ARTHROPODS OTHER THAN INSECTS

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Summary

Non-insect arthropods exhibit a diverse array of body plans. Particular sub-groups conform to particular body plans, but no common pattern can be applied to all forms. This great disparity of body plan accounts for the great diversity we see among all the arthropods. Phylogenetic relationships within body plans are still in some cases rather tentative, but the broad outline of higher arthropod relationships is becoming increasingly clearer as we expand our knowledge of the fossil record and the developmental genetics of groups.

1. Introduction

No more diverse an array of body plans can be conceived of than is found among the non-insectan arthropods. If we seek to define body plans by such features as location of the gonopores, total numbers of segments in the body, and body region specializations we can easily define insects into a common pattern [see *Insects*]. However, no such easy definition can be arrived at when examining all the other arthropods. While particular sub-groups may conform to a particular body plan, no such common pattern can be applied to all forms at once. This great disparity of body plan accounts for the great diversity we see among all the arthropods, a diversity not exceeded by any other group of animals [see *Classification and Diversity of Life forms*].

To focus on defining more restricted ground patterns, nevertheless, does allow us to recognize smaller, more discrete groups within the non-insectan arthropods even though our understanding of the relationships between and within these groups remains incomplete. Thus, we can take up the following living groups: myriapods, crustaceans, pycnogonids, and chelicerates. We will take up each of these in turn below.

2. Myriapoda

Myriapods are often treated as a natural class (Myriapoda) of the phylum Arthropoda, but this is far from universally accepted. The term, however, is still universally used as vernacular embracing four main groups of terrestrial, tracheate, polypodous arthropods. In all these forms, the trunk is not distinctly subdivided into a thorax and an abdomen. Four Recent classes of myriapods can be recognized.

2.1. Chilopoda

The chilopods, or centipedes, range in length between a few mm and the approximate 30 centimeters of the tropical American *Scolopendra gigantea*. The body is divided into a head and a trunk.

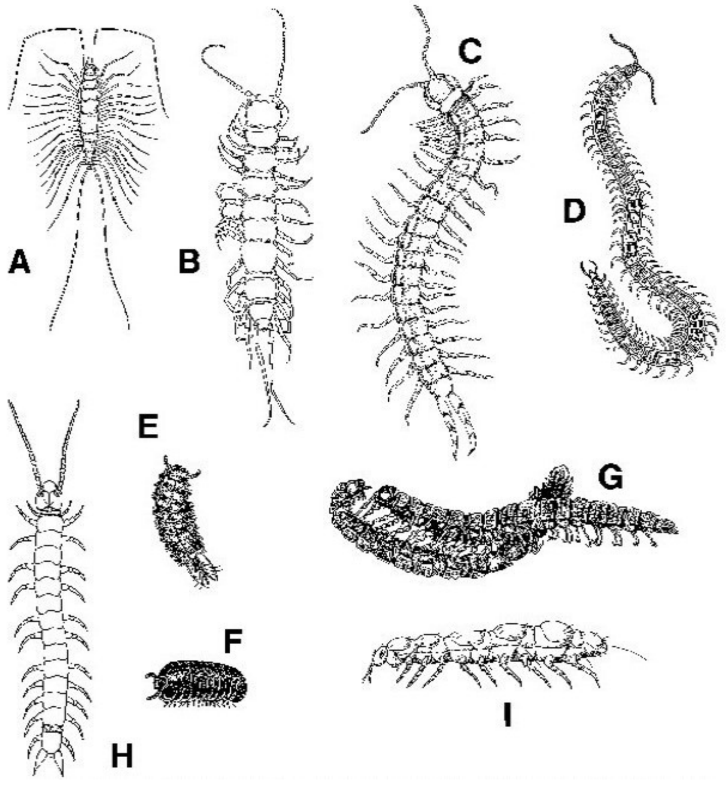

Figure 1. Representative Myriapoda. A-D) the major orders of Chilopoda: A) Scutigeromorpha, the house centipede, *Scutigera*; 2) Lithobiomorpha, *Lithobius*; C) Scolopendromorpha, *Scolopendra*, note the large pair of fangs extending forward just behind the head; D) Geophilomorpha. E-G) some representative orders of Diplopoda: E) Pselaphognatha, *Polyxenus*; F) Oniscomorpha, pill millipede, *Glomeris*; G) Polydesmoida, copulating pair of the genus *Polydesmus*. H) Symphyla, *Scutigerella*. I) Pauropoda, *Pauropus*. [Figures modified from Meglitsch and Schram, 1991]

Compound eyes are present in the scutigeromorphs, whereas groups of ocelli are present in many lithobiomorphs and scolopendromorphs; all geophilomorphs and many scolopendromorphs are blind, as are several cave-dwelling lithobiomorphs (Figure 1 E). In the Scutigeromorpha and in some Lithobiomorpha the antennae are longer than the whole body. In the other groups, the antennae are much shorter and comprise a fixed number of antennal articles (14 in all Geophilomorpha, 17 in many Scolopendromorpha). The first trunk segment bears specialized appendages called the poison claws or forcipules, which contain a poison gland and are used in the capture and immobilization of prey. Each of the remaining trunk segments bears one pair of legs. Curiously enough, the number of leg pairs in the adults is always an odd number, with 15 pairs to be found in all Scutigeromorpha (Figure 1A), Lithobiomorpha (Figure 1B), and Craterostigmomorpha; 21 or 23 in the Scolopendromorpha (Figure 1C); and 27 to 191 in the Geophilomorpha (Figure 1 D).

The Scutigeromorpha have a very peculiar respiratory system, with 7 dorsal openings, each of which leads to a thick bundle of very narrow tracheae that join the dorsal vessel. The oxygen is distributed to the body by help of the circulatory apparatus: the circulating hemolymph contains an oxygen-binding pigment (hemocyanin), related to the respiratory pigments found in several chelicerates and crustaceans. In all remaining centipedes, there are tracheae of the same kind as those of insects.

2.2. Diplopoda

The diplopods, or millipedes, range in length between a few mm and 35 cm. The body includes a head and a trunk. Groups of simple eyes are present in most millipedes, but are lacking in the Polydesmida and in the numerous specialized cavernicolous species. The antennae are generally short, consisting of 8 articles. The mouthparts are typically adapted for cutting and chewing wood or dead leaves. The trunk is normally elongate, more or less flattened dorso-ventrally, but often subcylindrical. The exoskeleton is rarely soft and flexible, as in the subclass Pselaphognatha (Figure 1 E) but is usually rigid in members of the subclass Chilognatha (Figures 1F-G) due to the presence of calcium salts in the internal layers (endocuticle).

The first trunk segment (the collum) does not bear legs; it is followed by 3 (rarely 4) "thoracic“ segments, each of which bears one pair of legs, and a further number of "abdominal“ segments, with two pairs of legs each. Overall, there are 11-17 pairs of legs in the Polyxenida and a variable number (at least 17, but usually many more) in the remaining orders, the highest number being the 375 pairs of legs (in *Illacme plenipes*).

Most millipedes have chemical defenses, in the form of repugnatorial, or stink, glands that produce noxious substances pouring from a series of lateral openings on the trunk tergites. Among the defense substances found in these animals there are benzoquinones, hydroquinones, phenol, benzoic acid, benzaldehyde, and hydrogen cyanide. Several millipedes can coil onto themselves (*volvation*): in this way they become a smooth ball that is difficult to seize; others can roll themselves into a spiral flat coil.

In the male sex, specially modified legs are transformed into clasping and/or genital organs. Posterior claspers are found in the pill millipedes (Figure 1F), and the male uses these appendages to fix the female during mating (Figure 1 G). In most other millipedes, one or, more commonly, two leg pairs are modified into gonopods. These are complex structures directly involved in sperm transfer.

2.3. Symphyla

Symphylans are tiny, blind, soft-bodied and generally whitish myriapods, mostly 2-9 mm long (Figure 1 H). They have one pair of elongate antennae, 12 (rarely 11) pairs of legs, and one pair of posterior appendages (spinnerets). The mouthparts are of a chewing type. Of all terrestrial arthropods, symphylans are the only group with respiratory openings on the head.

2.4. Pauropoda

Still smaller than the symphylans, the pauropods (Figure 1 I) are mostly 0.5-0.7 mm long, the largest species just reaching 1.9 mm. All species are blind. The antennae, of unique structure, are divided into two apical or subapical branches, each branch bearing in turn 1-2 flagella. The mouthparts are generally adapted for the suction of fluids. There are 9 to 11 pairs of legs. Most pauropods lack a structural respiratory system, gas exchange being achieved by simple diffusion through the thin cuticle.

2.5. General aspects of myriapod biology

The vast majority of myriapods are terrestrial. Most species live in forest leaf litter or in rotten wood, others under the bark of dead trees, in the soil or in caves. A few millipedes and symphylans, such as *Blaniulus guttulatus* and *Scutigerella immaculata* respectively, are agricultural pests. The bite of the largest tropical scolopenders can be quite nasty, but no lethal accident has apparently been recorded. Nevertheless, some Central American tribes for making poison arrows use the obnoxious secretions of some large millipedes.

The feeding habits of the myriapods are quite diverse. Basically, however, centipedes are predatory, whereas most millipedes are consumers of decaying plant matter. A few species may be qualified as omnivores; very few are carnivores. Symphylans are mainly vegetarian, whereas the tiny pauropods feed on fungal hyphae and spores.

All myriapods are oviparous. Among the centipedes, the scolopendromorphs and the geophilomorphs have evolved brood care independently, the female remaining coiled around her brood until hatching. Parental care is virtually unknown in the other myriapod classes.

The newborn millipedes may be qualified as larvae, because they do not have the full number of segments and legs they will have as adults. In most species, only three pairs of legs are present at hatching. Additional segments and leg pairs develop through a series of molts. Three different developmental schedules can be distinguished. The pill millipedes, e.g., *Glomeris* (Figure 1F) develop by *hemianamorphosis*: after a few molts, the final number of segments and leg pairs is reached, but the animal will undergo further molts before reaching adult size and sexual maturity. In the polydesmids (Figure 1G), developing by *teloanamorphosis*, the final number of segments and leg pairs is achieved at the same time as maturity, after which no further molt occurs. In other groups, such as the cylindrical julids, which develop by *euanamorphosis*, new segments are progressively added at every molt, but the animal continues molting even after sexual maturity is reached.

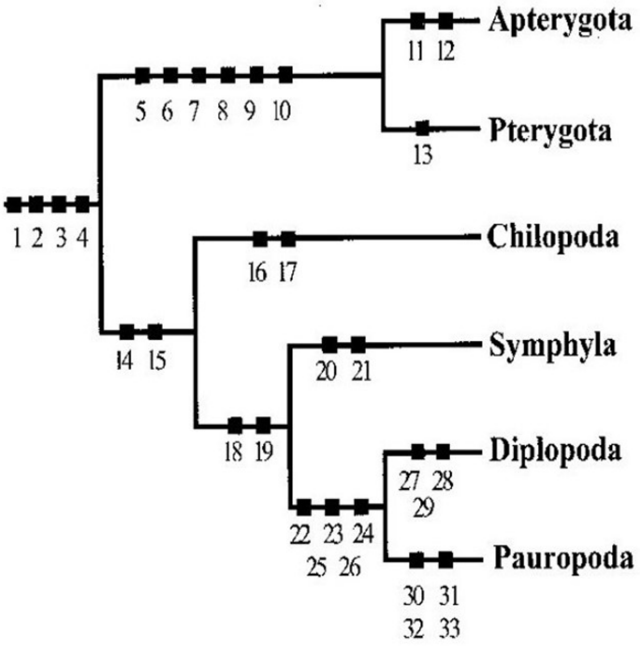

Figure 2. A cladogram portraying one hypothesis as to the relationships within the Myriapoda.
The Hexapoda, or insects, serve here as an out-group, i.e., a taxon outside the immediate area of concern but which can serve to help root the characters within the in-group. The derived characters are: 1) uniramous limbs; 2) excretory Malphigian tubules developed from proctodeum; 3) molar hooks on mandibles; 4) tritocerebral segment highly modified without limbs; 5) tendency to develop at least proto-wings; 6) mandible with promotor-remotor action; 7) first maxilla coxa divided into plates; 8) abdomen of 11 segments; 9) abdominal limbs suppressed except posteriorly; 10) trunk limbs reduced to three pairs in the thorax; 11) wingless; 12) no gonopodal limbs on the abdomen; 13) functional wings greatly elaborated; 14) gnathic lobe on mandible; 15) coxa articulated mid-ventrally with the trunk segments; 16) maxillipeds; 17) mandibles retracted into a head pouch; 18) first maxillae with reduced or absent palp; 19) tendency towards anterior gonopores; 20) head tracheae; 21) gonopod on the 4th trunk segment; 22) collum, or first trunk segment, free; 23) gonopod on 2nd trunk limb; 24) antennae generally short; 25) diplosegments; 26) hatchlings with 4 post-cephalic segments; 27) repugnatorial, or stink, glands; 28) rigid diplosegments; 29) solid tergo-scutal body rings; 30) antennae with several rami; 31) eyeless; 32) pseudoculi, a special chemo- or tacto-receptor on the head; 33) body reduced to a total of no more than 11-12 segments. [Modified from Meglitsch and Schram, 1991]

Many centipedes (scutigeromorphs, lithobiomorphs, and craterostigmomorphs) also develop by *hemianamorphosis*, hatching with 4, 7, and 12 pairs of legs, respectively. The final number of 15 leg pairs is reached following one or more molts, but these animals continue molting until they reach maturity. The remaining centipedes develop by *epimorphosis*: they already reach the final number of body segments before hatching; no segment or leg pair is added during the post-embryonic development.

In symphylans, 6 or 7 pairs of legs are present at hatching. Mature symphylans continue to molt, up to 40 times in *Scutigerella immaculata*. Pauropods hatch as motion-less pupoids with nothing more than rudiments of the antennae and the first two pairs of legs. After a molt they change into an active stadium with three pairs of legs. The following development is by *anamorphosis*, continuing to add a segment with each molt until the adult form is attained.

The exact relationship of myriapods to the other groups of arthropods is now a subject of debate. Long thought to be closely allied to the Hexapoda (insects), this is now questioned since several lines of evidence suggest that insects may be more closely allied to the crustaceans rather than to the myriapods. This issue will not be easily resolved. Nevertheless, the hexapods can still serve as an out-group to the myriapods in order to gain some insight into possible relationships within Myriapoda (Figure 2).

Essentially two major lines appear. The carnivorous chilopods are opposed to a more complex clade of essentially herbivorous taxa, groups that feed on fungi, decaying plant material, and occasionally live plants. While different authors may vary in interpreting the specific relationships within the myriapods, there seems little question that the myriapods as a whole form in fact a monophyletic clade.

3. Crustacea

True crustaceans have existed since the Cambrian and are usually easily recognizable as belonging to one of a number of diverse groups, treated here only summarily. Relatively recent discoveries of new living groups have heavily influenced phylogenetic considerations. The construction of a cladistic phylogeny, or tree of relationships, comprising all these crustacean groups have drawn on computers for little more than a decade. Several possible phylogenies have resulted from this, which we discuss, and while at least partial agreement exists on systematics at the lower levels, there are still significant problems in understanding the phylogenetic relationships of the four or five major groups. For instance substantial questions, such as which major groups are sister taxa, as well as which major taxon constitutes a sister group to all other crustaceans, still await answers, possibly through application of modern molecular techniques in combination with conventional fields like morphology and paleontology.

Living crustaceans and their close relatives from the fossil record are usually arranged in the following five major groups or classes.

3.1. Remipedia

The Remipedia is the most recently described class of Crustacea (in 1981). There are about 12 known species placed in a single living order Nectiopoda. Most of these occur in the Caribbean area; one species is on the Canary Islands, and one species occurs in Western Australia. All species inhabit anchialine caves, occurring in a brackish zone with an associated low level of oxygen. Field observations record that remipedes, while swimming ventral side up, fed on caridean shrimp, discarding the empty cuticles after the contents are sucked dry. The remipede subchelate mouthparts are specialized for gripping and holding prey and include unique maxillules equipped with terminal fangs that apparently puncture the prey cuticle and inject a toxic and/or histolytic secretion. It is suggested that this substance dissolves the prey tissues allowing the remipede to suck out the digestate not unlike what occurs among many arachnids.

While the mouthparts and mode of feeding of remipedes appear to be advanced traits, the posterior morphology of the class seems more primitive (Figure 3 A).

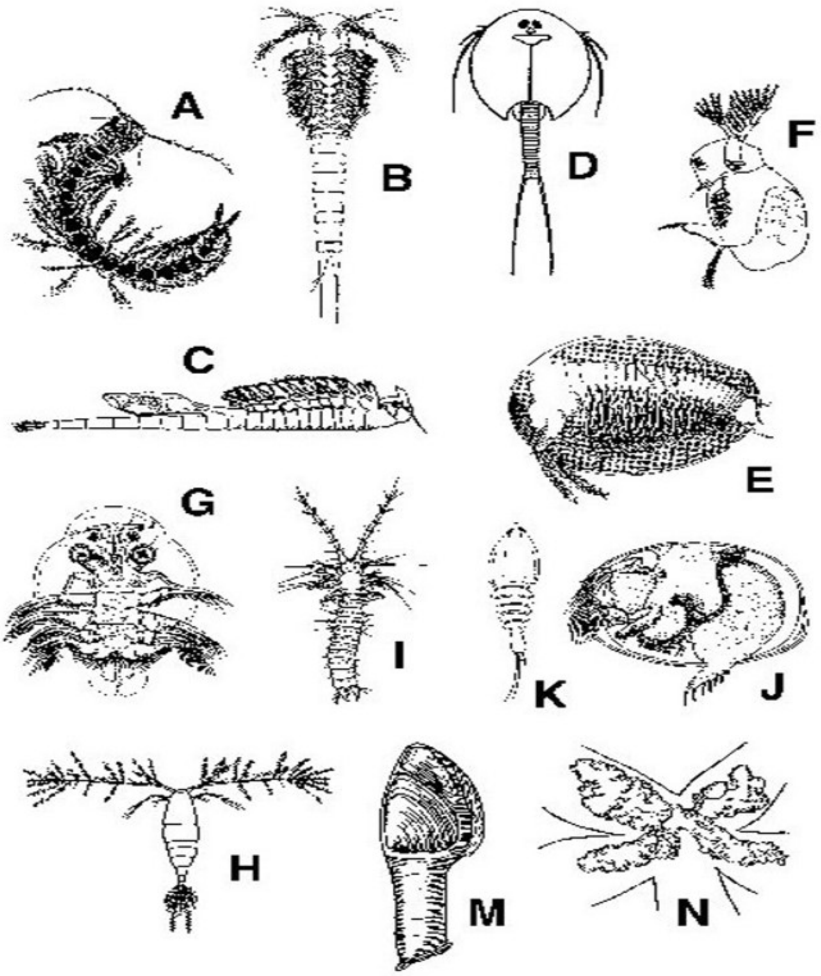

Figure 3. Representative non-Malacostraca crustaceans. A) Remipedia, ventral view, *Speleonectes*; 2) Cephalocarida, ventral view, *Hutchinsoniella*; C-F) Branchiopoda, C) Anostraca, fairy shrimp lateral view, *Branchinecta*, D) Notostraca, tadpole shrimp dorsal view, *Triops*, E) Conchostraca, clam shrimp lateral view with left valve removed to reveal body, *Limnadia,* F) Cladocera, water flea lateral view, *Sida*; G-N) Maxillopoda, G) Branchiura, ventral view, *Argulus*, H) Copepoda, free-swimming, planktonic genus, *Acartia*, I) Mystacocarida, *Derocheilocaris*, J) Ostracoda, lateral view with left valve removed to reveal body, *Vargula,* K) Tantulocarida, *Deoterthron,* M) Thoracica, goose-neck barnacle, *Lepas*, N) Ascothoracida, external view of female in host starfish, *Dendrogaster*. [Figures modified from Schram, 1986]

The trunk lacks post-cephalic tagmosis, that is, their body is not regionalized into a distinct thorax and an abdomen. Instead the trunk consists of up to 30 virtually identical segments each possessing a pair of biramous, paddle-like limbs. The animal swims with metachronal waves of the limbs. The internal morphology also includes some apparently primitive features such as ladder-like nerve system extending throughout the trunk, and gut diverticula in each segment. Remipedes appear to be simultaneous hermaphrodites, males and females at the same time, but with the gonopores of each sex opening on completely different segments: the female system on the eighth trunk segment, the male on the fifteenth. The embryology and early larval development of remipedes are still completely unknown.

The remipede fossil record begins with the fossil *Tesnusocaris goldichi* (order Enantiopoda) from the late-most Mississippian of western Texas in North America. Another species, *Cryptocaris hootchi*, occurs in the Middle Pennsylvanian of Illinois. The raptorial cephalic appendages clearly displayed in *Tesnusocaris* definitely ally that species with the extant remipedes.

The distinctive geographical distribution of the known extant remipedes indicates an ancestry in the ancient Tethys Sea. Even the Paleozoic enantiopods are found on that part of the ancient, tropical, island continent of Laurentia in an area that later became the Western Tethys. When the Gondwana and Laurasia landmasses drifted apart to eventually form the modern arrangement of the continents, the remipedes likely became isolated in their present day rather disparate locations.

3.2. Cephalocarida

Since Sanders described the first cephalocarid in 1955, the number of known species has slowly increased to only around 11 in the single order Brachypoda. All of them are only few mm long and are found worldwide. Long thought to typically live in the flocculent surface layer of muddy bottoms, recent collections seem to indicate that their prime habitat may be much deeper in the sediments than that. Although they have been collected in coastal areas in many parts of the world at relatively shallow depths, at least one species occurs deeper than 1 km.

Some 20 segments sit posterior to the head, of which the anterior eight are said to constitute the thorax and the remaining segments mark an abdomen that lacks appendages (Figure 3 B). Typically the segment after the last appendage-bearing somite has a single, anterior pair of reduced egg-bearing limbs. The anal segment carries a pair of long rami. The cephalocarid head consists of the usual 5 segments typical of crustaceans, but only the four anterior most appendages differ significantly from the thoracopods. The (second) maxillae essentially resemble the thoracic limbs. These maxillae supposedly function as post-cephalic limbs. The thoracic limbs move in a metachronal pattern at the same time achieving locomotion and feeding. Feeding is accomplished when sediment particles are trapped by setae on the median part of the post-cephalic limbs and conveyed forward to the mouth via the median food groove on the underside of the thorax. The animals are hermaphrodites, with both sets of gonads opening through a common set of gonopores on the sixth thoracic segment. Cephalocarids display anamorphic development (growing gradually through a series of

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Biographical Sketches

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