972
Superfamily Galatheacaridoidea Vereshchaka, 1997
Superfamily Pasiphaeoidea Dana, 1852
Superfamily Oplophoroidea Dana, 1852
Superfamily Atyoidea De Haan, 1849
Superfamily Bresilioidea Calman, 1896
Superfamily Nematocarcinoidea Smith, 1884
Superfamily Psalidopodoidea Wood-Mason, 1874
Superfamily Stylodactyloidea Bate, 1888
Superfamily Campylonotoidea Sollaud, 1913
Superfamily Palaemonoidea Rafinesque, 1815
Superfamily Alpheoidea Rafinesque, 1815
Superfamily Processoidea Ortmann, 1896
Superfamily Pandaloidea Haworth, 1825
Superfamily Physetocaridoidea Chace, 1940
Superfamily Crangonoidea Haworth, 1825
Infraorder Polychelida Scholtz & Richter, 1995
Superfamily Eryonoidea De Haan, 1841. (monotypal)
Family Coleiidae Van Straelen, 1924 †
Family Eryonidae De Haan, 1841 †
Family Palaeopentachelidae Ahyong, 2009 †
Family Polychelidae Wood-Mason, 1875
Family Tetrachelidae Beurlen, 1930 †
Infraorder Astacidea Latreille, 1802
Superfamily Enoplometopoidea de Saint Laurent, 1988
Superfamily Nephropoidea Dana, 1852
Superfamily Astacoidea Latreille, 1802
Superfamily Parastacoidea Huxley, 1879
Infraorder Glypheidea Winckler, 1882
Superfamily Glypheoidea Winckler, 1882
Family † Chimaerastacidae Amati, Feldmann & Zonneveld, 2004
Family Glypheidae Winckler, 1882
Family † Mecochiridae Van Straelen, 1924
Family † Pemphicidae Van Straelen, 1928
Family † Platychelidae Glaessner, 1969
Superfamily † Erymoidea Van Straelen, 1924
Family † Erymidae Van Straelen, 1924
Infraorder Axiidea de Saint Laurent, 1979b
Infraorder Gebiidea de Saint Laurent, 1979
Infraorder Achelata Scholtz & Richter, 1995
Infraorder Anomura MacLeay, 1838
Superfamily Aegloidea Dana, 1852
Superfamily Galatheoidea Samouelle, 1819
Superfamily Hippoidea Latreille, 1825a
Superfamily Kiwaoidea Macpherson, Jones & Segonzac, 2005
Superfamily Lithodoidea Samouelle, 1819
Superfamily Lomisoidea Bouvier, 1895
Superfamily Paguroidea Latreille, 1802
Infraorder Brachyura Linnaeus, 1758 (Crabs; Trias-Rec)
Section Dromiacea De Haan, 1833
Superfamily Dromioidea De Haan, 1833
Superfamily Homolodromioidea Alcock, 1900
Superfamily Homoloidea De Haan, 1839
Section Raninoida De Haan, 1839
Section Cyclodorippoida Ortmann, 1892
Section Eubrachyura de Saint Laurent, 1980
Subsection Heterotremata Guinot, 1977
Superfamily Aethroidea Dana, 1851

- Superfamily Bellioidea Dana, 1852
- Superfamily Bythograeoidea Williams, 1980
- Superfamily Calappoidea De Haan, 1833
- Superfamily Cancroidea Latreille, 1802
- Superfamily Carpilioidea Ortmann, 1893
- Superfamily Cheiragonoidea Ortmann, 1893
- Superfamily Corystoidea Samouelle, 1819
- Superfamily Dairoidea Serène, 1965
- Superfamily Dorippoidea MacLeay, 1838
- Superfamily Eriphioidea MacLeay, 1838
- Superfamily Gecarcinucoidea Rathbun, 1904
- Superfamily Goneplacoidea MacLeay, 1838
- Superfamily Hexapodoidea Miers, 1886
- Superfamily Leucosioidea Samouelle, 1819
- Superfamily Majoidea Samouelle, 1819
- Superfamily Orithyioidea Dana, 1852c
- Superfamily Palicoidea Bouvier, 1898
- Superfamily Parthenopoidea MacLeay,
- Superfamily Pilumnoidea Samouelle, 1819
- Superfamily Portunoidea Rafinesque, 1815
- Superfamily Potamoidea Ortmann, 1896
- Superfamily Pseudothelphusoidea Ortmann, 1893
- Superfamily Pseudozioidea Alcock, 1898
- Superfamily Retroplumoidea Gill, 1894
- Superfamily Trapezioidea Miers, 1886
- Superfamily Trichodactyloidea H. Milne-Edwards, 1853
- Superfamily Xanthoidea MacLeay, 1838

Subsection Thoracotremata Guinot, 1977

- Superfamily Cryptochiroidea Paul'son, 1875
- Superfamily Grapsoidea MacLeay, 1838
- Superfamily Ocypodoidea Rafinesque, 1815
- Superfamily Pinnotheroidea De Haan, 1833

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Decapoda: Dendrogram

Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           `--+--Anomura
              `--Brachyura
```

Contents

The phylogeny of the Decapoda here follows Schram and Dixon, 2004, , except for *Palaeopalaemon*, which is more conventionally placed a s abasal Astacidean (lobster)

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata (= "Natantia" in part)
   `--Pleocyemata
      |--Caridea  (= "Natantia" in part)
      `--+--Stenopodidea (= "Natantia" in part)
         `--Reptantia
            |--Palaeopalaemon
            |--Eryonoidea (= Polychelida)
            |  |--Tetrachela
            |  `--+--Eryonidae
            |     `--+--Palaeopentacheles
            |        `--+--Coleiidae
            |           `--Polychelidae
            `--Eureptantia
               |--Pemphicidae
               |--Astacura
                |  |--Glypheoidea
```

```
|  |  |--Glypheidae
|  |  `--Mecochridae
|  `--Astacidea
|     |--Astacida
|     |--Homarida
|     `--+--Erymida
|        `--Enoplometopidae
|--Thalassinidea
|--Palinuroidea (Achelata)
|  |--Palinuridae
|  `--Scyllaridae
`--Meiura  (see also Alternative phylogeny)
   |--Stem Anomura
   |   |--Platykotta
   |   `--+--Eocarcinus
   |      `--Crown Anomura
   |         |--Hippoidea
   |         `--Aeglidae
   |            |--Galatheoidea
   |            |--Kiwa
   |            |--Lomis
   |            `--+--Paguroidea
   |               `--Lithodoidea
   `--Brachyura
       |--Homolodromioidea
       `--+--Dromiacea
          |--Raninoida
          |  |--Cyclodorippoidea
          |  |--Dakoticancroidea
          |  `--Raninidae
          `--Eubrachyura
              |--Heterotremata
              `--Thoracotremata
```

Alternative phylogeny:

```
`--Meiura
   |--Platykotta
   `--+--Eocarcinus
      |--Anomura
      `--Brachyura
```

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Abbreviated Dendrogram

```
MALACOSTRACA
|
`--DECAPODA
   |--Dendrobranchiata
   `--+--Caridea
      `--Reptantia
        |--Eryonoidea
        `--Eureptantia
           |--Astacidea
           |--Palinuroidea
           `--+--Anomura
              `--Brachyura
```

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Hexapoda

The Insects

Abbreviated Dendrogram

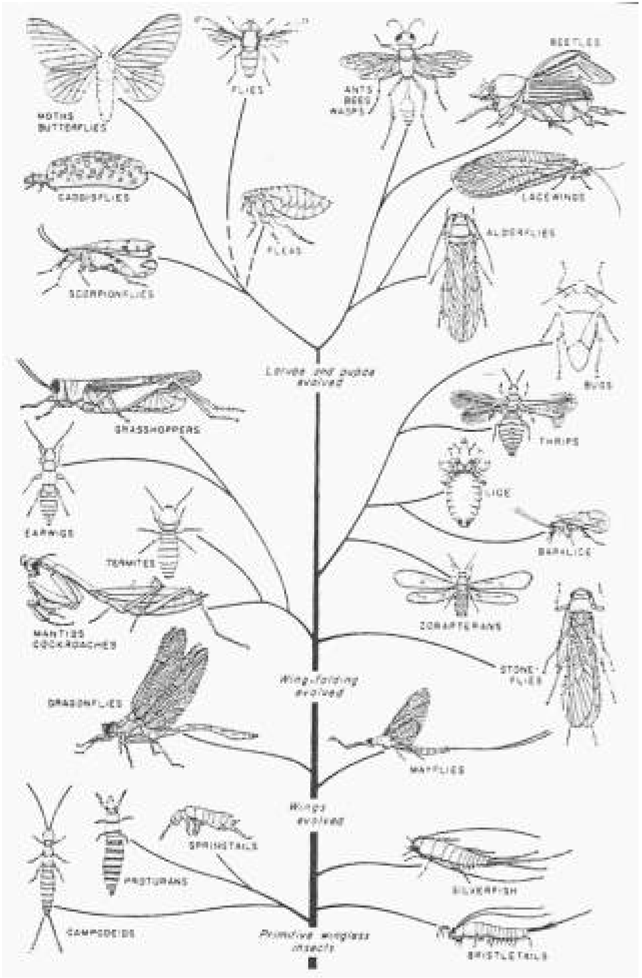
```
MANDIBULATA
|--MYRIAPODA
`--+--CRUSTACEA
   |
   `--HEXAPODA
      |--+--Protura
      |  `--Collembola (springtails)
      `--+--Diplura
         `--INSECTA (insects)
```

Contents

The Insects - Four hundred million years of glorious evolution

The most diverse and abundant (or perhaps second most abundant, after nematodes) type of animal life on Earth today, insects, or hexapods (six legged animals), are small terrestrial arthropod distinguished by their six legs and division of the body into three parts: head, thorax, and abdomen. they are also the only invertebnrates with the power and flight, and this may well be a factor in their success, although some wingless types, such as the tiny Collembola, are astonishingly successful and abundant.

The diagram shown at the right presents a simple "tree of life" representation of the evolutionary relationships of the insects. Insects through their long evolutionary history show a number of distinct evolutionary stages towards greater complexity, represented artistically and metaphorically as ascent up the tree (for reasons expressed elsewhere the present writer (MAK) does not agree with the current trend to reject all reference to evolutionary advancement to greater complexity). However if the time dimension were added, then the tree would resemble a sort of multiple bush, with sudden bursts of evolutionary novelty, then nothing happening for a hundred million years or so and the various lineages continuing alongside each other,



Evolution of the insects, from Prothero, 1990, url. Although insect evolution is not quite as linear as this, insect evolution, like that of other major groups, does involve a number of progressive evolutionary grades or stages.

then another burst of novelty, and so on. Hence during the Early Devonian there is a sudden evolutionary radiation of primitive wingless insects. Nothing much happens for a long time, then suddenly during the mid Carboniferous one of these lineages gives rise to paleopterous (dragonfly-like) insects, and there is another extraordinary adaptive radiation (while the flightless insects continue humbly in the background). One of these dragonfly-like types very quickly (geologically speaking) evolves into the ancestral folding wing insects, and there so there are two huge evolutionary radiations alongside each other, the dragonfly types (called Paleoptera) and the early cockroach and grasshopper types (called Neoptera). Nothing happens for a while, with both groups existing alongside each other. Then at some time during the middle Permian one of the folding wing types evolves into the ancestral holometabolic insects which, as their name indicates, undergo transformation through their life cycle. These last named are the most successful of the whole group, including flies (diptera), beetles (coleoptera) and, only much later, butterflies and moths (lepidoptera), and ants bees and wasps (hymenoptera)

Although "insect" has been used in the above paragraph in a colloquial sense, technically speaking we should distinguish here between hexapods and insects, as these two terms are sometimes confused or synonymised. Although colloquially, all hexapods are also insects, and although some (e.g. Cavalier-Smith 1998) have synonymised the two (in which case they are referred to by their earlier name, Class Insecta), in current cladistic classifications, insects are a subgroup of hexapods, albeit the largest and most diverse one. Hence we have divided these units according to evolutionary grades. The five grades are:

> **Hexapoda** - six legs, three tagma, spiracles (the latter shared with myriapods)
> **Insecta** - similar to above, but distinguished by further synapomorphies
> **Pterygota** - wings
> **Neoptera** - folding wings
> **Holometabola** (or just **Metabola** - ref) - change of form during life cycle

Updating the insect tree of life diagram, this can be arranged in the form of a dendrogram, as follows

```
Hexapoda
|==Several hexapod groups (primitive wingless insects)
 `--Insecta
   |==Wingless insects (silverfish and their relatives)
    `--Pterygota (winged insects, or secondarily wingless)
      |==Paleoptera ("ancient wings" - primitive winged insects)
```

```
`--Neoptera ("new wings" - can fold wings)
   |==Many different
   |==insect groups
   `--Holometabola (higher insects, with complete larval to adult metamorphosis)
```

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Hexapoda

Abbreviated Dendrogram

```
MANDIBULATA
|--MYRIAPODA
`--+--CRUSTACEA
   |
   `--HEXAPODA
      |--+--Protura
      |  `--Collembola (springtails)
      `--+--Diplura
         `--INSECTA (insects)
```

Contents

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1. Hexapoda

Introduction

While crustaceans are the dominant group of arthropods in marine environments, hexapods, including insects, rule the land. Their dominance among animals is evident in their numbers of species, with over 750,000 described (Wilson, 1988), as well as biomass (e.g. Fittkau and Klinge, 1973).

As the name indicates the Hexapoda have six legs, one pair per thoracic segment. Thebody segments are fused into three body regions: a head, thorax, and abdomen.. A single pair of preoral antennae are present. The waxy epicuticle protects against desiccation. The superclass Hexapoda includes so-called true insects and several orders or classes (depending on your preference) of primitive wingless proto-insects, the Collembola, Protura, and Diplura (Manton 1979). These are soil or litter dwellers. Collembola (springtails) are perhaps the most abundant arthropods on earth. Proturans are very small, pale arthropods that are rarely encountered. Diplurans (right) include a few families of larger, pale arthropods that are frequently found in moist soils. Of the four or so hexapod classes, only the Class Insecta possess wings. DRM 02xxxx ToL, MAK020507, 120515

Image: Campodeid (Diplura), photo Creative Commons Attribution © 2002 David R. Maddison

Evolution and Fossil Record

The oldest well-known fossil hexapod is called *Rhyniella praecursor*, a collembolan from the Early Devonian-age Rhynie Chert. This and other small, wingless forms may have been an important part of the early terrestrial ecosystem, mainly detritivores foraging in soil and plant litter (the most primitive of the true insects, the Thysanura or silverfish, have a similar lifestyle, and have adapted well to human habitats). By the middle Carboniferous, a number of insect lineages appeared Carpenter 1992, and insects have dominated the terrestrial microfauna ever since.

Hexapod Phylogeny

Morphological and embryological evidence points to the Hexapods being related most closely either to the Myriapods; molecular sequencing and some morphology however argues for Crustacea as the sister group; molecular evidence alone - but not morphology!, - has Crustacea as the parent clade MAK020507, 120515

The position of Diplura in the hexapods is unclear. Traditionally, it has been placed with the Collembola and Protura in a group called "Entognatha",

```
o Hexapoda
|--Entognatha
|    |--+--Collembola
|   |   `--Protura
|    `--Diplura
`--Insecta
```

so named because members of these three orders all have the base of the mouthparts internalized, so that the mandible and maxilla are partly contained within the head capsule. In addition to this derived similarity in mouth structure, these three orders share reduced Malpighian tubules and compound eyes. However, there is some evidence that diplurans may instead be the sister group of insects:

```
o Hexapoda
|--+--Collembola
|  `--Protura
`--+--Diplura
   `--Insecta
```

Derived characteristics linking diplurans with insects include the presence of filiform cerci, and an extra set of nine single tubules in the axoneme of the sperm. For a more detailed discussion of the evidence, with additional references, see Kristensen (1991). - DRM 02xxxx ToL

Hexapods as uniquely terrestrial

All known recent and fossil hexapods are air breaters. The few aquatic insects are usually able to live in the water by trapping air bubbles against their spiracles (respiratory openings). This shows that they developed from an arthropod group that was already breathing air, although the precise ancestry remains uncertain, as no transitional fossil types are known. Terrestrial arthropods - insects, arachnids, and myriapods, are one of only two groups of animals that are truly adapted to terrestrial life, in that they manage water to an extent that allows them to explore the terrestrial habitat fully; the other being the Amniota vertebrates - MAK120515, adapted from UA Geosciences.

Descriptions

Hexapoda

Range: Early Devonian to Recent

Phylogeny: Mandibulata **:** Myriapoda + (Crustacea + * **:** (Protura + Collembola) + (Diplura + Insecta))))

Comments: The most distinctive feature of the hexapods is the reduction in walking appendages to six, with three body segments consolidating to form the thorax, which provides much of the locomotory ability of the animals. (n contrast to other arthropods, most of which have more than three pairs of legs.) - David R. Maddison, ToL CC-BY 2002

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Abbreviated Dendrogram

```
MANDIBULATA
|--MYRIAPODA
`--+--CRUSTACEA
   |
   `--HEXAPODA
      |--+--Protura
      |  `--Collembola (springtails)
      `--+--Diplura
         `--INSECTA (insects)
```

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Insecta

Abbreviated Dendrogram

```
HEXAPODA
|
`--INSECTA (insects)
   |--Archaeognatha
   `--+--Monura
      `--+--Thysanura
         `--PTERYGOTA
```

Contents

The common silverfish *Lepisma saccharina* (Thysanura - Lepismatidae). This primitive creature has proved remarkably adept at co-existing with humans
Photograph by Miroslav Deml, via Encyclopedia of Life, Creative Commons Attribution.

Whether one defines hexapoda as synonymous with, or the more inclusive clade that includes, the insects doesn't really matter much, as all the small wingless forms that evolved during the Devonian evolutionary radiation of life on land are basically very similar. The various groups considered here constitute an evolutionary seqyuence that in its broad lines can be quite clearly traced. The problem of whether the nearest relative of hexapods/insects are myriapods or crustaceans has been discussed elsewhere.

Actually, dividing the wingless insects among two units is really just an artifact of cladistic analysis, as both morphological and molecular studies agree that some wingless insects are more clearly further from the winged insects than others, and therefore some are more basal (primitive) and go in a more inclusive clade, others more derived (specialised, advanced) and so should be considered separately. Hence this unit can also be called "Wingless Insects part 2,". But because it is also about Insects as such, we have dedicated a whole page just to insects of all kinds, regardless of whether they are with or without wings MAK120516

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Insecta

Abbreviated Dendrogram

```
HEXAPODA
|
`--INSECTA (insects)
   |--Archaeognatha
   `--+--Monura
      `--+--Thysanura
         `--PTERYGOTA
```

Contents

Insecta-1

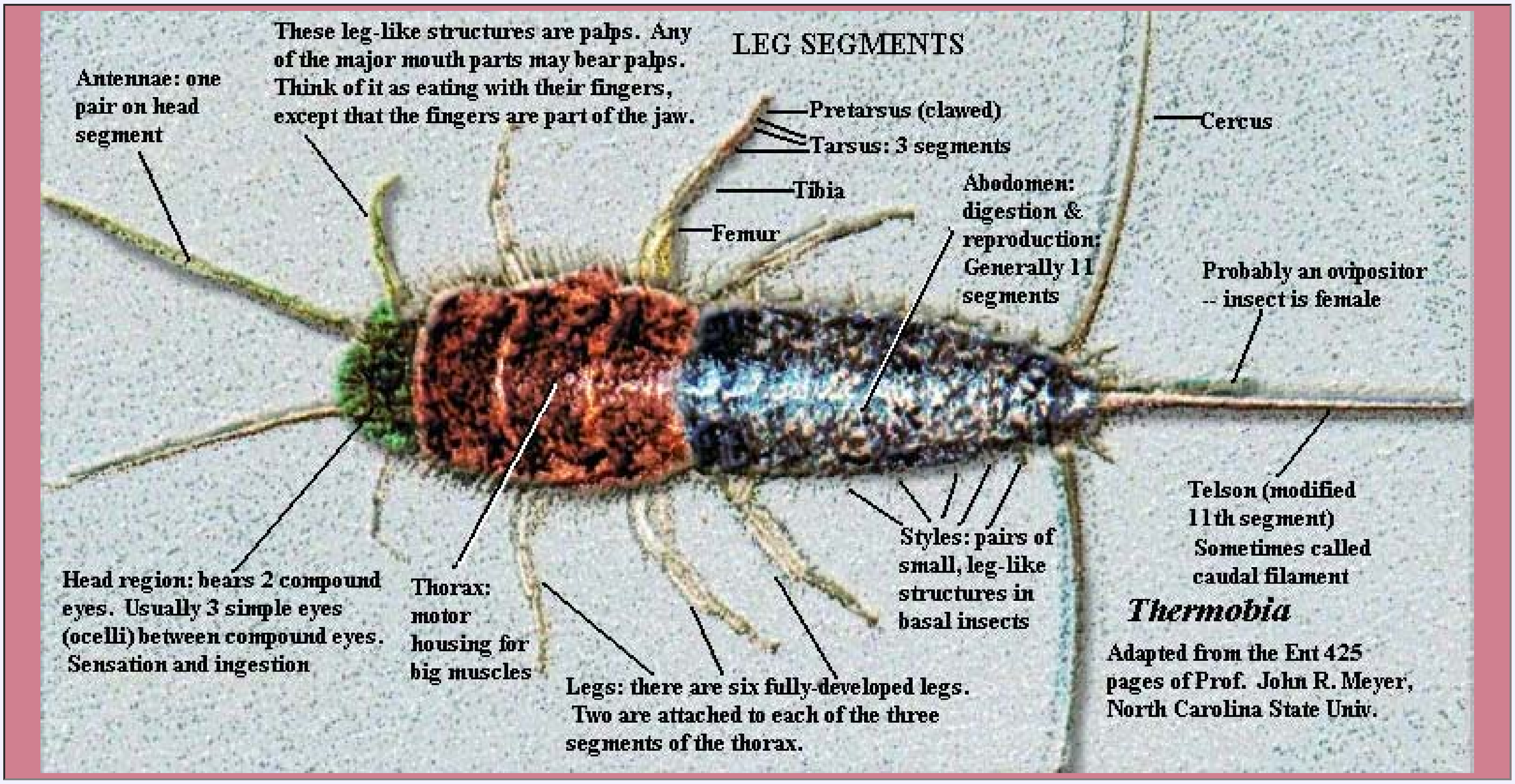
One of the most extraordinary groups of living organisms, insects account for many more species than all other groups of animals and plants combined. Although there are more than 800,000 known species, this is believed to be only a small fraction of total, which may run as high as ten million or more. Add to this innumerable species from Earth's past ages (only a tiny fraction of which have left any fossil remain) and one might guess that the number of species that have ever lived on Earth, past and present, may well amount to a billion (a thousand million).

Insects include among their number parasites, parasitoids, carnivores, herbivores, scavengers, and detritivores. As adaptations to different food different types of insects are distinguished by any of several types of mouthparts - chewing, sucking etc. Finally, all more advanced insects go through a metamorphosis of some kind. This may be a partial metamorphosis (*Hemimetabolous*) in the case of the exopterygotan insects, or a complete metamorphosis

(*Holometabolous*) in the case of the endopterygotan insects

Insects, both in the strict sense of Class Insecta and the broader sense of Superclass Hexapoda ("six-legged") - are characterized by having three tagmata - that is, a body divided into head, thorax, and abdomen - and three pairs of legs on thorax.

Insect Anatomy



Adapted from the Ent 425 pages of Prof. John R. Meyer, North Carolina State Univ.

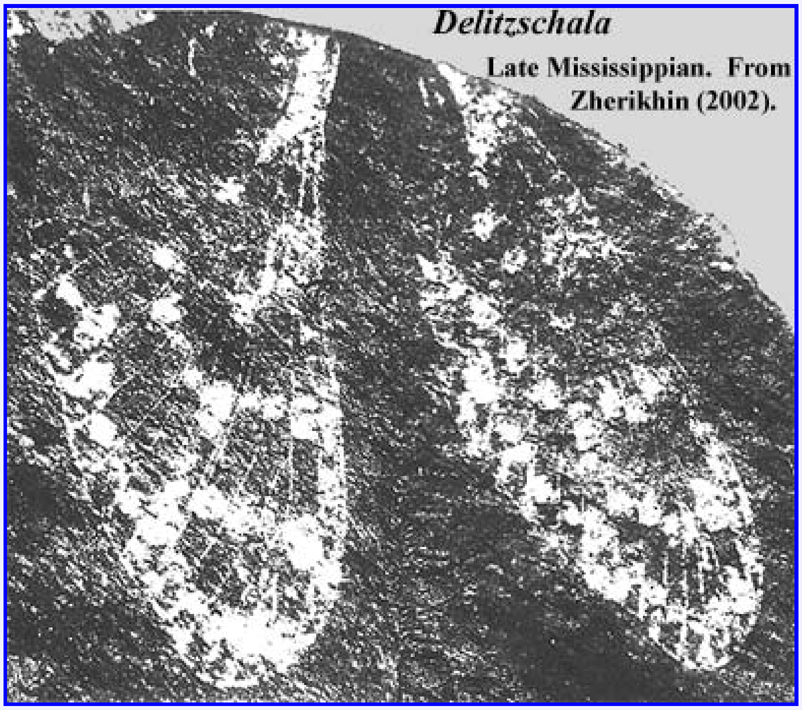
The very basic external anatomy of insects is all we're going to cover here, and most of the information is in the image above. The head has a single pair of antennae (Crustacea, in contrast, are distinguished by possession of two pairs), and a pair of compound eyes. Compound eyes - a common arthropod feature - differ from vertebrate eyes in that, instead of a single lens, each eye has a large number of small lenses, around 4,000 in the case of the common fly. While not good for seeing precisely at long distances, compound eyes are very good at detecting movement. Between the compound eyes are usually three simple eyes, or *ocelli*. The head also contains the mouth and jaws which we will take up elsewhere. It is worth noting that most of the basal insects have mouths which are *prognathous*. The mouth faces forward here at the root of the insect tree. More derived insect have *hypognathous*, or downward- facing, mouths. Any of the major mouth parts may develop grasping *palps*.

The middle part of the body, the thorax, contains the three pairs of legs. Insects have fewer legs than any other arthropod. Depending on the adaptation and lifestyle, the legs are used for walking, swimming, jumping or digging. The overall structure of the thoracic legs is described in the figure of *Thermobia*. In addition to the pretarsus, tarsus, tibia and femur, insects have two proximal (closer to the body) segments not shown in the figure. These are the *trochanter*, which acts as a swivel joint for the leg, and the *coxa*, which anchors the leg to the body. Each of the thoracic and abdominal segments has an upper plate (*tergum*) and lower plate (*sternum*). The region which joins them is called the *pleuron*. It is pierced with openings (*spiracles*) for the insect respiratory system.

In most insects (the Pterygota) the thorax posses one or two pairs of wings for flying. The wings are lost in some groups - e.g. fleas. In the very primitive insects discussed on this page, wings did not evolve.

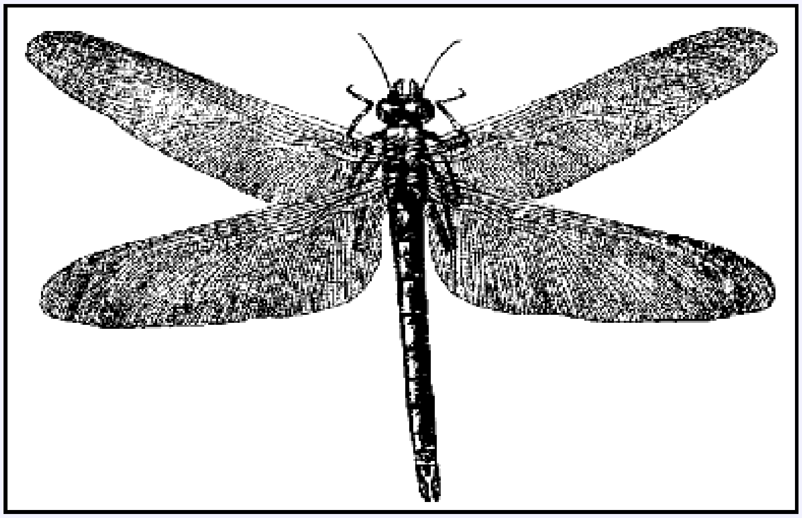
The abdomen is distinguished by 11 segments, and contains the main body organs, such as the heart, respiratory system, digestive system and reproductive system. The Parainsecta (springtails and proturans) and Diplura (diplurans) are not true insects, for their numbers of abdominal segments vary. These basal Hexapoda are not true insects. Thus, you will note, Insecta is an apomorphy-based definition. That is, it is defined by physical characteristics allegedly shared uniquely by this group. See cladograms.

The Evolutionary History of the Insects



The earliest known proto-insects were tiny wingless forms from the Early Devonian, perhaps somewhere near the paleoequator. Eskov (2002). The best known Devonian forms are the archaic collembellan (springtail), *Rhyniella praecursor*. The first true insect may be *Rhyniognatha praecursor* from the Early Devonian (Pragian) of the Rhynie Chert. However, insects remained very rare and marginal members of the terrestrial fauna through the Mississippian. The arthropod communities were dominated by arachnids and myriapod-like animals Zherikhin (2002). These earliest insect species were probably detritivores, scavenging for organic matter in the thin soils of the time, although some species may have been herbivores feeding on live plants. It is almost certain that detritivory appeared first. Zherikhin (2002). Most earlier insects, to the extent they fed on living plants at all, seem to have been specialist feeders on pollen or other enriched plant products. It is only recently that true insect herbivory - leaf-eating -- has been securely documented in the Jurassic, although this mode of life presumably developed earlier. Rasnitsyn & Krassilov (2000).

Insect flight developed suddenly during the Middle Carboniferous -- in the latest Serpukhovian/earliest Bashkirian. The evolutionary radiation of winged insects was a dramatic, exponential event, like the origin of multi-celled animals (Metazoa) at the base of the Cambrian, which only took about five million years. It is unlikely that winged insects existed during the mid Serpukhovian or the late Viséan Age, as none have been found at high preservation sites like Dora in Scotland. The tropical Euramerican province seems to have become a factory of insect diversity in the Carboniferous. All fifteen insect orders known from the Carboniferous are first known from Euramerica, a pattern that continued into the Permian. Eskov (2002).



Several distinct types of insects are known from the late Serpukhovian and early Bashkirian Ages. These include the palaeopteran *Erasipteron larischi* (Meganisoptera), the orthopteroid *Stygne roemeri* (Paraplecoptera), the fragmentary *Metropator pusillus* (uncertain relationships), pollen-eating(?) Palaeodictyoptera, like *Severinopsis vetusta*, and othopterid-like forms representing the very earliest herbivores. By the end of the Carboniferous, the insects had evolved into a large number of distinct orders, including many dragonfly-like forms. This was the heyday of the Palaeoptera.

The Permian period saw the continuation of all the Carboniferous types, plus a number of important new forms. The Palaeopterans continued to be well-represented, the blattoid and orthopteroid orders attained their greatest diversity, and new groups like the Psocoptera, homopteran Hemiptera, Mecoptera and Coleoptera, were all abundant and diverse.

But hard times were ahead. The Permian extinction events took out at least nine orders of insects, and the Mesozoic saw the decline and extinction of many more of the Permo-Carboniferous lineages. On the other hand, there was diverse evolution within the surviving orders, the Neuroptera, Mecoptera, and Diptera, and Coleoptera being notable examples. Many suborders and families were established, many of which survive to this day. In contrast to the Permo-Carboniferous pattern of evolution, the Triassic spike in diversity was diffuse, with new types of insect developing simultaneously in widely-separated locations. During most of the later Mesozoic, the pattern actually reversed, with most new taxa appearing first in cooler climates. Eskov (2002).

From the Late Cretaceous, and even more so the early Cenozoic period, insects were essentially of modern type. This is illustrated by the many Recent families and genera that have been found preserved in Baltic amber and elsewhere. Of the orders recorded with certainty for the first time from Tertiary beds, the Strepsiptera and Siphonaptera may have been relatively late developments, but the others were probably more ancient.

Image: *Meganuera monyi* - order Meganisoptera a giant dragonfly (order Protodonata) wingspan 60 to 75 cm Carboniferous of Europe. Graphic from Modelování v paleontologii - Michal Rybka. (originally from Zittel & Eastman *Text-Book of Paleontology* 2nd ed. vol.1 1937 MacMillan & Co. London, p.809, fig.1567)

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Continued on Next Page

Descriptions

Insecta

Range: Early Devonian to Recent

Phylogeny: Hexapoda **:** (Protura + Collembola) + (Diplura + * **:** Archaeognatha + (Monura + (Thysanura + Pterygota))))

Characteristics: lack of musculature beyond the first segment of antenna; Johnston's organ in pedicel (second segment) of antenna (this organ is a collection of sensory cells that detect movement of the flagellum; a transverse bar forming the posterior tentorium inside the head; tarsi subsegmented; females with ovipositor formed by gonapophyses from segments 8 and 9; annulated, terminal filament extending out from end of segment 11 of abdomen (subsequently lost in most groups of insects) - Kristensen 1991, via Tree of Life - Insecta

Links Tree of Life, Encyclopedia of Life, Wikipedia; Insectclopedia - lots and lots of links, arranged by topic; Prehistoric Insects - notes on insects through the ages (the images don't load);Insects at Mikko's Phylogeny pages; Fossil Insects & Alternative Order Names; Cultural Entomology Digest MAK120516

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Insecta (2) - Wingless Insects

Abbreviated Dendrogram

```
HEXAPODA
|
`--INSECTA (insects)
   |--Archaeognatha
   `--+--Monura
      `--+--Thysanura
         `--PTERYGOTA
```

Contents

The Diversity of (Basal) Insects ("Zygentoma")

In simplified form, the higher level classification of the basal insects looks like this:

```
Insecta
|--Archaeognatha
`--+--Monura
   `--+--Thysanura
      `--Pterygota (i.e. all other insects)
```

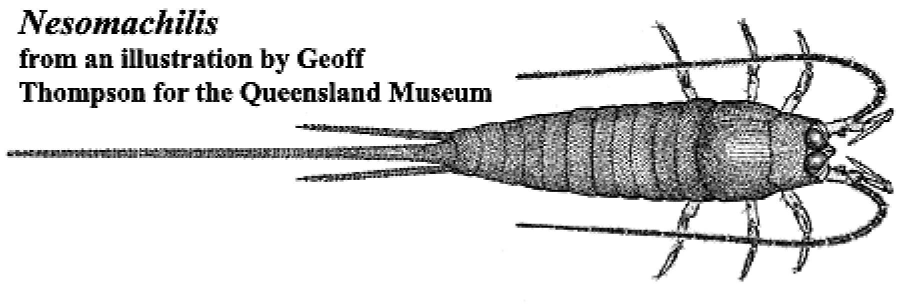
There seems to be general agreement about who belongs here, but no consensus on how to sort them into Archaeognatha, Monura, and Thysanura. Many, otherwise sensible, people continue to use the term "Zygentoma" to refer to the paraphyletic group containing all of these taxa except the Pterygota. We will use the following scheme, which probably keeps everyone together with their closest relatives, but may not put things in the proper buckets.

```
Insecta
|--Archaeognatha
|  |--Cercopodata
|  `--Machiloidea
|     |--Triassomachilis
|     |--Meinertelidae
|     `--Machilidae
`--+--Monura (4 assorted extinct genera)
   `--+--Thysanura
      |  |--+--Lepidotrichidae
      |  |  `--Nicoletiidae
      |  `--+--Lepismatidae
      |     `--Maindroniidae
      `--Pterygota
```

The particular arrangement of thysanuran families adopted here is stitched together from a few comments about the views of Jules Barlet in Bitsch (2003). Since this is hearsay authority, our arrangement should be taken with even less seriousness than is usual.

We will deal with these basal insects in the same three unequal blocks: the Archaeognatha, the Monura, and the Thysanura. The Pterygota, constituting all the other insects, will be discussed elsewhere. The three groups of immediate interest are sometimes collectively called the "Apterygota," the wingless insects. However, that term is more usually used in the older literature to refer to the paraphyletic group containing springtails and other Parainsecta, in addition to Archaeognatha, Monura, and Thysanura.

Archaeognatha (= Microcoryphia)



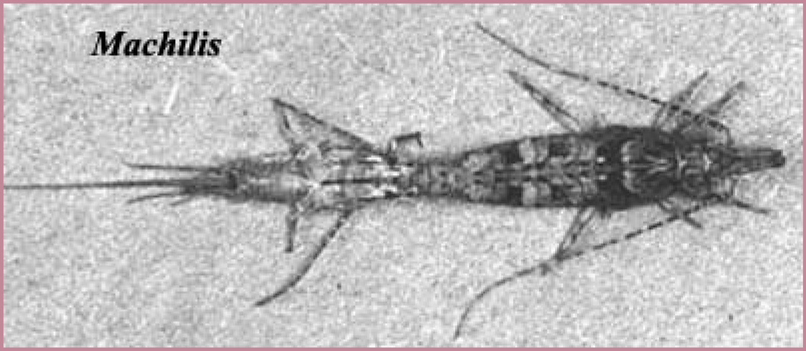
The archaeognaths are the most basal of the true insects and diverged from the Columbella before the close of the Emsian Age of the Early Devonian. Zherikin (2002). Recent Archaeognathae are known as *bristletails* and are, as the image indicates, quite similar to the Thysanura, or silverfish, with which they are often grouped. They differ from the Thysanura in their form of locomotion, which relies more on jumping (up to 10 cm). This is acheived by flexing the abdominal segments and releasing them like a spring.

These are all relatively small insects, never longer than 2 cm, most of which is "tail." The head is small, but surrounded by a large *notum* and appears large. Archaeognaths have rather large, compound eyes, which meet medially and glow if illuminated at night. And wouldn't *that* be an amusing thing to wake up to? Their name derives from the primitive articulation of the mandibles. The mandibles articulate with the body at only a single condyle (joint). All other insects have two condyles. The antennae are long and divided into many short segments. The thorax is stiff and raised at an angle, giving the insect a hump-backed appearance in lateral view. The abdominal body is soft and flexible. It is long, tapers posteriorly, and is covered in tiny scales. Abdominal segments 2-9 bear tiny auxilliary limbs (*styles*) which are moveable and aid in locomotion. Abdominal segments 1-7 bear eversible vesicles. The body terminates in three long, thin *cerci* ("tails"). The longer middle cercus is actually the 11th abdominal segment. Like all basal insects, Archaeognathae lack wings.

Cercopodata

This is a Permo-Carboniferous fossil group with abdominal appendages and leg- like, segmented cerci. However, cercopodates may have two mandibular condyles, which would be anomalous for true Archaeognatha. Note that, since the "tail" is derived from the 11th abdominal segment, the implication is that the *cerci* maybe evolved from the limbs of the 11th segment.

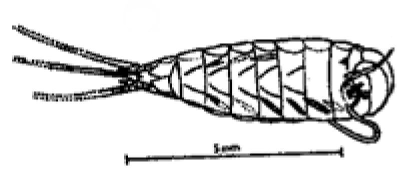
Machiloidea



This group may or may not have formal taxonomic status. It includes Archaeognaths of essentially modern form. These extant archaeognaths lay a relatively small number (~12) orange-coloured eggs in crevices or holes bored with their long ovipositors. Fertilization is external. Some species are parthenogenetic (eggs may mature without fertilization). Nymphs are virtually identical to adults, other than in size. They require two or three years for full development. Maturation involves 7-8 molts, and molting continues into adulthood. Bristletails are nocturnal herbivores and detritivores with a very broad dietary range. Significantly, they can survive on algae and lichen -- probably the mainstay of their diet in the

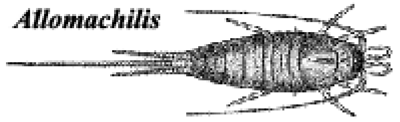
Devonian. Archaeognaths inhabit damp environments which may range from coastal cliffs to forest leaf litter in tropical to temperate climates. One species is even known from Alaska.

Triassomachilis (= *Mesoneta?*)



Shown in ventral view. This is, as the name suggests, a Triassic fossil form. Note that there appear to be only 6-7 abdominal segments, but segments 2-7 do bear styles -- possibly multiple styles. So each abdominal segment probably results from the fusion of two segments. The structure of the region around the *cerci*, as well as the mandibles, appear simplified when compared with Recent forms. The notum (1st thoracic) is well-developed, but it is impossible to tell if the eyes are large or meet medially.

Meinertellidae



*Allomachilis, Hypomachiloides, Machilellus, Machilinus, Machilis**, *Machiloides, Nesomachilis, Praemachilellus,* and others. This is the more common group in most parts of the world and can be distinguished from Machilidae by (a) the absence of scales at the base of the antennae and legs and (b) having very small abdominal styles (pseudo-legs).

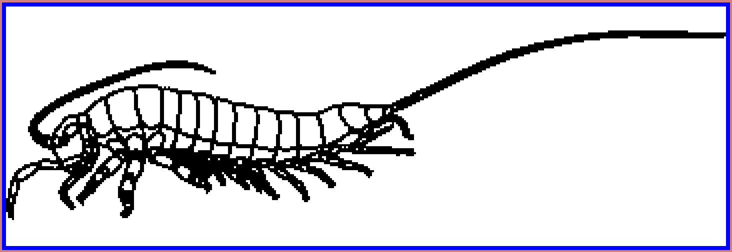
* Yes. Apparently, *Machilis* is not a member of the Machilidae. Go figure.

Machilidae

Dilta, Leptomachilis, Machilanus, Mesomachilis, Pedetontinus Petrobius. The Machilids tend to be slightly smaller than Meinertellids, with a more cylindrical body and more strongly inflected thorax. The thoracic sternals (ventral plates) are triangular. Abdominal segments 1-6 have 1-2 pairs of eversible vessicles. Scutes are present at the base of the antennae and legs.

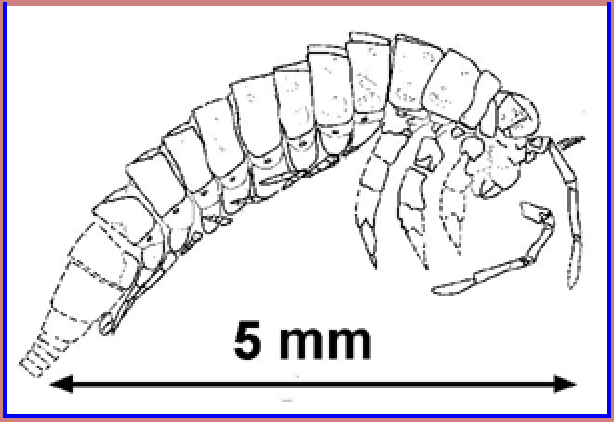
The Monura are a group of vague and doubtful affinities. There is a sense in some of the literature that Monura was erected because something *ought* to occupy this phylospace -- not because the fossil evidence actually compelled that conclusion.

Monura



Dasyleptus, Lepidodasypus, Tonganoxichnus. Carboniferous to Permian. This a group of questionable status. Specifically, there is a substantial body of opinion that the fossils assigned to this group are simply immture archaeognaths. One source states that the Monura are all Cercopodata, which seems very plausible. Grimaldi (2001). On the other hand, the argument that "the holotype of taxon *X* is actually an immature taxon *Y*" is heard rather often in paleoentomology to explain inconvenient discrepancies. Material from this taxon, if it is a taxon, is extremely scarce, so it is difficult to make judgments.

The characters which have been ascribed to the Monura include: supernumary ocelli (unique), segmented jaw parts (hard to accept on theoretical grounds), mandibles with a single condyle (primitive character shared with



Archaeognathae), abdominal styles divided into leg-like segments (a much-sought intermediate state), abdominal cerci absent (or simply missing?), annulated (segmented!?) caudal filament. Kukalová-Peck, who was responsible for many of the extraordinary claims for the Monura, has also argued that the cerci are present as short, leg-like structures with apical claws.

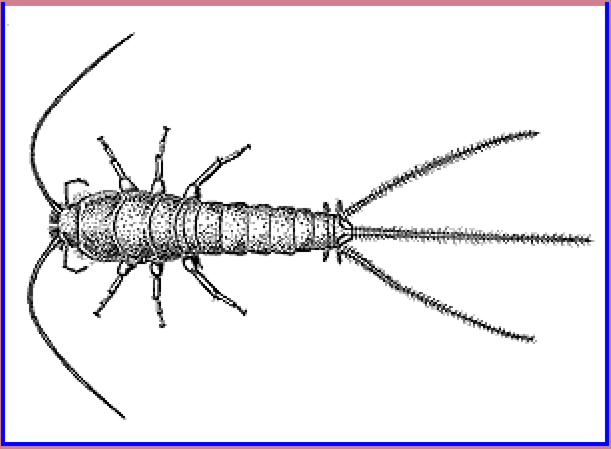
Perhaps the truth of the matter is that we simply have too little data to draw a firm conclusion at the moment.

With the Thysanura, we return to firmer phylogenetic ground. Recently, a few mischievous junior members of the Molecule Mob have suggested that mayflies evolved from within the Thysanura. In other words, they suppose that flight evolved twice in insects. Nardi *et al.* (2003). This is unlikely. However, flight is a demanding business. Flying animals tend to diverge far and quickly from their non-flying cousins because of the stringent mechanical demands of flight and the selective pressures faced (and avoided) as a result of the ability to fly. For that matter, mayflies are not morphologically so different from thysanurans that we can reject Nardi's suggestion out of hand. Certainly, this hypothesis is infinitely preferable to the semi-molecular work of Giribet *et al.* (2001), who require three independent origins of flight (its either that, or flying lobsters -- the choice is yours, folks) and place fruit flies as the sister group of diplurans and barnacles! Nevertheless, more senior Moleculons have intervened, bearing reams of Beyesian statistics showing that no definite conclusions can yet be drawn. Delsuc *et al*. (2003). Thus the public fisc is once again impoverished to support contending, fruitless speculations -- but, undoubtedly, our discourse is much enriched in compensation.

What all these molecular studies *do* show is that the Pancrustacea hypothesis is correct. Generations of morphologists have been unable to determine the branching order of Chelicerata, Myriapoda, Crustacea and Insecta. By repeatedly and strongly supporting Pancrustacea, the molecular results shift the weight of evidence decisively in favor of an insect-crustacean clade. We reluctantly concede that molecules have helped immensely to resolve this intractable issue. Flight may have developed more than once, but there are theoretical, as well as morphological, reasons to doubt this. Zherikhin (2002).

Thysanura

Common names: *silverfish* and *firebrats*. Estimates of the age of the earliest known Thysanura vary from the Pennsylvanian to the Oligocene. Since this represents a range of almost 300 My, someone's geological clock may have stopped. The earliest estimate is probably correct. Extant silverfish are so named because of the silvery scales that easily separate from the body when the insects are rubbed. It is unclear to us why anyone of even marginal sanity would wish to rub a silverfish -- they are not known to grant wishes or bring good luck. "Firebrats" are thysanurans adapted to high temperatures, and are frequently found as pests in human kitchens, where, like



other brats, they attempt to consume anything of even vaguely organic composition -- at no small expense to the family wage-earners, we might add.

The body is dorsoventrally flattened. The compound eyes are reduced or absent. If present, the compound eyes are always well-separated. One to three ocelli may be present. Then again, they may not. The mandibles are notable for being covered by a 'beard' of small hairs, as are other parts of the body, including the caudal filament, the tail-like extension at the posterior end. The abdomen has ten segments, and bears two posterior cerci in addition to the aforesaid caudal filament (actually the 11th abdominal segment), just as in the Archaeognathae. However, unlike archaeognaths, the cerci of thysanurans are almost as long as the "tail." This is the source of the taxon name, which combines the Greek word for *tasseled* (θυsανοις) with a common suffix for *tail* (-ουρος). Thus, once again, the Ancient Greeks prove their superior powers of common sense, since only a moron would rub these noxious vermin before giving them a name.

Like other basal insects, silverfish are long-lived, and may survive for up to four years. Compare mice, for example, with a laboratory life-span of two years, the average rock band at 18 months, or the average Ancient Greek at about 30 years. There is surely a lesson here, but it escapes us. Most silverfish occupy the same ecospace presumably occupied by their Carboniferous ancestors -- *e.g.*, under damp plant litter or rocks. Other species of silverfish have crawled out from under the rocks, so to speak, and have evolved adaptations allowing them to live with humans. This, if you think about it, is more than can be said for many humans. Several species are "commensals" in ant or termite colonies, where they may steal the colony's food reserves and devour its young. How, exactly, this behavior qualifies as "commensalism" is unclear. By this measure, a neighborhood drug dealer would qualify as a "commensal." But that is what the textbooks state.

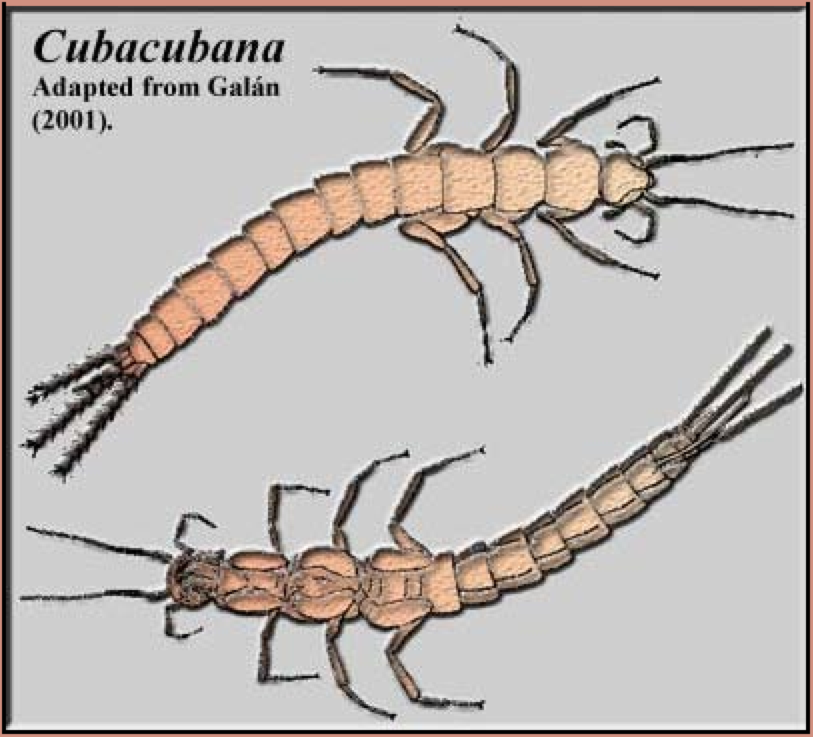
Links: Thysanura (with identification key to thysanuran families).

Lepidotrichidae

Lepidothrix, Tricholepidion (extant). This is a relict group, now reduced to one species in northern California (and Oregon?). Ocelli are present. The body lacks scales, and the tarsus has five segments. Interestingly, *Tricholepidion* is associated with red carpenter ants (genus *Camponotus*) and is tolerated in their tunnels. *Tricholepidion* does not digest wood, and appears to be a strict herbivore. We have no information on why it hangs around in this peculiar environment. *Tricholepidion* may also be found, more conventionally, under leaf and bark litter. The interesting implication is that all surviving Thysanura are descended from a group which was associated with colonial insects -- an insect type which evolved only in the Mesozoic.

Nicoletiidae

Common names: Fishmoths, naked silverfish. Genera: *Atelura*,



Battigrassiella, Coletinia, Cubacubana, Gastrotheus, Lepidospora, Metrinura, Nicoletia, Texoreddellia, Trinemura. Range: The nicoletiids are cosmopoltan, but usually cave or termite-associated forms.

The nicoletiids are small-bodied (7-18 mm). They are blind and often without pigments in the exoskeleton. Galán (2001). The maxillary palps have five segments. The abdomen almost always lacks eversible vesicles. The tarsus has fewer than 5 segments. Galán recognizes two families. The Atelurinae associate with colonial insects. They have scales, and are short, with ovoid bodies. The Nicoletiinae are elongate, predominantly lack scales, and live in forest litter, under rocks, underground, or in caves.

Maindroniidae

Maindronia. This taxon consists of one genus and three species found in arid regions of Chile, India and Ceylon, where it lives under rocks. This genus lacks ocelli and scales and is closely related to the Lepismatidae, and is often subsumed into that family.

Lepismatidae

Acrotelsa, Ctenolepisma, Lepisma, Thermobia. These are the typical silverfish and firebrats found in households world-wide. The common household silverfish is *Lepisma*. Compound eyes are present, but small & well-separated. The maxillary palps have 5 segments. The body is flattened and rather carrot-shaped. The abdomen usually lacks eversible vessicles. If present, there are only a songle pair per segment. All lepismatids prefer warmer temperatures, and firebrats are particularly thermophilic. Some species are associated with ant colonies.

Image: *Lepisma*, from **Forestry Images**. Photograph by Joseph Berger. It appears that the caudal filament and cerci have been truncated in this specimen. There's another excellent image at **Lepismatidae** with full-length appendages.

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Insect Dendrogram

Abbreviated Dendrogram

```
HEXAPODA
|
`--INSECTA (insects)
   |--Archaeognatha
   `--+--Monura
      `--+--Thysanura
         `--PTERYGOTA
```

Contents

The following dendrogram is posted as is from the old Palaeos edition MAK120516

```
<==o INSECTA
    |--o Archaeognatha (= Microcoryphia) (bristletails)
    |  |--†Cercopodata
    |  `--o Machiloidea
    |     |--†Triassomachilis
    |     |-- Meinertellidae
    |     `-- Machilidae
    `--o DICONDYLIA sensu lato
       |--†Monura
       `--o DICONDYLIA sensu stricto
          |--< THYSANURA (silverfish)
          |  |--+-- Lepidotrichidae
          |  |  `-- Nicoletiidae
          |  `--+-- Maindroniidae
          |     `-- Lepismatidae (common silverfish and firebrats)
          `--< PALEOPTERA
             |--†Rhyniognatha
             `--+--o†PALEODICTYOPTEROIDEA
                |  |--†Palaeodictyoptera
                |  `--+--†Megasecoptera
                |     `--+--†Permothemistida
                |        `--†Diaphanopterodea
                `--+-- Ephemeroptera
                   `--+-- Odonatoptera [Odonata sensu lato]
                      `--o NEOPTERA
                         |--†Paraplecoptera
                         |--†Protoperlaria
                         |--†Titanoptera
                         |--o POLYNEOPTERA
                         |  |--+--+-- Embiidina
                         |  |  |  `-- Plecoptera
                         |  |  `--+-- Orthoptera
                         |  |     `-- Phasmida
                         |  `--+--o Grylloblattodea
                         |     |-- Zoraptera
                         |     |--+?-†Protelytroptera
                         |     |  `-- Dermaptera
                         |     `-- Dictyoptera
                         `--o EUMETABOLA
```

```
|-- o PARANEOPTERA
|   |-- Hemiptera
|   `--+-- Thysanoptera
|      `--+-- Psocoptera
|         `-- Phthiraptera
`--o ENDOPTERYGOTA  [Holometabola sensu lato]
   |?-†Miomoptera
   `--o HOLOMETABOLA
      |--+-- Neuroptera
      |  `-- Coleoptera
      `--+-- Hymenoptera
         `--o MECOPTEROIDEA
            |--+-- Trichoptera
            |  `-- Lepidoptera
            |?- Glosselytrodea
            `--+-- Mecoptera
               |-- Siphonaptera
               `--o HALTERIA
                  |-- Strepsiptera
                  `-- Diptera
```

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Insect References

Abbreviated Dendrogram

```
HEXAPODA
|
`--INSECTA (insects)
   |--Archaeognatha
   `--+--Monura
      `--+--Thysanura
         `--PTERYGOTA
```

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Pterygota

Abbreviated Dendrogram

```
INSECTA
|
`--PTERYGOTA
   |--Rhyniognatha
   `--+--Palaeodictyopteroida
      |--Ephemeroptera
      |--Odonatoptera
      `--NEOPTERA
```

Contents

The Triumph of the Insects

The gigantic proto-dragonfly *Meganeura*, from the Latest Carboniferous (Stephanian - Gzhelian age) of France. Wingspan 70 cm.

Image courtesy Muséum de Toulouse - Meganeura, Creative Commons Attribution Non-Commercial Non-derivative.

At some point during the mid Carboniferous, insects evolved wings, even though the evolutionary line of winged insects derives from a tiny wingless Devonian ancestor. In a geological instant, the Carboniferous terrestrial ecology was transformed, and the world would never be the same again. So successful was this adaptation that the Pterygota (winged insects) are the most abundant and diverse of all the hexapod clades. During the Paleozoic, most insects belonged to the paleopteran or ancient-winged grade, but by the start of the Mesozoic, the Neoptera or "new wings" had become predimonant. In this unit however we focus on the Paleoptera MAK120517

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Pterygota: Paleoptera

Abbreviated Dendrogram

```
INSECTA
|
`--PTERYGOTA
   |--Rhyniognatha
   `--+--Palaeodictyopteroida
      |--Ephemeroptera
      |--Odonatoptera
      `--NEOPTERA
```

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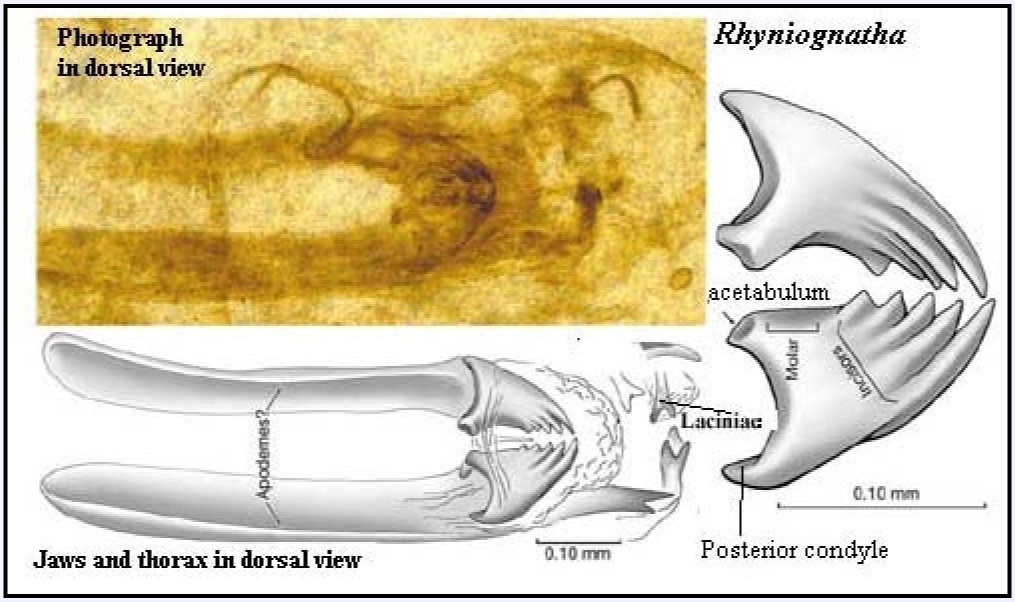
Taxa on This Page

1. *Rhyniognatha*

Introduction

Classically, the Paleoptera have been defined both apomorphically and paraphyletically..... That's a mouthful. Perhaps we should try again. Paleoptera are usually defined as "primitive winged insects." So, all paleopterans, and no other arthropods, are supposed to have a particular physical characteristic (wings) in common. That's the "apomorphic" part. However, the Paleoptera don't include *all* winged insects -- just the "primitive" ones. That's the "paraphyletic" part. This sort of definition is hopelessly vague and invites problems of classification.



Those problems recently surfaced in this group with the discovery -- actually, the redescription – of *Rhyniognatha*, an insect from the Pragian (Early Devonian) of Scotland. Engel & Grimaldi (2004). *Rhyniognatha* is like other Paleoptera in most respects, but it probably had no wings. On the other hand, it is not a silverfish (Thysanura). The mouth parts are all wrong for a silverfish. The mouth parts are entirely correct for a paleopteran – but there are no wings and no reason to believe there ever were any wings.

The reaction to *Rhyniognatha* in the semi-scientific press has been interesting. It was speculated by Engel & Grimaldi that *Rhyniognatha*'s early Devonian date might imply that insects began even earlier, in the Silurian. The press duly reported that *Rhyniognatha* was Silurian. Much more importantly, Engel & Grimaldi stated, quite correctly, that *Rhyniognatha* appeared to be a paleopteran. It was duly reported that flying insects were present in the Silurian ... .

In fact, there are no flying insects known for almost a hundred million years after the Ludlow (Late Silurian). Flying insects are first found in the Carboniferous, specifically, the Late Mississippian. The acquisition of flight in insects was followed -- just as in pterosaurs, birds, and bats -- by an explosive radiation of flying forms and non-flying taxa related to them. So, were the press out of line? Maybe, but the real problem is that silly definition: "primitive winged insects." It invites precisely the misunderstandings which followed the article by Engel & Grimaldi. The irony is that the Paleoptera are some of the very insects studied by Willi Hennig, the founder of cladistics, whose influence on evolutionary theory is exceeded only by Darwin. Here, if anywhere, we would expect to see the hand of the cladistic Reformation which Hennig began.

But we don't. However, in homage to Hennig, we will ignore traditional usage and give Paleoptera a proper phylogenetic definition: **fire ants (*Solenopsis*) > fire brats (*Thermobia*)**. For an explanation of this terminology, see Dendrograms. This makes *Rhyniognatha* a paleopteran because, very probably, it shares a more recent common ancestor with *Solenopsis* than with *Thermobia* -- whether or not *Rhyniognatha* had wings.

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Paleopteran Relationships and Diversity

Paleopteran relationships are a contentious field. [1] Fortunately there are relatively few who care enough to contend, so collateral damage to civilians has been slight. Our own take on the subject is summarized in the following cladogram:

```
PALEOPTERA
|--†Rhyniognatha
`--+--o†PALEODICTYOPTEROIDEA
   |   |--†Palaeodictyoptera
   |   `--+--†Megasecoptera
   |      `--+--†Permothemistida
   |         `--†Diaphanopterodea
   `--+-- Ephemeroptera
      `--+-- Odonatoptera [Odonata sensu lato]
         `--o NEOPTERA
```

Hennig himself favored a monophyletic Paleoptera. In this scheme, Paleoptera and Neoptera represent a fundamental divergence between two designs for flight, which diverged long ago, something like this:

```
ANCESTRAL THYSANURAN-LIKE THINGY
|--PALEOPTERA
|  |--†Palaeodictyopteroida
|  `--+-- Ephemeroptera
|     `-- Odonatoptera [Odonata sensu lato]
`--NEOPTERA
```

Unfortunately, our principled defense of Hennigian historic primacy in the previous section has pretty much exhausted our meager supply of principle. Thus we unctuously defer to current orthodoxy and treat the relationship as paraphyletic.

The main groups of paleopterans are all treated on separate pages, with the exception of the Megasecoptera, which we now summarize in the following fashion.

ATW041022. Text and *Protohymen* image public domain. No rights reserved.

Notes

[1]While the relationships of the extinct paleodictyopteroid orders (Diaphanopterodea, Palaeodictyoptera, Megasecoptera, and Permothemistida) to each other and to other orders have not been extensively examined, the relationships of the three living lineages (Ephemeroptera, Odonata, and Neoptera) to each other have been the subject of much debate. Each of the three possible relationships are supported by various authors.

A monophyletic Paleoptera was advocated by Hennig (1981) and Hovmöller et al. (2002):

```
Insecta
|--Paleoptera
|    |--Odonata
|    `--Ephemeroptera
`--Neoptera
```

Boudreaux (1979) favored monophyly of Ephemeroptera + Neoptera:

```
Insecta
|--Odonata
`--+--Ephemeroptera
   `--Neoptera
```

Kristensen (1975, 1991) Wheeler et al. (2001) and Grimaldi & Engel (2005) present evidence in support of monophyly of Odonata + Neoptera:

```
Insecta
|--Ephemeroptera
`--+--Odonata
   `--Neoptera
```

David R. Maddison, ToL CC-BY 2002

Descriptions

Rhyniognatha

Range: Early Devonian

Phylogeny: Pterygota **:** (Ephemeroptera + Palaeodictyopteroida + Odonatoptera + Neoptera) + *

Comments: Ancestral/basal pterygotan. See main essay

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checked ATW060202, revised MAK120516; Creative Commons Attribution;

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Pterygota

Abbreviated Dendrogram

```
INSECTA
|
`--PTERYGOTA
   |--Rhyniognatha
   `--+--Palaeodictyopteroida
      |--Ephemeroptera
      |--Odonatoptera
      `--NEOPTERA
```

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1. Pterygota

The following text is by David Maddison, from the Tree of Life page on Pterygota, and is reproduced here under teh Creative Commons license - MAK120516

Introduction

Insects were the first organisms on Earth to evolve active flight. It is likely that the ability to fly arose only once in insects, over 300 million years ago in the Carboniferous period. About 70 million years later active flight arose within vertebrates (pterosaurs), followed by separate origins in birds and bats. Winged insects, or pterygotes, have radiated into over 100 times more species than all of the winged vertebrate lineages combined.

Many groups of insects have subsequently lost the ability to fly. Some of these (lice and fleas, for example) have lost all remnants of wings. It is only through their evident relationship with particular groups of winged insects (lice are closely related to psocids [book lice]; fleas are related to flies) that it is clear that their ancestors had wings.

Paleopterous and neopterous insects

Two groups of pterygotes evolved the ability to fold their wings back flat against their abdomens. The largest of these is the clade Neoptera ("new wing"). Remaining insects are sometimes referred to as Paleoptera ("old wing"), because they lack the sophisticated wing-folding mechanism of neopterous insects. Members of paleopterous insects cannot fold their wings back over their abdomens, with the exception of the extinct order Diaphanopterodea, which could fold their wings using a mechanism different than Neoptera. (Some neopterous insects, such as butterflies, can no longer fold their wings against their abdomen, but this clearly represents a secondary loss.)

David R. Maddison, ToL CC-BY 2002

Descriptions

Pterygota

Range: Early Devonian to Recent

Phylogeny: Insecta : Archaeognatha + (Monura + (Thysanura + * : *Rhyniognatha* + (Ephemeroptera + Palaeodictyopteroida + Odonatoptera + Neoptera)))

Comments: veined wings on the second (meso-) and third (meta-) thoracic segment. - DRM02

Links Tree of Life, Encyclopedia of Life, Wikipedia; Fossil Insects by Roy J. Beckemeyer (focus on the Permian fossil insect Lagerstätten of Kansas and Oklahoma (The Wellington Formation sites) MAK120516

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Pterygota Dendrogram

Abbreviated Dendrogram	**Contents**

```
INSECTA
|
`--PTERYGOTA
   |--Rhyniognatha
   `--+--Palaeodictyopteroida
      |--Ephemeroptera
      |--Odonatoptera
      `--NEOPTERA
```

This is, as you may have gathered, yet another holding page. MAK120522

MAK120522

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Pterygota: References

Abbreviated Dendrogram

```
INSECTA
|
`--PTERYGOTA
   |--Rhyniognatha
   `--+--Palaeodictyopteroida
      |--Ephemeroptera
      |--Odonatoptera
      `--NEOPTERA
```

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Cladistics 17:113-169.
Paleoptera - phylogeny note

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Palaeodictyopteroida

Abbreviated Dendrogram

```
PTERYGOTA
|--Ephemeroptera
|--Odonatoptera
|--NEOPTERA
|
`--PALAEODICTYOPTEROIDA
   |--Palaeodictyoptera
   `--+--Megasecoptera
       `--+--Permothemistida
          `--Diaphanopterodea
```

Contents

Palaeodictyopteroida

Dunbaria fasciipennis described from the Early Permian (Artinskian) Welington Formation of Kansas. The original colour patterns are preserved in fossils (but not the actual colour), including bright and dark patches. Like other members of the family Spilapteridae, the wings relatively broad and rounded at the corners. Image and some text from Zoological excursions on Lake Baikal .

The Palaeodictyopteroida (also spelled Palaeodictyopter-*ida*, but we have chosen to use the original spelling) constituted the first major adaptive radiation of herbivorous insects, and hence the first herbivores that would have impacted very strongly on plant ecosystems. They also shifted the Paleozoic terrestrial foodchain from an inefficient detritivore-carnivore based system to an efficient photosynthesis-herbivore based one. On the one hand the most primitive of all flying insects, many retaining the primitive extra wing flaps (paranota), and yet on the other the most specialised of the three branches of Paleozoic "ancient wings", Their unique adapation was the evolution of long biting and sucking mouthparts, as opposed to the more conventional and less specialised jaws of their contemporaries. They were by far the most numerous and diverse of all Paleozoic insects, as well as the most colourful; with wing markings preserved on fossils hundreds of millions of years old; in a sense they were the butterflies of the ancient world. They also have the unhappy reputation of being the only major clade of insects to become extinct; the result perhaps, of the end Permian ecosystem collapse. That this extraordinary evolutionary experiement is virtually unkown today outside the paleoentomological community is a shame, because these ancient wonders have much of interst about them MAK120521

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Palaeodictyopteroida

Abbreviated Dendrogram

```
PTERYGOTA
 |--Ephemeroptera
 |--Odonatoptera
 |--NEOPTERA
 |
 `--PALAEODICTYOPTEROIDA
      |--Palaeodictyoptera
      `--+--Megasecoptera
         `--+--Permothemistida
            `--Diaphanopterodea
```

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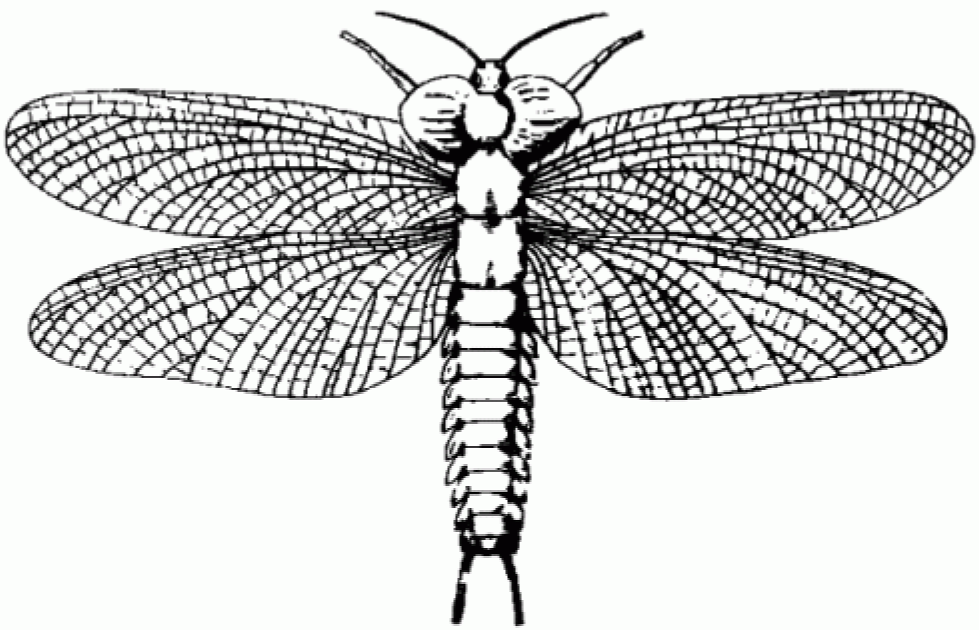


Lithomantis carbonarius Woodward 1876 (Palaeodictyoptera - Lithomantidae), Lanark: Scotland, Westphalian B (Early Moscovian, early Late Carboniferous).

The Palaeodictyopteroida were a diverse assemblage of mostly large, rather solidly built paleopterous insects, which were widespread in the Late Carboniferous. We treat them as a paraphyletic assemblage, but cover our backsides by reserving the use of "Palaeodictyoptera" for some possible monophyletic group of these insects. Thus comfortably talking out of both sides of our mouths, we proceed to a description.

The largest had wingspans 20 to 50 cm across. The Palaeodictyopteroida are usually regarded as the most primitive winged insects so far known to have existed. The wings were subequal (i.e. fore and hind pairs similar), sometimes widened, occasionally triangular. The most interesting thing about these insects is the presence of paranota (fore-wings) on the first thoracic segment. These are quite large and sometimes with rudiments of venation.

Despite their ancient status, the Palaeodictyopteroida already displayed specializations in that most, if not all, had mouth-parts modified into a long, suctorial rostrum - that is, piercing-sucking mouthparts for feeding upon plant sap. This was not, however, the same as the hemipteran rostrum, but rather represented an independent (an earlier) adaptation to feeding on spores, pollen, fruit, etc.

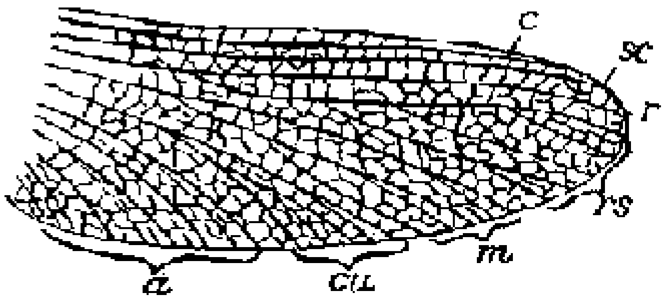


Diagram of the neuration of a Palaeodictyopteran-grade primitive insect wing. The principal longitudinal veins are connected by a network of cross -veins, c, Costa ; sc, Subcosta; r, Radius; rs, Radial sector; m, Media; ru, Cubitus; a, Anal veins or nervures (after Handlirsch), from Zittel & Eastman 1913, fig 1531

The paleodictyopteroid wing (*left*) is generally taken as the ancestral type from which the other types evolved. There is a complete system of venation, typically with the concave components (Rs, MP, CuP) arising as posterior branches from the convex components, and with a fully developed cubito-anal field which was sometimes more or less expanded. The cross-veins are numerous, and regular or irregular.

The antennae are setose (bristly), the legs slender, abdominal segments usually with prominent lateral lobes, with cerci (two "tails") that are usually rather short, and no caudal style. Some species were more slender, with reduced lateral processes and long cerci. MAK000108, slightly modified by ATW

Descriptions

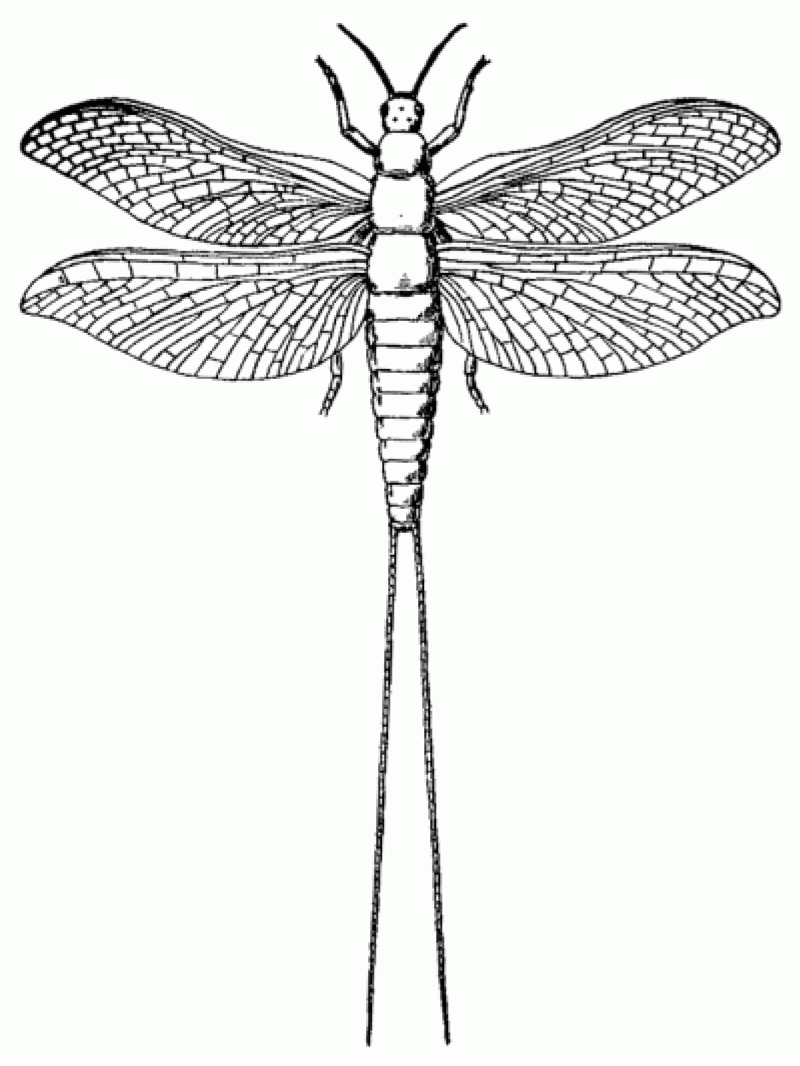
Palaeodictyopteroida (Rohdendorf, 1961) (*sensu* Bechly 1996)

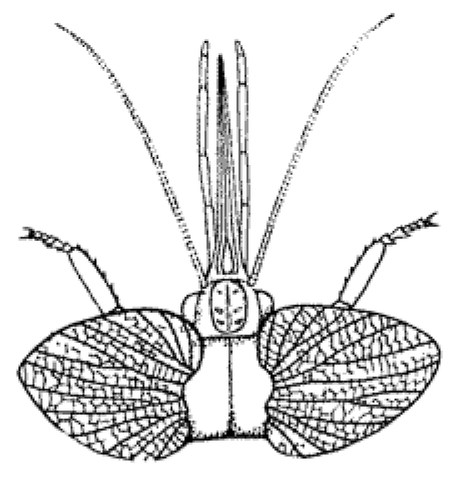
Synonyms: Dictyoneuridea Handlirsch, 1906, Palaeodictyopteroidea Rohdendorf, 1961, Palaeodictyopteroida Müller 1978, Palaeodictyopterida Grimaldi & Engel 2005

Range: Mid Carboniferous to Late Permian

Phylogeny: Pterygota : *Rhyniognatha* + (Ephemeroptera + Odonatoptera + Neoptera + * : Palaeodictyoptera + (Megasecoptera + (Permothemistida + Diaphanopterodea))))

Characters: highly derived sucking-





piercing mouthparts forming a prominent rostrum or proboscis (Haustellum) that consists of 5 stylets (most likely the two mandibles, two galaeo-laciniae, and the hypopharynx), correlated with a highy domed clypeus (clypeal sucking pump); presence of hollow filamentous projections on the posterior edges of thoracic and abdominal terga (dubious character); adult epiproct (paracercus or terminal filum) suppressed (convergent to Neoptera and Panodonata); well developed prothoracic and abdominal paranota expanded laterally (maybe caused by a secondary fusion of winglets or gills with the terga, correlated with a terrestrial mode of life of the larvae); terrestrial larvae without abdominal gills. - Günter Bechly, 2007

Characters: Head moderately large, rounded, ivith simple antennae, mouth parts adapted for biting, and well-developed jaws. Two pears of wings, subequal in size, of similar form and frimitive venation, incapable of being folded backward over the abdomen ; sometimes a rudimentary third pair present on the first thoracic segment. Abdomen consisting of ten nearly homonomous segments which often exhibit pleural lobes. Terminal segment often with much elongated cerci. Thoracic legs similar. - Zittel & Eastman 1913

Comment: Palaeozoic beaked insects, characterised by unique mouthparts consisting of 5 stylets. They represent the first important terrestrial herbivores, and the first major group of herbivorous insects. They appear during the Middle Carboniferous (late Serpukhovian/early Bashkirian), along with the other major winged insect clades, and continue through to the Late Permian; being teh only major group of iunsects to duie out at the end Permian extinction. Exact phylogenetic relationships with other paleopterans are unclear, we follow Grimaldi & Engel (2005) out of convenience. This large and diverse group includes 50% of all known Paleozoic insects. MAK120516, incorporating Wikipedia

The oldest name for this taxon, according to Russian entomologist N.D. Sinitshenkova Dictyoneuridea Handlirsch, 1906, but this is almost never used. The most common name seems to be Palaeodictyopteroidea Rohdendorf 1961, which is used, for example by the Tree of Life project. Bit according to Professor N.J. Kluge's Nomina Circumscribentia Insectorum database this refers to Palaeodictypotera + Archodonata + Ephemeroptera , and is therefore a paraphyeetic or polyphyletic taxon. Palaeodictyopteroida Müller 1978 would be prefereble as referring to Palaeodictyoptera only. this amended spelling was independently used by Bechly, who pointed out that the suffix "-oidea" is reserved for superfamilies. Grimaldi & Engel 2005 suggested a slightly different spelling again, replacing "-oida" with "-ida", in order to give the taxon superordinal rank, and this spelling was been widely adopted and hence has become the standard one. But as superorders, unlike superfamilies, seem to have variable suffixes, and can just as easily end in -oida as -ida, there probably is little necessity for this latter change MAK120522

Image: Top right, *Homaloneura ornata* Brongniart 1893 (Palaeodictyoptera - Spilapteridae) from Commentry Shales Formation of France, a Gzhelian lacustrine deltaic shale (ref Paleobiology database)., Upper left, *Stenodictya*, unfortunately I don't remember where I found either of these images

Links: Phylogenetic Systematics of basal Pterygota and Stem-Group Odonates - Günter Bechly,Wikipedia, Paleobiology database, Evolution of Insects in terms of the Implicate and Explicate Orders. MAK120522

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Palaeodictyopteroida: Diaphanopterodea

Abbreviated Dendrogram

```
PTERYGOTA
|--Ephemeroptera
|--Odonatoptera
|--NEOPTERA
|
`--PALAEODICTYOPTEROIDA
   |--Palaeodictyoptera
   `--+--Megasecoptera
      `--+--Permothemistida
         `--Diaphanopterodea
```

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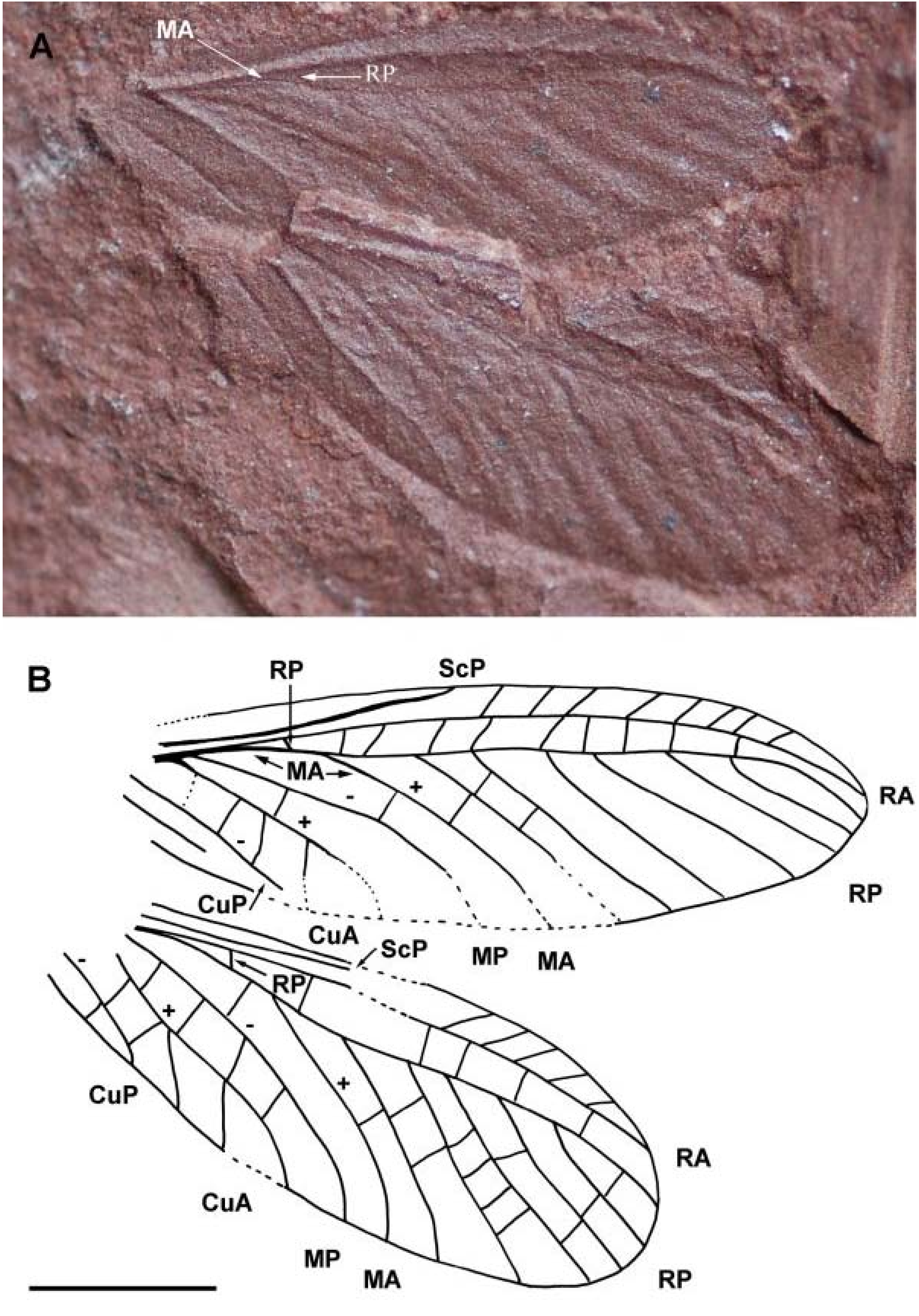
1. Diaphanopterodea

This order of paleopterous insects appeared during the Carboniferous but is best known known from the Permian of Russia and North America, and more recently, Europe. They resembled mosquitoes in size, suctoral mouthparts, and structure, the head being armed with a beak with piecing mouthparts, and they may have been blood-sucking forms like some Diptera.

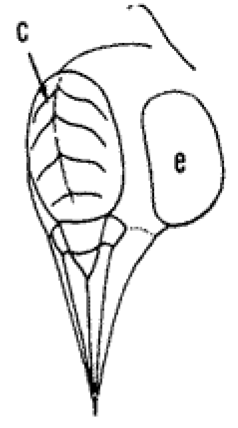
The fore and hind wings were similar, with the R vein was bent back at the base in the fore-wings, less so in the hind wings. The main veins were closely aligned in the basal part of the wing. As with the neoptera, these insects were able to fold their wings back over the top of their abdomen, but the mechanism of folding is not clear. They constitute a separate neopterous development that is unrelated to the true Neoptera.



Alexrasnitsynia permiana (Diaphanopterodea: Alexrasnitsyniidae), from the Middle Permian (Guadalupian) of Salagou Formation in the Lodève Basin (South of France), **A** photograph of wings, **B** drawing of wings (Scale bar represents 3 mm). From Prokop & Nel 2011, New Middle Permian palaeopteran insects, Creative Commons Attribution .

Descriptions

Diaphanopterodea



Range: Carboniferous (Bashkirian) to Late Permian

Phylogeny: Palaeodictyopteroida **::** Palaeodictyoptera + (Megasecoptera + (Permothemistida + *))

Comments: the paleozoic equivalent of the mosquito

Image: Head of *Asthenohymen* sp. (probably Wellington Formation of Oklahoma (Early Permian), showing biting mouthparts. Source of this image not recorded.

References: E. F. Reik, 1970, "Fossil History", in *Insects of Australia*, Melbourne University Press, p.175; Behrensmeyer et al 1992 *Terrestrial Ecosystems Through Time* - p.272

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page MAK000107; checked ATW041127; revised MAK120517;

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Palaeodictyopteroida: Megasecoptera

Abbreviated Dendrogram

```
PTERYGOTA
|--Ephemeroptera
|--Odonatoptera
|--NEOPTERA
|
`--PALAEODICTYOPTEROIDA
   |--Palaeodictyoptera
   `--+--Megasecoptera
       `--+--Permothemistida
          `--Diaphanopterodea
```

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1. Megasecoptera

Megasecoptera

There are 22 families of megasecopterans and only about 35 known genera, so -- right out of the box -- we should be suspicious that the diversity of the group is undersampled and poorly understood.

Like many other paleopterans, the megasecopterans had sucking mouthparts, which doesn't fit the usual party line about detritivory. Instead, it is quite clear that the Megasecoptera were "plant vampires." The suctorial wouth parts were used to pierce plant casings and extract high-quality plant materials, such as spores and pollen.

Protohymen after Kukalova-Peck (1974)

Megasecoptera bore two pairs of wings (some very basal paleopterans had three), which are nearly of the same size. The wings were held horizontally, as in dragonflies (Odonata, Anisoptera). The wing bases tend to be very slender, as in damselflies (Odonata, Zygoptera). The body is long and thin. The illustrated *Protohymen* is rather stouter and shorter than a typical megasecopteran.

During their relatively brief existence, the Megasecoptera were extremely succesful. It has been estimated that this order accounted for 50% of the insect biomass in some locations. This may be an overestimate, because Megasecoptera tended to be rather large. Some reached almost unbelievable dimensions, with wingspans close to 100 cm. As a result they are over-represented in the fossil record. It has been suggested that insects of this size would be capable of soaring flight, like an albatross or large pterosaur.

Links: ELMO INSECTS IN BRIEF, Insect Flight- Evolution

Descriptions

Megasecoptera

Range: Pennsylvanian to Guadalupian.

Phylogeny: Palaeodictyopteroida **::** Palaeodictyoptera + ((Permothemistida + Diaphanopterodea) + *)

Comments: see above

Page Back: Palaeodictyoptera | **Unit Home** | **Page Top** | **Page Next: Permothemistida**

Page Back: Palaeodictyopteroida | Unit Up: Arthropoda | Unit Home | Clade Up: Palaeodictyopteroida | Page Next: Megasecoptera
Unit Back: Pterygota | Clade Down: None | Dendrogram | References | Unit Next: Ephemeroptera

Palaeodictyopteroida: Palaeodictyoptera

Abbreviated Dendrogram

```
PTERYGOTA
|--Ephemeroptera
|--Odonatoptera
|--NEOPTERA
|
`--PALAEODICTYOPTEROIDA
   |--Palaeodictyoptera
   `--+--Megasecoptera
       `--+--Permothemistida
          `--Diaphanopterodea
```

Contents

Taxa on This Page

1. Palaeodictyoptera

The Palaeodictyoptera are among the least derived of all flying insects, corresponding very nearly to the hypothetical common ancestral type (Zittel & Eastman 1913; a paraphyletic assemblage or ancestral grade, like Thecodontia, Condylartha, etc) although more recently it is argued that the Palaeodictyopteroida as a whole constitute a clade (Grimaldi & Engel 2005). Whether or not this is an artifact of cladistic analysis, like the old "Ceratosauria", remains to be seen. Many species are distinguished by a pair of winglets in front of the two standard wing pairs. MAK120522.

Descriptions

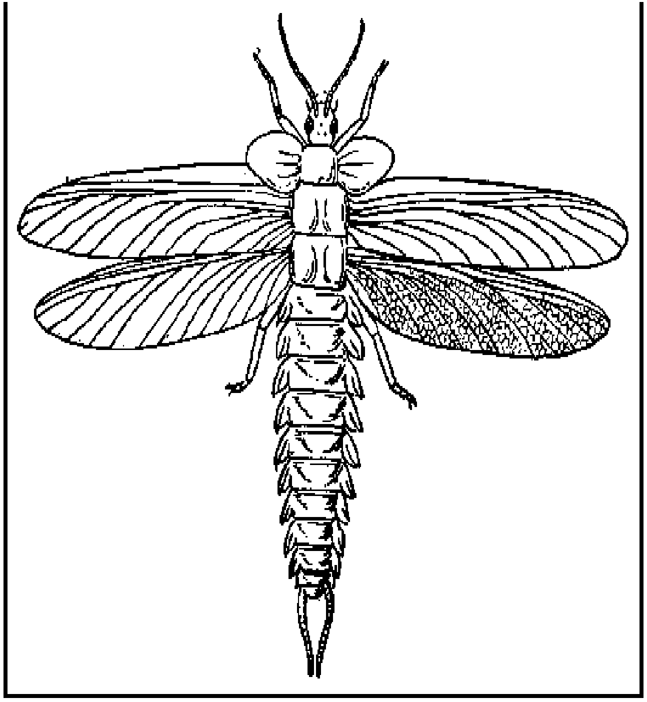
Palaeodictyoptera

Range: Middle Carboniferous (Serpukhovian/Bashkirian) to Permian

Phylogeny: Palaeodictyopteroida :: Palaeodictyoptera + (Megasecoptera + (Permothemistida + Diaphanopterodea) + *))

Comments: pollen- spore- or fruit- feeding insect - piercing mouthparts, probably frequented open areas with suitable vegetation, MAK120516. The wing itself is very primitive: the cross-veins are numerous and more or less irregular; tlie anal lobe is not separated by a fold ; the anal veins are always well developed, more or less branched, C and curved regularly backward to the SC posterior margin ; and there is no anal fold nor fan - like plaitings. The Larvae are similar to the imago - Zittel & Eastman 1913 (public domain text) - slightly modified

Links: Wikipedia, Paleobiology database, Stenodictya, from Arthur's Prehistoric Life Clipart;



Stenodictya lobata Brongniart; wingspan 10 cm. Carboniferous, Stephanian Epoch (Upper Productive Coal Measures) - Gzhelian epoch, Commentry (Allier), France
graphic from Rozvoj letenja - JTV page

Page Back: Palaeodictyopteroida | Unit Home | Page Top | Page Next: Megasecoptera

page MAK000108, revised ATW041020, checked ATW060202, revised MAK120516;

Palaeodictyopteroida: Permothemistida

Abbreviated Dendrogram

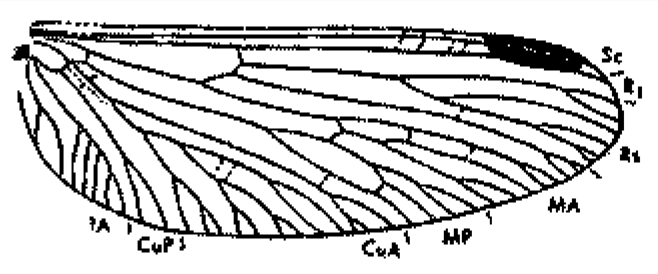
```
PTERYGOTA
 |--Ephemeroptera
 |--Odonatoptera
 |--NEOPTERA
 |
 `--PALAEODICTYOPTEROIDA
    |--Palaeodictyoptera
    `--+--Megasecoptera
        `--+--Permothemistida
           `--Diaphanopterodea
```

Contents

Taxa on This Page

1. Permothemistida

Order Permothemistida



Permothemis libelluloides, fore wing (modified from Jeannel, 1949a)

This is a small order of insects known from fossils from the Permian of North America and Russia. The mesothorax was greatly developed, the fore wing had a well-developed pterostigma and few cross-veins, and the abdomen ended in a pair of long cerci. It has been compared with the Megasecoptera (Protodonata), but was more probably a two-winged development from the Palaeodictyoptera. It has left no recognizable descendants.

Descriptions

Permothemistida

Range: Permian

Phylogeny: Palaeodictyopteroida **::** Palaeodictyoptera + (Megasecoptera + (Diaphanopterodea + *))

References: E. F. Reik, 1970, "Fossil History", in *Insects of Australia*, Melbourne University Press, p.174

Page Back: Palaeodictyoptera | Unit Home | Page Top | Page Next: Diaphanopterodea

Palaeodictyopteroida Dendrogram

Abbreviated Dendrogram

```
PTERYGOTA
|--Ephemeroptera
|--Odonatoptera
|--NEOPTERA
|
`--PALAEODICTYOPTEROIDA
   |--Palaeodictyoptera
   `--+--Megasecoptera
       `--+--Permothemistida
          `--Diaphanopterodea
```

Contents

The following dendrogram is copied verbatum from the dendrogram on Palaeos org by Christopher Taylor. This concerns the Palaeodictyoptera only, and even then only some Palaeodictyopteran groups (others still rto be added). References included below, indicated by the letter -number code. MAK120521

```
Palaeodictyoptera [Dictyoneurida, Paleodictyoptera]
   |  i. s.: Rochdalia parkeri K-P83
   |         Idoptilus onisciformis K-P83
   |         Stenodictya lobata GE05
   |         Mazothairos GE05
   |         Moravia grandis GE05
   |--Frankenholziina S02
   |    |--Frankenholzioidea S02
   |    |    |--Psychroptilus Z02 [Psychroptilidae S02]
   |    |    `--+--Frankenholziidae S02
   |    |       `--Dictyoneurellidae S02
   |    `--Arcioneuroidea S02
   |         |--Arcioneuridae S02
   |         |--Elmoboriidae S02
   |         `--+--Eubrodia Carpenter 1967 [Eubrodiidae] S02
   |            `--Eukuloja [Eukulojidae] S02
   |                 `--E. cubitalis S02
   `--Dictyoneurina S02
        |  i. s.: Archaeoptilidae S02
        |         Lithoptilidae S02
        |         Mecynoptera tuberculata S02
        |--+--+--Eugereonoidea [Dictyoptiloidea] S02 [Taxon diversity]
        |  |   |--Archaemegaptilidae S02
        |  |   |--Graphiptilidae S02
```

```
|  |   |--Jongmansiidae S02
|  |   |--Lycocercidae S02
|  |   |--Megaptilidae S02
|  |   |--Polycreagridae S02
|  |   |--Protagriidae S02
|  |   |--Synarmogidae S02
|  |   |--Lithomantis GE05 [Lithomanteidae S02]
|  |   |    `--L. carbonarius GE05
|  |   |--Eugereon [Dictyoptilidae, Eugereonidae] S02
|  |   |    `--E. boeckingi S02
|  |   `--Tchirkovaeidae S02
|  |      |--Paimbia fenestrata Sinichenkova 1979 K-P83
|  |      `--Tchirkovaea Zalessky 1931 BN03
|  |           `--T. guttata S02
|  `--Dictyoneuroidea S02
|       |--Peromapteridae S02
|       |--Saarlandiidae S02
|       `--Palaeoneura [Dictyoneuridae] S02
|            `--P. giligonensis S02
`--+--+--Breyerioidea S02
   |  |    |--Breyeriidae S02
   |  |    |--Stobsiidae S02
   |  |    `--Cryptoveniidae S02
   |  `--Calvertielloidea S02
   |       |--Mongolodictyidae S02
   |       `--Sharovia [Calvertiellidae] S02
   |            `--S. sojanica S02
   `--+--Spilapteroidea S02
      |   |--Aenigmatidiidae S02
      |   |--Fouqueidae S02
      |   |--Homothetidae S02
      |   |--Lamproptilidae S02
      |   |--Mecynostomatidae S02
      |   `--Spilapteridae [Neuburgiidae] S02
      |        |--Delitzschala bitterfeldensis Brauckmann & Schneider 1995 S02, FT05
      |        |--Dunbaria fascipennis S02, GE05
      |        |--Paradunbaria pectinata S02
      |        `--Vorkutoneura variabilis S02
      `--Homoiopteroidea S02
           |--Heolidae S02
           `--Homoiopteridae S02
                |--Homoioptera vorhallensis S02 [=Homaloneura vorhallensis Z02]
                |--Parathesoneura carpenteri Sharov & Sinichenkova 1977 K-P83
                |--Mazonopterum wolfforum Kukalová-Peck & Richardson 1983 K-P83
                |--Ostrava nigra (Kukalová 1960) K-P83
                |--Adolarryia bairdi Kukalová-Peck & Richardson 1983 K-P83
                `--Monsteropterum moravicum Kukalová-Peck 1972 K-P83
```

* Type species of generic name indicated

References

[BN03] Bethoux, O., & A. Nel. 2003. Revision of Diaphanoptera species and new diagnosis of Diaphanopteridae (Palaeoptera: Diaphanopteridae). Journal of Paleontology 77 (5): 1016-1020.

[FT05] Fayers, S. R., & N. H. Trewin. 2005. A hexapod from the Early Devonian Windyfield Chert, Rhynie, Scotland. Palaeontology 48 (5): 1117-1130.

[GE05] Grimaldi, D., & M. S. Engel. 2005. Evolution of the Insects. Cambridge University Press: New York.

[K-P83] Kukalová-Peck, J. 1983. Origin of the insect wing and wing articulation from the arthropodan leg. Canadian Journal of Zoology 61: 1618-1669.

[S02] Sinitshenkova, N. D. 2002. Superorder Dictyoneuridea Handlirsch, 1906 (=Palaeodictyopteroidea). In History of Insects (A. P. Rasnitsyn & D. L. J. Quicke, eds) pp. 115-124. Kluwer Academic Publishers: Dordrecht.

[Z02] Zherikhin, V. V. 2002. Ecological history of the terrestrial insects. In History of Insects (A. P. Rasnitsyn & D. L. J. Quicke, eds) pp. 331-388. Kluwer Academic Publishers: Dordrecht.

Palaeodictyopteroida: References

Abbreviated Dendrogram

```
PTERYGOTA
|--Ephemeroptera
|--Odonatoptera
|--NEOPTERA
|
`--PALAEODICTYOPTEROIDA
   |--Palaeodictyoptera
   `--+--Megasecoptera
      `--+--Permothemistida
         `--Diaphanopterodea
```

Contents

D. Grimaldi & M. S. Engel 2005. Evolution of the Insects. xv + 755 pp. Cambridge, New York, Melbourne: Cambridge University Press.

Jakub Prokop & André Nel, 2011, New Middle Permian palaeopteran insects from Lodève Basin in southern France (Ephemeroptera, Diaphanopterodea, Megasecoptera), ZooKeys 130: 41–55, doi: 10.3897/zookeys.130.1311, **WWW**
Diaphanopterodea

Page Back: Palaeodictyopteroida	Unit Up: Arthropoda	Unit Home	Clade Up: Pterygota	Page Next: Ephemeroptera
Unit Back: Palaeodictyopteroida	Clade Down: None	Dendrogram	References	Unit Next: Odonatoptera

Ephemeroptera

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Odonatoptera
|--NEOPTERA
|
`--EPHEMEROPTERA
   `--+--Triplosobidae
      `--+--Permoplectoptera
         `--Euplectoptera
```

Contents

Ephemeroptera: the not so ephemeral Mayfies

One of the most ancient of insects, on one of the most ancient of plants. A female subimago of *Rhithrogena germanica* . Ephemeroptera: Euplectoptera: Schistonota: Heptagenioidea: Heptageniidae, resting on *Equisetum hyemale*. Despite this being a modern photo, this exact same image could belong with barely any change to any time over the last quarter of a billion years
Photo by Richard Bartz,Wikipedia, Creative Commons Attribution Share Alike

There is something ironic about creatures that live barely a few days as adults existing with very little change over several hundred million years. the Mayflies, whose scientific name Ephemeroptera is derived from the Greek *ephemeros*, short-lived, hence ephemeral are one of the four most ancient clades of winged insects. Like their relatives the dragonflies and damselflies, they have a long aquatic immature stage (called a *naiad* or nymph), a heritage, no doubt, of their ancestral home in the mighty Carboniferous wetlands. Experts disagree on which of the three "ancient wing" (paleopteran) groups stand at the base of the insectan evolutionary tree. MAK120521

Page Back: Palaeodictyopteroida | Unit Home | Page Top | Page Next: Ephemeroptera

Ephemeroptera

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Odonatoptera
|--NEOPTERA
|
`--EPHEMEROPTERA
   |--Triplosobidae
   `--+--Permoplectoptera
      `--Euplecoptera
```

Contents

Taxa on This Page

1. Ephemeroptera
2. Euplecoptera
3. Permoplectoptera X
4. Triplosobidae X

Ephemeroptera

Mayflies

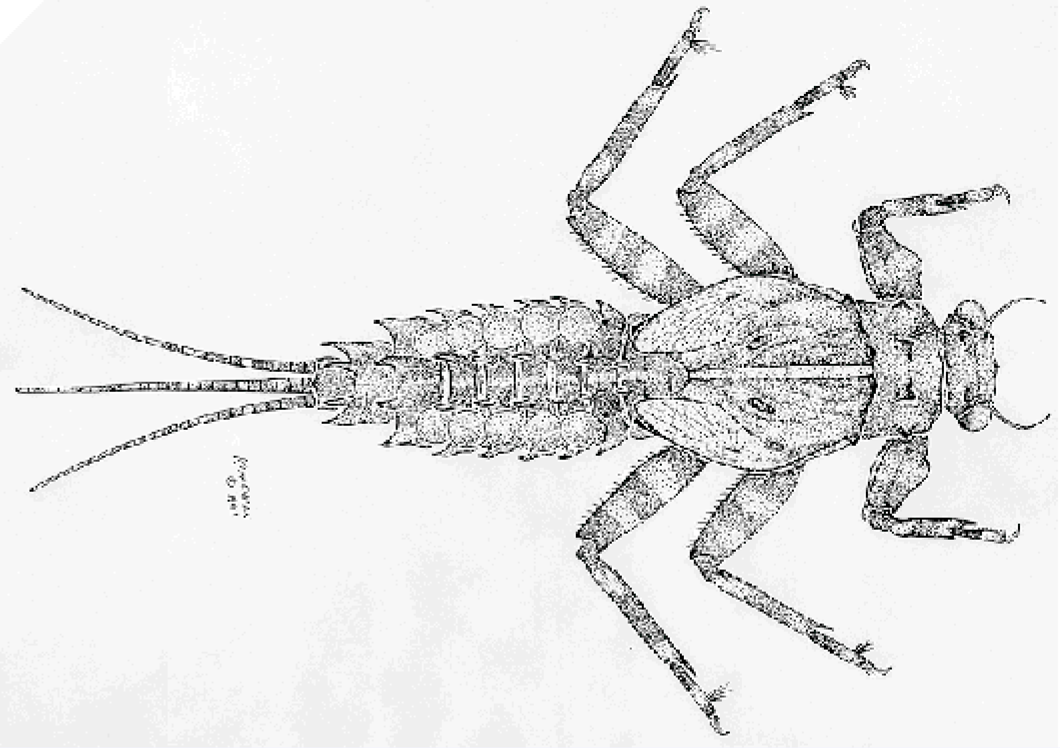
The following page was written some years ago, from a mostly Linnaean perspective, and is in need of revision and updating, as well as conversion to the current Palaeos format. In the meantime it has been posted as is MAK120517

```
PALEOPTERA
|-
```

```
-Palaeodictyopteroida
|  |--Megasecoptera
|  `--+--Permothemistida
|     `--Diaphanopterodea
`--+--Ephemeroptera
   |  |--Schistonota
   |  `--Pannota
   `--+--Odonatoptera
      |  `--Panodonata
      `--Neoptera
```

Rhithrogena sp - family Heptageniidae
image from Ephemeroptera Galactica

The Ephemeroptera are among the most primitive of flying insects. They are delicate, elongate Palaeopteran insects with net-veined wings, of which the second-pair is reduced in size and function and in advanced forms may be absent. The wings are held vertically over the body at rest. There are two or three causal ("tail") filiform appendages. The eyes are large and compound, the antennae short. The prothorax is small, the legs slender, the first pair elongate.



Drunella grandis nymph (family Ephemerellidae) length 1.4 centimeters

Illustration by B.C. Kondratieff, Colorado State University, from Ward, J.V. and B.C. Kondratieff.

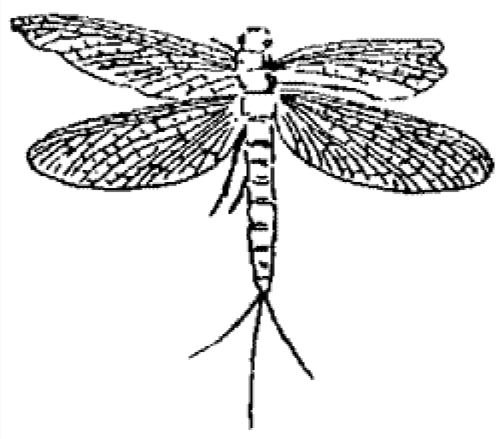
The aquatic larvae or *nymphs* possess respiratory abdominal tracheal gills. Modern forms live in streams as they require running water (Paleozoic types probably preferred ponds swamps, and rivers). Most mayfly larvae are collector-gatherers or scrapers, being herbivores or scavengers (usually feeding on diatoms, bottom detritus, etc). Only a few forms being carnivorous. Most mayflies in temperate regions spend most of their one-year life cycle as nymphs, although some species may live for two or three years. In adult Euephemeroptera the mouthparts are vestigial, they do not feed, but live only briefly to breed. Depending on the weather and the species, adults live from one hour to several days.

There are three suborders Protephemeroptera, the Permoplectoptera, and the Euephemeroptera or Euplecoptera, which last group includes all surviving forms. The following dendrogram (modified from one on Mikko's Phylogeny pages with the addition of a number of extinct taxa) shows a very approximate and simplistic representation of these groups. In fact it is almost certain that the Permoplectoptera are paraphyletic, including among their number the direct ancestors of modern groups

```
o EPHEMEROPTERA (sensu lato)
|--o PROTEPHEMEROPTERA Handlisch 1906
|   `-- Triplosobidae [Kasimovian to Gzhelian]
 `--o EPHEMEROPTERA
     |--o SYNTHONOPTERODEA
     |   `-- Bojophlebiidae (Moscovian)
      `-o PLECOPTERA (sensu Tillyard) = EUPHEMEROPTERA (sensu Julievich and others)
         |--o PERMOPLECOPTERA
         |  |--o PROTERISMATOIDEA
         |  |  |-- Protereismatidae [Asselian? - Kungurian?]
         |  |  |-- Misthodotidae [Asselian? - Kungurian?]
         |  |  |-- Jarmilidae [Asselian? - Kungurian?]
         |  |  |-- Oboriphlebiidae [Asselian? - Kungurian?]
         |  |  `-- Palingeniopsidae [Permian]
         |  `--o MESEPHEMEROIDEA
         |      `-- Mesephemeridae [Ufimian?/Tartarian - Tithonian]
          `--o EUEPHEMEROPTERA = EUPLECOPTERA (mayflies)
             |--- Hexagenitidae [Hettangian?/Toarcian - Berriasian?/Albian]
             |--- Paedephemeridae  [Jurassic]
             |--- Epeoromimidae [Hettangian?/Toarcian - Berriasian?/Albian]
             |--o SCHISTONOTA
             |  |--o BAETOIDEA
             |  |  |-- Siphlonuridae [Hettangian?/Toarcian - Recent]
             |  |  |-- Baetidae [Priabonian - Recent]
             |  |  |-- Oniscigastridae [Recent]
             |  |  |-- Ameletopsidae [Recent]
             |  |  `-- Ametropodidae [Aptian - Recent]
```

```
|  |--o HEPTAGENIOIDEA
|  |  |?- Aenigephemeridae [?Oxfordian/?Portlandian]
|  |  |-- Coloburiscidae [Recent]
|  |  |-- Oligoneuriidae [Aptian - Recent]
|  |  |-- Isonychiidae [Recent]
|  |  `-- Heptageniidae [Priabonian - Recent]
|  |--o LEPTOPHLEBIOIDEA
|  |  `-- Leptophlebiidae [Hettangian?/Toarcian - ?Aptian - Recent]
|  `--o EPHEMEROIDEA
|     |?- Palaeoanthidae [Santonian]
|     |-- Behningiidae [Recent]
|     |-- Potamanthidae [Berriasian?/Albian - Recent]
|     |-- Euthyplociidae [Berriasian?/Albian - Recent]
|     |-- Polymitarcydae [Aptian - Recent]
|     |-- Ephemeridae [Aptian - Recent]
|     `-- Palingeniidae [?Oxfordian/?Portlandian - Recent]
`--o PANNOTA
   |--o EPHEMERELLOIDEA
   |  |-- Ephemerellidae [Hettangian?/Toarcian - Recent]
   |  |-- Leptohyphidae [Recent]
   |  `-- Tricorythidae [Recent]
   `--o CAENOIDEA
      |-- Neoephemeridae [Rupellian?/Chattian - Recent]
      |-- Baetiscidae [Recent]
      |-- Caenidae [Recent]
      `-- Prosopistomatidae [Recent]
```

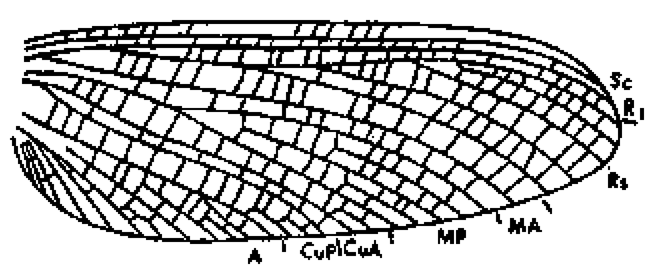
Suborder Protephemeroptera



Triplosoba pulchella
family Triplosobidae
wingspan about 4 cm
Stephanian Epoch (Upper Productive Coal Measures) - Gzhelian epoch
Commentry (Allier), France
graphic from Karl Von Zittel's *Text-Book of Paleontology*

The Suborder Protephemeroptera contains the species *Triplosoba pulchella*, from the latest Carboniferous of Europe. This is so different to later mayflies that it has in the past been placed in a separate order (the tendency nowadays is to include it under the Ephemeroptera proper). Unlike modern mayflies, these creatures fed normally upon attaining adulthood. Also unlike modern mayflies, the larvae apparently did not require flowing water. The fore- and hind-wings are similar, with a very primitive pattern of wing venation, and numerous cross-veins, although with some intercalary veins extending longitudinally. The thorax and abdomen consist of similar segments, the legs likewise are similar. The cerci are long.

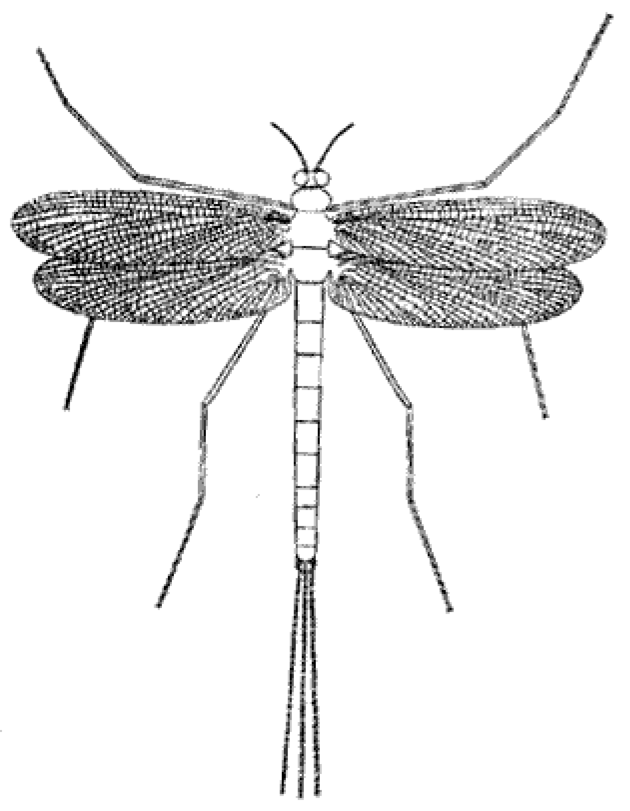
Although similar in appearance to the true Ephemeroptera, its wing veneation (*left*) (unbranched MA and pectinately branched Rs) exdudes it from the direct line of mayfly descent. Nevertheless it does represent something of a transitional form (in a sense a grand-uncle rather than a grand-father) between



the Palaeodictyoptera and the true Ephemeroptera

Triplosoba pulchella - wing (after Edmunds and Traver 1954) from Riek, p.174

Suborder Permoplecoptera

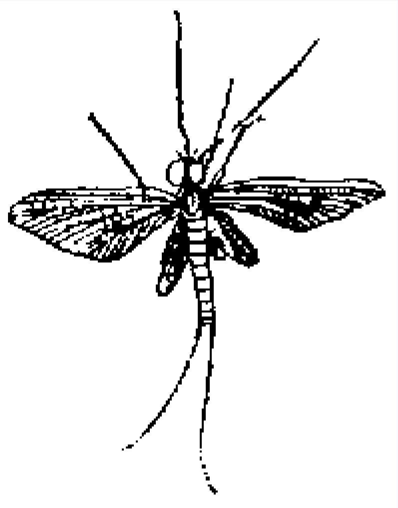


Protereisma permianum,
Early Permian
Note the fore and hind-wings are of more or less equal size.
graphic from Carpenter, 1933, reprinted in Reik

The Suborder Permoplecoptera includes a number of more typical forms known from the Permian of North America Russia, Australia, and a single Mesozoic lineage. They differ from some of the more slender Palaeodictyoptera of the time, which they otherwise resembled, chiefly in venational characters and in possessing a long caudal style. Unlike recent mayflies, which do not have functional mouths as adults, the Permoplectoptera had chewing mouthparts as adults. Another way they differed from modern species of mayflies is in the wings, the fore and hind wings being approximately the same size (technically, in which fore and hind wings were "subequal" in size). Apart from a few doubtful nymphs, there is no further record of the Ephemeroptera until the Jurassic, when two families of the surviving suborder Euephemeroptera (Euplectora) appeared. The Mesephemeridae, which retained the nearly homonomous wings of the Permoplectoptera, survived well into the Cretaceous as a sort of "living fossil" alongside its more derived Euplectopteran descendents.

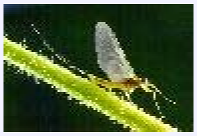
Roy Beckemeyer has a number of illustrations of Permoplecoptera on his Fossil Insects site

Suborder Euplecoptera



Cronicus anomalus (Pictet)
An extinct genus of the family Siphlonuridae
Early Oligocene - Baltic Amber
wingspan about 2 cm
graphic from Karl Von Zittel's *Text-Book of Paleontology*

(*note* - this drawing shows the eyes too large in proportion to the body - c.f. the figure in Carpenter, *Treatise* O24, fig.16-2)



The suborder Euephemeroptera or Euplectoptera can be used to distinguish all recent mayflies and their immediate ancestors and relatives. These more typical forms have vestigial mouthparts, and the hind wings are smaller or even absent. A number of families appeared during the early Jurassic, representing some seven or eight distinct lineages. In fact during the Jurassic the diversity of the Ephemeroptera reached its highest extent, fossils of nine families have been found during this period. Although there are more living families known, the Jurassic diversity would have been much higher, as only a small proportion of types would ever be fossilized. It is possible that most of these forms evolved during the latest Triassic, a time of great evolutionary diversification. Among the Jurassic forms, the Paedephemeridae had considerably reduced hind wings. A several of these families represent Recent groups.

Links:

Note: following links have not been revised

UCMP -Ephemeroptera - Mayflies - the best coverage of the group

Fossil Insects - by Roy J. Beckemeyer

Günter Bechly, Ephemeroptera - technical diagnosis of the group, including extinct forms. Excludes the Protephemeroptera/Triplosobidae from the Ephemeroptera.

The Fossil Record II (ed. Mike Benton) - on-line database

Tree of Life project Ephemeroptera

Palaeoptera - Mikko's Phylogeny - dendrogram and a few references

---

images not loading? | error messages? | broken links? | suggestions? | criticism?

contact us

Ephemeroptera Dendrogram

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Odonatoptera
|--NEOPTERA
|
`--EPHEMEROPTERA
   `--+--Triplosobidae
      `--+--Permoplectoptera
         `--Euplectoptera
```

Contents

The following dendrogram is copied verbatim from the dendrogram on Palaeos org by Christopher Taylor. It doesn't cover the phylogeny of crown-group ephemeroptera. MAK120521

Ephemeroptera Dendrogram

```
PTERYGOTA
|--Rhyniognatha
`--+--Palaeodictyopteroida
   |--Odonatoptera
   |--NEOPTERA
   |
 EPHEMEROPTERA  [Ephemerida, Euephemeroptera]
   |  i. s.: Tintorina Krzeminski & Lombardo 2001 [Tintoriniidae]
   |           `--*T. meridensis Krzeminski & Lombardo 2001 (see below for synonymy)
   |         Litophlebia [Litophlebiidae, Xenophlebiidae]
   |           `--L. optata (Riek 1976) [=Xenophlebia oplata]
   |         Torephemeridae
   |           |--Archaeobehningia
   |           `--Torephemera
   |         Blasturophlebia
   |         Brevitibia
   |         Cronicus
   |         Siphoplecton
   |         Philolimnias
   |         Turingopteryx Kuhn 1937
   |         Geisfeldiella
   |         Aphelophlebodes
   |         Siphangarus
   |         Bolbonyx ludibriosus
   |         Mesopalingea lerida
   |         Cratoligoneuriella
   |         Povilla adusta
   |         Stenonema interpunctatum
   |           |--S. i. interpunctatum
   |           |--S. i. canadense
   |           |--S. i. frontale
   |           `--S. i. heterotarsale
   |         Sharephemera Sinitshenkova 2002 [Sharephemeridae]
   |           `--*S. cubitalis Sinitshenkova 2002
```

```
      |         Siphlonisca aerodromia
      |--Euplectoptera
      |    |  i. s.: Triassomachilis Sharov 1948
      |    |         Turphanella Demoulin 1954
      |    |         Mesogenesia Tshernova 1977
      |    |         Clephemera Lin 1986
      |    |--Ephemerina  (extant mayflies and their immediate ancestors)
      |    `--Baetiscina [Posteritorna]
      |         |--Baetisca [Baetiscidae]
      |         `--Myanmarella [Prosopistomatidae]
      |              `--M. rossi
      `--Protereismatina [Permoplectoptera]
           |  i. s.: Phtharthus netshaevi Handlirsch 1904 [incl. P. rossicus Handlirsch 1904]
           |--Oboriphlebia [Oboriphlebiidae]
           |--Jarmila [Jarmilidae]
           |--Mesoplectopteron [Mesoplectopteridae]
           |--Palingeniopsis [Palingeniopsidae]
           |    `--P. praecox
           |--Misthodotes [Misthodotidae]
           |    `--M. sharovi
           |--Protereismatidae [Kukalovidae]
           |    |--Protereisma latum
           |    `--Kukalova americana
           `--Mesephemeridae
                |--Montralia
                `--Palinephemera
```

---

*Tintorina meridensis Krzeminski & Lombardo 2001 [=T. triassica Krzeminski & Lombardo 2001 (n. n.)]

*Type species of generic name indicated

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Ephemeroptera: References

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Odonatoptera
|--NEOPTERA
|
`--EPHEMEROPTERA
   `--+--Triplosobidae
      `--+--Permoplectoptera
         `--Euplectoptera
```

Contents

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Odonatoptera

Dragonflies and their prehistoric relatives

Abbreviated Dendrogram

```
PTERYGOTA
 |--Palaeodictyopteroida
 |--Ephemeroptera
 |--NEOPTERA
 |
 `--ODONATOPTERA
    |--Eugeropteridae
    `--Holodonata
       |--Meganisoptera
       `--Odonata
```

Contents

Griffenflies, Dragonflies, and Damselflies

Zdenek Burian's (whose magnificent artwork, like that of Charles R Knight, shaped several generations of young paleo enthusiasts) evocative representation of the huge griffenfly *Meganeura* in a primordial Carboniferous forest. From *Prehistoric Animals* (Paul Hamlyn Ltd)

There has to be something magical about a group of insects named Dragonflies and Damselflies, and more recently Griffenflies, the largest known insects. Currently we only have a few holding pages on this fascinating group; hopefully more content will be added later. MAK120522

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Pterygota: Odonatoptera

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Ephemeroptera
|--NEOPTERA
|
`--ODONATOPTERA
   |--Eugeropteridae
   `--Holodonata
      |--Meganisoptera
      `--Odonata
```

Contents

Taxa on This Page

1. Eugeropteridae
2. Holodonata
3. Odonatoptera

This is a holding page, pending the addition of more content on basal Odonatoptera MAK120516

The Odonatoptera contain the living Odonata (dragonflies and damselflies) plus all fossil taxa more closely related to odonates than other living insects. The earliest known odonatopterans are recorded from the Upper Carboniferous. The best known of the basal odonatopterans are the meganeurids which had the largest wingspans of any known insect, up to about 640 mm in Meganeuropsis permiana (Grimaldi & Engel 2005).- CKT110413

Descriptions

Odonatoptera

Range: From Mid Carboniferous

Phylogeny: Pterygota **:** *Rhyniognatha* + (Ephemeroptera + Palaeodictyopteroida + Neoptera + * **:** Eugeropteridae + (Meganisoptera + Odonata)))

Characters: (from Grimaldi & Engel 2005): Wings with anal region reduced; distinctive form of bracing with kink in CuP where it meets AA; only two articular plates at wing base. CKT110413

Eugeropteridae

Range: Mid Carboniferous (Bashkirian)

Phylogeny: Odonatoptera Holodonata **:** + *

Holodonata

Range: From Mid Carboniferous

Phylogeny: Odonatoptera **:** Eugeropteridae + * **:** Meganisoptera + Odonata

page uploaded 25 June 2002, new page with same name MAK120516, content Christopher Taylor.

Odonatoptera: Meganisoptera

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Ephemeroptera
|--NEOPTERA
|
`--ODONATOPTERA
   |--Eugeropteridae
   `--Holodonata
      |--Meganisoptera
      `--Odonata
```

Contents

Taxa on This Page

1. Meganisoptera

Order Meganisoptera - the Griffenflies

The Meganisoptera (commonly but incorrectly referred to as Protodonata [1]) or Griffenflies (Grimaldi & Engel) were a group of large to gigantic predatory flying insects, with wingspans of 12 to 75 cm. Like dragonflies, to which they were related, they had long narrow bodies, huge eyes, and strong jaws and spiny legs for grasping prey. The wing veination is extremely primitive, with all the main veins except one (the Rs vein) having separate origins at the base of the wing, and the cubito-anal area represented by a single vein. The characteristic structure of the true Odonata (dragonfly) wing are not developed. There was also a dense reticulation of cross-veins.

The Meganisoptera were closely related to true dragonflies (Odontata). Almost certainly the larvae were aquatic and carnivorous (like modern dragonfly larvae), and fed on small aquatic vertebrates (fish, and amphibia) or larger invertebrates. It is likely that the adults frequented open spaces where they had room to maneuver, and may well have spread to upland environments. Only a few families and genera are known; this appears to have been a small group, or alternatively to have frequented areas where they would not have easily fossilized.

Meganeura as featured in the BBC science documentary *Walking With Monsters*

Fossil remains of Meganisoptera are known from the late Carboniferous of France, the early Permian of North America, the late Permian of Russia and Australia. A single species recorded from the Triassic of France is most likely a true dragonfly. . It can be assumed that they evolved some time during the mid Carboniferous, flourished until the end of the Paleozoic. MAK020625 slightly revised 120517

Cladistic diagram - from Günter Bechly, Phylogenetic Systematics of the Odonates

- Meganisoptera
  - Namurotypidae
  - Meganeuromorpha
    - Paralogidae (sedis mutabilis)
    - Kargalotypidae (sedis mutabilis)
    - Kohlwaldiidae (sedis mutabilis)
    - Meganeuridae (sedis mutabilis)
      - Carpentertypinae (sedis mutabilis)
      - "Tupinae" (sedis mutabilis)
      - Meganeurinae (sedis mutabilis)

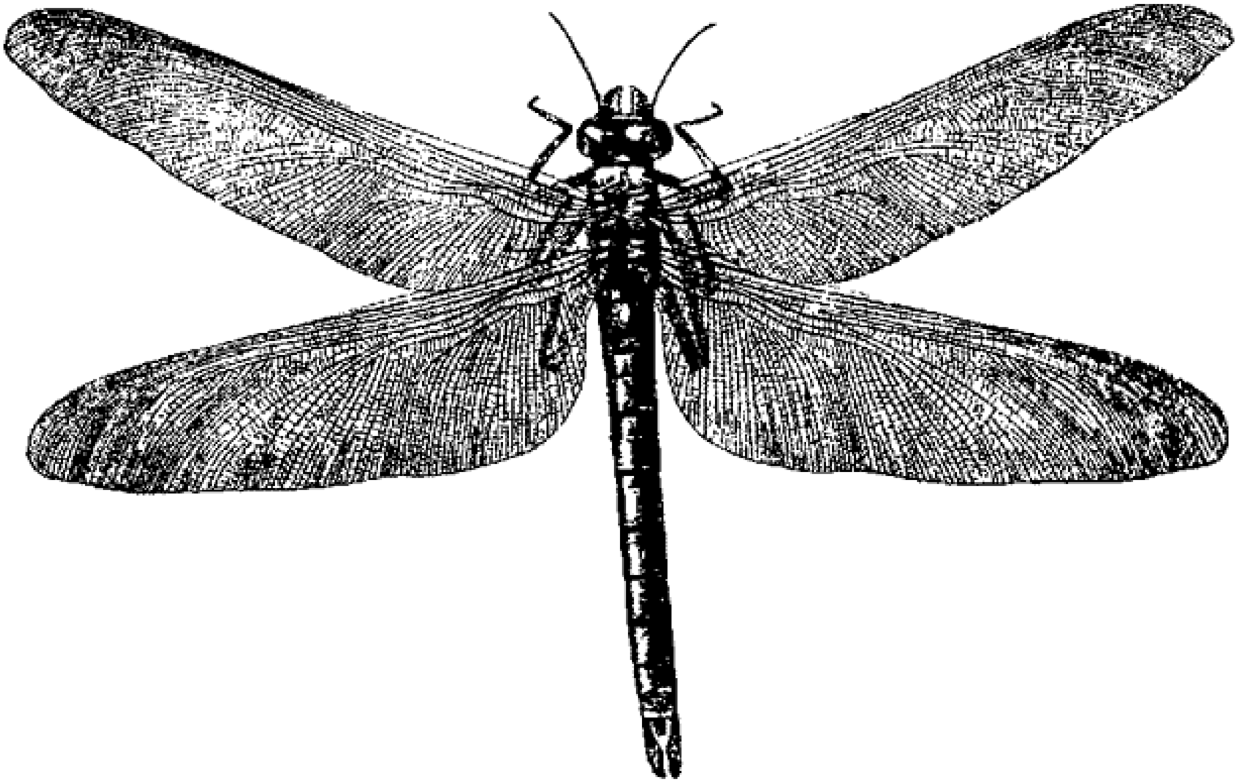
Note

[1] Although Protodonata is the term used in Grimaldi & Engel's definitive *Evolution of the Insects*, it is not technically correct. As Professor N.J. Kluge points out in his wonderfully titled Nomina Circumscribentia Insectorum database:

> "Initially the family Protodonata Brongniart 1885 was established for a single genus *Protagrion*, while the genus *Meganeura* was placed to another family, named Sthenaropterida. Later (Lameere 1900, Handlirsch 1906-1908) added *Meganeura* and other insects, recently attributed to Meganisoptera, to the taxon Protodonata. Because *Protagrion* is no longer regarded to be close to *Meganeura* or even include din the Odonatoptera at all, but rather placed in the Protorrhynchota (Martynov 1932, Carpenter 1943, Bethoux & Nel 2003, et al.); the usage of the name Protodonata for the taxon which includes *Meganeura* and does not include *Protagrion*, contradicts to its original circumscription. The name Meganisoptera is therefore the preferred and widely accepted name for this taxon. The name Meganeuroptera Tillyard 1918 (from words "Meganeura" and "ptera") is older, but at the same time is peoccupied, because the same name Meganeuroptera Crampton 1916 (from words "mega" and "Neuroptera") was given for the taxon Corydalus/f1=Chauliodes/g1. The names Prototyloptera Crampton 1924 and Protaeshnoptera Crampton 1928 were given as synonyms of "Protodonata" in unknown sense, so they can be only presumably attributed to this taxon."

(slightly edited to clarify the English) MAK120522

Descriptions



Meganuera monyi Brongniart, from the Latest Carboniferous (Stephanian Epoch (Upper Productive Coal Measures) Gzhelian age) Commentry (Allier), France. Graphic from Zittel & Eastman 1913 p.809, fig.1567.

Meganisoptera Martynov 1932

Synonym: Protodonata Brongniart 1885 (invalid for this taxon)

Range: Carboniferous (Bashkirian) to Late Permian

Phylogeny: Odonatoptera **:** Eugeropteridae + (Odonata + *)

Comments: large airborne diurnal predators, larvae (nymph) predatory, fed on small vertebrates, small fish, larval ("tadpole") and small adult amphibians, most likely frequented pond margins, lakes and watercourses, although adults could no doubt cover large distances and may have ranged wider afield

References: Karl Von Zittel's *Text-Book of Paleontology* ed. Charles R. Eastman, 2nd ed. vol.1 1937 MacMillan & Co. London; E. F. Reik, 1970, "Fossil History", in *Insects of Australia*, Melbourne University Press

Links: The magnificent, giant (and unfortunately extinct) griffenflies **best on the web**; Phylogenetic Systematics of basal Pterygota and Stem-

Group Odonates - Günter Bechly,; Wikipedia; *Meganeura* Life reconstruction by Surface Vision; *Meganeura* Life reconstruction by Dinoraul, *Meganeuropsis* Life reconstruction by Karen Carr MAK120522

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page MAK020625; checked ATW050625, last modified MAK120522;

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ARTHROPODA | **ODONATA**

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Odonata

Abbreviated Dendrogram

```
PTERYGOTA
 |--Palaeodictyopteroida
 |--Ephemeroptera
 |--NEOPTERA
 |
 `--ODONATOPTERA
     |--Eugeropteridae
     `--Holodonata
         |--Meganisoptera
         `--Odonata
```

Contents

Taxa on This Page

1. Odonata

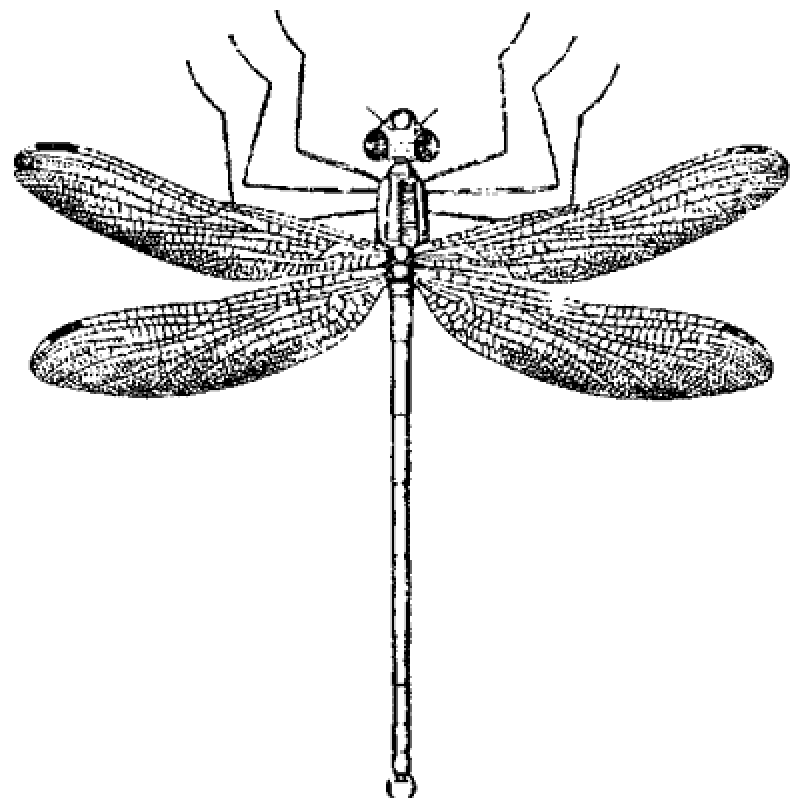
This is a holding page, posted as is, pending the addition of content MAK120517

Odonata

dragonflies and their kin

"There is general agreement that the Odonata and Meganisoptera (Meganisoptera) were derived from the same stock. Excluding the Upper Carboniferous Campylopteridae, the position of which is disputable, the earliest records of Odonata are from the Permian of North America and Russia, where the main lines of zygopterous and anisopterous descent were already differentiated. Six suborders are recognized, of which three have survived. The Protozygoptera, best known from *Kennedya* and its allies, may have been ancestral to the Zygoptera, and the Protanisoptera, through the Anisozygoptera which replaced them in the Mesozoic, to the Anisoptera; the Mesozoic Archizygoptera appear to have been a divergent line that has left no descendants."

E. F. Reik, 1970, "Fossil History", in *Insects of Australia*, Melbourne University Press



Tarsophlebia eximia
a late Jurassic (early Tithonian) dragonfly from Europe
Lithographic Shale, Bavaria
wingspan 3.5 to 4 cm

Descriptions

Odonata

Range: From the Permian

Phylogeny: Odonatoptera **:** Eugeropteridae + (Meganisoptera + *)

References: Karl Von Zittel's *Text-Book of Paleontology* ed. Charles R. Eastman, 2nd ed. vol.1 1937 MacMillan & Co. London; E. F. Reik, 1970, "Fossil History", in *Insects of Australia*, Melbourne University Press

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Palaeos	Παλαιός	ODONATOPTERA
ARTHROPODA		DENDROGRAM

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Odonatoptera Dendrogram

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Ephemeroptera
|--NEOPTERA
|
`--ODONATOPTERA
   |--Eugeropteridae
   `--Holodonata
      |--Meganisoptera
      `--Odonata
```

Contents

The following dendrogram is combines the material on the old Palaeos edition with a newer but only partial dendrogram by Christopher Taylor. . MAK120516

Odonatoptera Dendrogram

```
ODONATOPTERA [Odonata sensu lato]  [= Libellulida, Libellulidea, Meganeurina, Odonatoidea,
Odonatomorpha]
|  i. s.: Hemeroscopus [Hemeroscopidae] R02
|           `--H. baissicus Pritykina 1977 R02
|         Eocordulia cretacea R02
|         Erasipteroides [Erasipteridae] GE05
|           `--E. valentini GE05
|         Namurotypus [Namurotypidae] RP02
|         Titanophasma fayoli RP02
|         Parahemiphlebia mickoleiti GE05
|--o Eugeropteridae [GEROPTERA] GE05
|    |--Eogeropteron lunatum RP02
|    `--Geropteron arcuatum RP02
`--o NEODONATOPTERA
   |--o "EOMEGANISOPTERA"
   |  `--"Erasipteridae"
   `--o HOLODONATA GE05 (= Euodonatoptera)
      |--o MEGANISOPTERA [Protodonata, Meganeuroidea, Meganeuromorpha] GE05
      |  |--Namurotypidae
      |  `--o MEGANEUROMORPHA (Meganeura)
      |    |--Paralogidae GE05
      |    |--Kohlwaldiidae NB01
      |    |--Kargalotypus Rohdendorf 1962 [Kargalotypidae, Kargalotypinae] NB01
      |    |    `--*K. kargalensis (Martynov 1932) [=Megatypus kargalensis] NB01
      |    `--Meganeuridae GE05
      |         |--Arctotypus sinuatus GE05
      |         |--Meganeuropsis permiana Z02 [incl. M. americana GE05]
      |         |--Meganeura monyi GE05
      |         |--Megatypus schucherti GE05
      |         `--Tupus gracilis GE05
      `--o ODONATOCLADA RP02
```

```
|--o Campylopteridae [Campylopterodea] RP02
`--Panodialata NB01
   |--Lapeyria [Lapeyriidae] NB01
   |    `--L. magnifica Nel, Gand & Garric 1999 NB01
   `--o NODIALATA RP02
      |--o PROTANISOPTERA  (= Pandiscoidalia RP02)  (alternative (and less resolved) phylogeny)
      |  |--Polytaxineuridae
      |  `--o DITAXINEUROMORPHA
      |     |--Permaeschnidae
      |     `--o DITAXINEURIDA
      |        |--Callimokaltaniidae
      |        `--o DITAXINEUROIDEA
      |           |--Hemizygopteridae
      |           `--Ditaxineuridae
      `--o DISCOIDALIA
         |--o TRIADOPHLEBIOPTERA
         |  |--o TRIADOTYPOMORPHA
         |  |  |--Triadotypidae
         |  |  `--Piroutetiidae
         |  `--o TRIADOPHLEBIOMORPHA
         |     |--o ZYGOPHLEBIOIDEA
         |     |  |--Xamenophlebiidae
         |     |  `--Zygophlebiidae
         |     `--o TRIADOPHLEBIIDA
         |        |--Mitophlebiidae
         |        `--o TRIADOPHLEBIOIDEA
         |           |--Triadophlebiidae
         |           `--Paurophlebiidae
         `--o STIGMOPTERA
            |--o PROTOZYGOPTERA
            |  |--o PERMAGRIONOIDEA
            |  |  |--Permagrionidae
            |  |  `--Permolestidae
            |  `--o ARCHIZYGOPTERA
            |     |--Permepallagidae (sedis mutabilis)
            |     |--Kennedyidae (sedis mutabilis)
            |     `--o PROTOMYRMELEONTOIDEA (sedis mutabilis)
            |        |--Batkeniidae
            |        `--Protomyrmeleontidae
            `--o PANODONATA
               |--Tarsophlebiidae
               `--o ODONATA sensu stricto (modern dragonflies)
                  |-- EPIPROCTOPHORA
                  `-- ZYGOPTERA
```

---

[1] Alternative classification:

```
`--Ditaxineuroidea [Protanisoptera] RP02
     |   i. s.: Hemizygopteron Zallesskiy 1955 NB01
     |--Ditaxineuridae GE05
     |--Permaeschna Martynov 1931 NB01 [Permaeschnidae GE05]
     |--Polytaxineura Tillyard 1935 NB01 [Polytaxineuridae RP02]
     |--Callimokaltaniidae RP02
     `--Kaltanoneuridae RP02
```

*Type species of generic name indicated

Reference(s):

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[NB01] Nel, A., O. Bethoux, G. Bechly, X. Martínez-Delclòs & F. Papier. 2001. The Permo-Triassic Odonatoptera of the "protodonate" grade (Insecta: Odonatoptera). Annales de la Société Entomologique de France (N.S.) 37 (4): 501-525.

[R02] Rasnitsyn, A. P. 2002. Special features of the study of fossil insects. In History of Insects (A. P. Rasnitsyn & D. L. J. Quicke, eds) pp. 8-12. Kluwer Academic Publishers: Dordrecht.

[RP02] Rasnitsyn, A. P., & L. N. Pritykina. 2002. Superorder Libellulidea Laicharting, 1781. Order Odonata Fabricius, 1792. The dragonflies. In History of Insects (A. P. Rasnitsyn & D. L. J. Quicke, eds) pp. 97-104. Kluwer Academic Publishers: Dordrecht.

Werner Söderström Osakeyhtiö, Porvoo-Helsinki-Juva, 1980. Alkuperäisteos: Beaut, Du Monde Animal XI & XII Invertébrés. Rizzoli Editore, Milano 1968.

[Z02] Zherikhin, V. V. 2002. Ecological history of the terrestrial insects. In History of Insects (A. P. Rasnitsyn & D. L. J. Quicke, eds) pp. 331-388. Kluwer Academic Publishers: Dordrecht.

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Odonatoptera: References

Abbreviated Dendrogram

```
PTERYGOTA
|--Palaeodictyopteroida
|--Ephemeroptera
|--NEOPTERA
|
`--ODONATOPTERA
   |--Eugeropteridae
   `--Holodonata
      |--Meganisoptera
      `--Odonata
```

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