EVOLUTION

We will begin this semester with a discussion of the evolution leading to the Arthropoda, and then the phylogenetic relationships within the Arthropoda itself. There has been a tremendous change in our thoughts about these relationships in recent years, due primarily to the use of DNA data, and then a re-interpretation of the morphological data.

Traditionally, we considered the Arthropoda to be most closely related to the Annelida. In fact, we either thought the Arthropoda descended from the Annelids, or that both the Annelida and the Arthropoda descended from a common ancestor. In your handouts, you will see the proposed hypothesis of how the insects may have evolved from an annelid like ancestor. Also, we have usually indicated that the Onychophora were probably related (perhaps an intermediate between the Annelida and the Arthropoda). There may still be some truth to this process, but the ancestor may be different.

Recent work, especially molecular studies (see handout - Mallatt, 2004 paper), have called into question the above scenario. It has now been proposed that the Arthropoda should be grouped together with the Nematoda and a few other small phyla into a group called the **Ecdysozoa**. Not only are the ribosomal DNA sequences similar, but all of these animals have in common a cuticle that is periodically molted. The Annelida have now been placed in a group called the **Lophotrochozoa** along with Molluscs, Platyhelminthes, and the Rotifera. This is supported by other recent studies from different sources. There is no current agreement on where the Onychophora belong, except that it probably does not belong with the Arthropoda (it appears that it is still related to the basal stem of the Arthropoda). There is still much research going on to either confirm or refute the above classification.

There are three basic arthropod body plans:

1. arachnoid - 2 main body regions, the cephalothorax (prosoma) and abdomen (epistoma); no locomotor appendages on the abdomen.
2. myriapod - 2 main body regions, the head and the trunk; locomotor appendages occur on the trunk.
3. insectan - 3 main body regions, the head, thorax, and abdomen; generally no locomotor appendages on the abdomen.

Evolution within the Arthropoda - Again, there is much debate on the actual evolution of the arthropod groups. Traditionally, it was thought that the Phylum Arthropoda split early on into 3 main groups: the Trilobita, the Chelicerata, and the Mandibulata. Others say that the Trilobita is a subgroup of the Mandibulata. More recently, the Phylum Arthropoda has been divided into 4 subphyla: the Trilobita (trilobites), the Chelicerata (arachnoids and relatives), the Crustacea (crustaceans), and the Atelocerata (millipedes, centipedes, insects, etc.) (remember, some people lumped the Crustacea and the Atelocerata together and call it the Mandibulata). The latest data, however, based upon molecular work, has now significantly changed our thoughts. It is now thought that the Arthropoda early on split into two major lineages: the Pancrustacea (containing a paraphyletic Crustacea + Hexapoda) and the Paradoxopoda (Chelicerata + Myriapoda).

I. Subphylum Trilobita: The **Trilobita** contained the **trilobites**. They are now extinct. They were marine animals. They were the most generalized group of arthropods due mainly to the general undifferentiation of the segmental appendages. They were oval, flattened ventrally with a double series of jointed limbs on all segments except the last. They had 3 body regions: the head, thorax, and pygidium, and the body had two longitudinal furrows. The anterior part of the body was covered by a shield like structure called a **carapace**. They had one pair of antennae, one pair of compound eyes, and no simple eyes. The endite lobes of the anterior legs apparently functioned as jaws. We do have some fossil examples.

II. Subphylum Chelicerata: The Chelicerata can be distinguished from the remaining arthropod groups by two distinctive characters: the loss of antennae, and the development of the first pair of postoral appendages into chelicerae, which are pincer-like feeding organs. They also have only 2 main body regions: the prosoma (cephalothorax) and the abdomen (opisthosoma). The prosoma normally bears 6 pairs of limbs: the chelicerae and 5 pairs of leg-like appendages. There are usually no appendages on the abdomen.

The Chelicerata is divided into 3 classes: the Merostomata, the Pycnogonida, and the Arachnida. Be aware that some workers also split out another extinct group, the Eurypterida, into a separate class; here they are considered as a Subclass in the Merostomata.

A. Class Merostomata: This class includes extinct Eurypterids (just mentioned) and the Subclass Xiphosura. The eurypterids were fairly large (less than a foot to 6-7 feet long; they often had a spine-like tail, and were aquatic or in mud.

The Xiphosura are the king crabs or horseshoe crabs. They do exist today and are also aquatic. They are relatively common along the Atlantic Coast where the feed primarily on marine worms. They are relatively easy to identify by their oval shape with the hard dorsal covering, and the long spine-like tail. The reproductive organs are located anteriorly, near the base of the abdomen. We have examples of these in the laboratory.

B. Class Pycnogonida: This is the sea spiders. They are marine animals, and look somewhat like spiders with their legs bent many times. They have a partial cephalothorax and a rudimentary abdomen. They are predaceous and have sucking mouthparts. They generally are deep-water organisms, but occasionally are found in shallow water under stones. They are relatively rare. We do have examples of these in the laboratory.

C. Class Arachnida: The Arachnida has 2 main body parts: the cephalothorax and the abdomen. The 1st pair of postoral appendages are the chelicerae, the 2nd pair are called pedipalps and the remaining 4 pairs are leg-like. Respiration is by book lungs and/or tracheae. There are groups of simple eyes, but no compound eyes.

The Arachnida is divided into quite a few orders, some of the more common are the Scorpiones, the Araneae, the Opiliones, the Acari, the Pseudoscorpiones, and the Solifugae.

1. Order Scorpiones: The Scorpiones, of course, includes the scorpions. The scorpions are relatively easy to recognize. The juncture between the prosoma and the abdomen is fairly broad and the prosoma is covered by an undivided carapace bearing 2 median and 3-5 pairs of lateral eyes. The opisthosoma is composed of two parts: a broad anterior part (mesosoma) and a narrow tail-like posterior part (metasoma) that distally bears the telson and a sting. They have on the ventral surface of the 2nd segment of the opisthosoma a pair of comb-like structures called pectines; the function of the pectines is unknown (may be tactile), but they may be derived from gills. Has small chelicerae, larger pedipalpi, and 4 pairs of legs. They respire via 4 pairs of book lungs.

They are largely nocturnal, hiding under rocks, etc. during the day. They are fairly common in the southern and southwestern parts of the U.S. They feed on insects and other arthropods, which they catch with their pedipalps and sometimes sting.

2. Order Aranae: These are the spiders. The spiders have two body regions: the cephalothorax and the abdomen. The abdomen is usually unsegmented and bears the genital structures, spiracles, anus, and spinnerets. The cephalothorax is usually covered with a carapace and bears the legs, eyes, and mouthparts. The first segment of the abdomen is reduced and forms a pedicel, the narrow joint between the prosoma and abdomen. Most spiders have 8 simple eyes (some fewer) which are often arranged differently according to the species - this is an important character used in identification. The anus is terminal, without telson. The spinnerets are involved in spinning silk. All spiders can spin silk, but not all make

webs. Some spiders will also spin a single line of silk and hang from the end letting the wind blow them, sometimes many miles. This type of dispersal is called ballooning. Respiration may be by book lungs, trachea, or both. There are a pair of chelicerae, a pair of pedipalps, and 4 pairs of legs.

Spiders live in many different types of habitat where they usually feed on other arthropods. Some do spin silk webs, some hunt on the ground, and some build traps underground. There are a few species that are sometimes considered to be pests: the black widow spider and the brown recluse.

3. Order Opiliones: These are the harvestmen or daddy-long-legs. The body is rounded or oval with the prosoma and the opisthosoma broadly fused (no pedicel); the prosoma is covered by an unsegmented carapace. They usually have 2 eyes. Many species have scent glands which produce a scent to ward off predators. The bodies in a knee-high position with body lower than joints between the femur and tibia. They have one pair of chelicerae, one pair of pedipalps, and 4 pairs of legs.

   Most species are predacous or some feed on other dead arthropods, etc.

4. Order Acari: These are the mites and ticks. Once again the prosoma and the opisthosoma are broadly joined. Newly hatched young are called larvae and have only 3 pairs of legs; they gain the fourth pair of legs after the first molt and are then called nymphs; adults have 4 pairs. They often lack eyes. They have one pair of chelicerae, one pair of pedipalps, and 4 pairs of legs. Eyes (if present) are located at the lateral corners of the scutum. The mouthparts are collectively called the capitulum and consist of an anterior hypstome with rows of posteriorly directed teeth, and a pair of palpi. Laterally on the opisthosoma are roughened areas called spiracular plates, the shape of which can also be important in identification. Some species have indentations along the posterior margin forming squared off areas called festoons. Also important in species identification is the presence and shape of the anal groove.

   Mites and ticks occur almost everywhere and are important economically. Many mites feed on plant material and can cause much damage. There are also mites which cause diseases in both plants and animals, for example, scabies or mange in dogs. There are also some mites which are predaceous on other mites and are considered to be beneficial. Of course, everyone is familiar with ticks and the problems they can cause. They feed on the blood a variety of animals and can transmit many different diseases. The most recent disease receiving much attention is Lyme disease which is vectored by deer ticks (*Ixodes* spp. - *scapularis* in our area). Ticks are the most important vector of diseases of domestic animals, and second only to mosquitoes in vectoring diseases to humans.

5. Order Pseudoscorpiones: These are the pseudoscorpions (there are about 200 species in North America). They look much like scorpions but they lack the tail with the sting, and they are usually much smaller than scorpions. The prosoma is covered with an undivided carapace which bears not more than 2 pairs of eyes. They have the enlarged pedipalps, like scorpions, but they are usually relatively flattened. They have one pair of chelicerae, one pair of pedipalps, and 4 pairs of legs. No pedicel or telson.

   They are most commonly found under stones or under bark where they feed on other small arthropods. Some do have venom glands and some can spin silk with silk glands on their chelicerae - they spin silk coccoons to overwinter in.

6. Order Solifugae: These are the wind scorpions (there are about 120 species in North America). The body is often hairy and somewhat constricted in the middle. The most distinctive character is the greatly enlarged chelicerae. There are usually 4-6 eyes. No telson. They may bite but they do not have venom glands. They have one pair of chelicerae, one pair of pedipalps, and 4 pairs of legs. The fourth pair of legs have a series of 5 malleoli or rachet-organs on their coxae and trochanters, the function of which is unknown (your text indicates that they are probably sensory structures).

   They are relatively common in the arid areas of the western U.S and does occur in western North Dakota.

III. Subphylum Crustacea: this group has has two pair of antennae; most of the appendages are biramous, that is they are bifurcating or divided into two parts. They have two body regions: the cephalothorax and the abdomen. They have well-developed mandibles. They also usually have 5 to 7 pairs of walking legs, and may have smaller appendages on the abdomen called swimmerets. Most are aquatic.

There are many classes of crustaceans, many of which are small, but you may have heard of such as branchiopods or copepods. We will only look at one class, the Malacostraca, and two of its included orders: the Isopoda and the Decapoda.

A. Class Malacostraca (We will only be discussing the two orders below, but we do occasionally see members of the Amphipoda - beach fleas):

1. Order Isopoda: These are the sowbugs and pillbugs. They lack a carapace and have seven pairs of legs. Many isopods are marine living under stones or in seaweed. The terrestrial forms are often found under stones or under bark. Some can roll up into tight balls for defense. Occasionally can be pests of cultivated plants.

2. Order Decapoda: These are the more commonly encountered and recognizable crustaceans including crayfish, shrimp, lobsters, crabs, etc. They are mainly marine animals. The entire thoracic area is usually covered with a carapace and they have five pairs of legs.

IV. Subphylum Atelocerata: This group (excluding the Hexapoda) is often called the Myriapoda. The myriapod classes have 2 body regions (myriapod body style) with a head and trunk region. The Hexapoda has 3 body regions. These organisms have a single pair of antennae and uniramous appendages. We will discuss 5 classes: the Diplopoda, the Chilopoda, the Pauropoda, the Symphyla, and the Hexapoda.

A. Class Diplopoda: This is the millipedes; the name means two footed and refers to the fact that there are 2 pairs of legs per segment. It does have two body regions: the head and the abdomen or trunk. They usually have 30 or more pairs of legs and the bodies are rounded to slightly flattened. Newly hatched millipedes only have three pairs of legs, additional legs are added at each succesive molt. The reproductive openings are located at the anterior end of the body and they lack the poisen fangs found in the centipedes. They usually do have a pair of compound eyes. They usually occur in damp places where there is an abundance of detritus such in the soil or under stones or bark. Most millipedes are scavengers and feed on decaying material, but some do feed on living plants and can be a pest. They do not generally bite humans.

B. Class Chilopoda: These are the centipedes. The name means lip foot and refers to the fact that the first pair of legs are modified into poisen fangs. They have only one pair of legs per segment (usually 15 or more total pairs), and the genital opening is located at the posterior end of the body. They have the two body regions: the head and abdomen or trunk which is often very flattened. They are usually found in protected areas such as in the soil, or under bark, or in rotten logs. They are predaceous feeding on small insects and other arthropods. Some species can inflict a painful bite.

Some species can spin silk: the male spins web and deposits sperm on it which is then picked up by the female.

C. Class Pauropoda: These are minute, whitish insects that can be recognized by the branched antennae. They have 9 pairs of legs, situated one pair per segment; the reproductive opening is at the anterior part of the body. They are generally found in soil and leaf litter.

D. Class Symphyla: These are also very small and slender organisms. They are pale in color and have a pair of long many segmented antennae. They will have 10-12 pairs of legs and the reproductive organs are located near the anterior end of the body. These also occur in the soil or leaf litter. There is one species that is known to feed on the roots of plants and occasionally can be a pest of vegetables. These have been collected in the Fargo area.

E. Class Hexapoda: This is the six-legged arthropods which we will spend the rest of the semester discussing. They have 3 main body regions: the head, thorax, and abdomen; they have 3 pairs of legs, 1 pair of antennae, and usually 2 pairs of wings.

Evolution of the Insectan Body Plan:

Evidence gained from various sources has now enabled us to develop a theory of the development of the insectan body form from a primitive 20-segmented worm-like organism **[see handout]**.

STAGE I - Worm-like Prototype: The prototype was hypothetically a 20-segmented worm-like animal. The mouth was located posteroventrally in the first anterior metamere called the archeocephalon or prostomium. The anus was located on the last metamere called the periproct. There is some disagreement as to the actual number of segments in the prototype - many workers believe that the prostomium and periproct should not be considered as true metameres, but rather more or less as lobe-like outgrowths of the first and last metameres.

STAGE II - Development of Appendages: The first major change that separated the arthropods from the annelids was the development of paired appendages on all major divisions of the body. Appendages 3-18 were probably fairly uniform in size and composition and used for locomotion. The appendages on the prostomium, the 2nd metamere, and the 19th metamere were sensory; the anterior sensory structures are antennae (2 pairs) and the posterior sensory structures are the cerci. Antennae and cerci of present day insects cannot be readily homologized with typical walking legs, so it is believed that they evolved directly as sensory structures rather than being modified from ambulatory appendages - both antennae and cerci appeared very early in the evolution of insects. No known insects (present-day or extinct) have 2 pairs of antennae, but there is sufficient evidence that this 2nd pair probably existed (embryological evidence and some adults have small lobes near mandibles).

Photoreceptors probably evolved early; well-developed compound eyes were already present in Trilobita, Eurypterida, and Xiphosura in the early Cambrian. Some people believe that the eyes evolved from another pair of appendages, but this is doubtful; the dioptic arrangement is simply a modification of the integument and development from appendages seems illogical. Ocelli also appeared in early Cambrian forms.

STAGE III - Cephalization and Differentiation of Appendages: Cephalization is the coalescence or unification of sensory structures and the mechanisms designed for food ingestion into a composite unit usually called the head. The first logical step was to combine the prostomium (bearing primary antennae and photoreceptors) with the first postoral metamere (bearing the second pair of antennae) - this is called the protocephalon.

The locomotor appendages on segments 3-5 were probably utilized as and later modified to aid in the ingestion of food; they eventually evolved to become the 3 principal appendages of the mandibulate mouthparts (mandibles, maxillae, and labrium). As such, it can be assumed that these 3 segments also coalesced bringing the feeding structures closer to the mouth - this is called the gnathocephalon. The utility of the 2nd pair of antennae decreased and they were eventually discarded.

From the study of the nervous system of present day insects we can tell that the gnathocephalon probably is composed of 3 fused metameres (the suboesophageal ganglion is a composite of 3 segmental ganglia) although there is some evidence in primitive insects that there may have been a fourth segment. There is some disagreement about the protocerebrum, but we now believe it is composed of the prostomium plus one metamere. So depending upon which theory, and whether you count the prostomium as a true metamere, the number of segments that coalesced to form the head is from 4-6.

The appendages on segments 6-8 began to develop. Segmentation of the primary locomotory appendages would be more efficient, as well as a corresponding reduction of the appendages on the remaining body segments.

The primitive genital pore of the female probably was situated on the conjunctival membrane behind the sternum of the 15th metamere. In today's insects, this pore is located on the 16th metamere. There is good evidence that the prototype also had an ovipositor that had its valvulae modified from two pairs of walking legs. A modification of the abdominal appendage on metamere 17 evolved into the clasping device of the male copulatory device.

To increase flexibility a longitudinal suture probably developed dividing each metamere into a dorsal tergum and a ventral sternum.

STAGE IV - Differentiation of Tagmata: A tagma is a principal body region of the arthropod's body; for example the head, thorax, and abdomen.

The protocephalon fused with the gnathocephalon to form the head tagma where the division of function was then related to sensory perception and food ingestion. The locomotor appendages on metameres 6-8 further developed into efficient waling legs with a corresponding elaboration of the metameres to accomodate the legs.

Early in the evolution of the Pterygota, the thoracic terga probably developed lateral expansions called paranotal lobes which may have been precursors of wings on the 7th and 8th metameres.

The rest of the metameres did not change much except that they coalesced to some extent and became the abdominal tagma which housed the important visceral systems and also functioned for reproduction.

- Some evidence that Collembola-like arthropods may have occurred during the Devonian geological period about 350 million years ago.

- There is unquestionable records that insects were present during the Upper Carboniferous Age about 250 million years ago; wings were already well-developed.

- Because fossil records are very incomplete, we must rely on three areas of study to gain insight on the origin of insects:
  1. comparative morphology of modern and ancient arthropods.
  2. comparative morphology of modern insects, and how they relate to fossil forms.
  3. study of embryonic forms of modern insects.