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Arthropods

Concept Outline

46.1 The evolution of jointed appendages has made arthropods very successful.

Jointed Appendages and an Exoskeleton. Arthropods probably evolved from annelids, and with their jointed appendages and an exoskeleton, have successfully invaded practically every habitat on earth.

Classification of Arthropods. Arthropods have been traditionally divided into three groups based on morphological characters. However, recent research suggests a restructuring of arthropod classification is needed.

General Characteristics of Arthropods. Arthropods have segmented bodies, a chitinous exoskeleton, and often have compound eyes. They have open circulatory systems. In some groups, a series of tubes carry oxygen to the organs, and unique tubules eliminate waste.

46.2 The chelicerates all have fangs or pincers.

Class Arachnida: The Arachnids. Spiders and scorpions are predators, while most mites are herbivores.

Class Merostomata: Horseshoe Crabs. Among the most ancient of living animals, horseshoe crabs are thought to have evolved from trilobites.

Class Pycnogonida: The Sea Spiders. The spiders that are common in marine habitats differ greatly from terrestrial spiders.

46.3 Crustaceans have branched appendages.

Crustaceans. Crustaceans are unique among living arthropods because virtually all of their appendages are branched.

46.4 Insects are the most diverse of all animal groups.

Classes Chilopoda and Diplopoda: The Centipedes and Millipedes. Centipedes and millipedes are highly segmented, with legs on each segment.

Class Insecta: The Insects. Insects are the largest group of organisms on earth. They are the only invertebrate animals that have wings and can fly.

Insect Life Histories. Insects undergo simple or complete metamorphosis.



FIGURE 46.1

An arthropod. One of the major arthropod groups is represented here by *Polistes*, the common paper wasp (class Insecta).

The evolution of segmentation among annelids marked the first major innovation in body structure among coelomates. An even more profound innovation was the development of jointed appendages in arthropods, a phylum that almost certainly evolved from an annelid ancestor. Arthropod bodies are segmented like those of annelids, but the individual segments often exist only during early development and fuse into functional groups as adults. In arthropods like the wasp above (figure 46.1), jointed appendages include legs, antennae, and a complex array of mouthparts. The functional flexibility provided by such a broad array of appendages has made arthropods the most successful of animal groups.

46.1 The evolution of jointed appendages has made arthropods very successful.

Jointed Appendages and an Exoskeleton

With the evolution of the first annelids, many of the major innovations of animal structure had already appeared: the division of tissues into three primary types (endoderm, mesoderm, and ectoderm), bilateral symmetry, a coelom, and segmentation. With arthropods, two more innovations arose—the development of *jointed appendages* and an *exoskeleton*. Jointed appendages and an exoskeleton have allowed arthropods (phylum Arthropoda) to become the most diverse phylum.

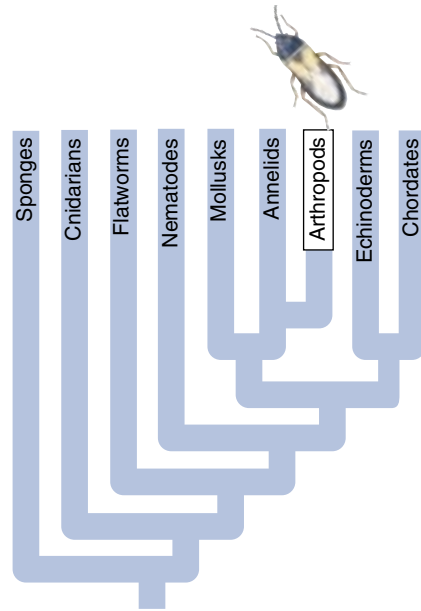
Jointed Appendages

The name “arthropod” comes from two Greek words, *arthros*, “jointed,” and *podes*, “feet.” All arthropods have jointed appendages. The numbers of these appendages are reduced in the more advanced members of the phylum. Individual appendages may be modified into antennae, mouthparts of various kinds, or legs. Some appendages, such as the wings of certain insects, are not homologous to the other appendages; insect wings evolved separately.

To gain some idea of the importance of jointed appendages, imagine yourself without them—no hips, knees, ankles, shoulders, elbows, wrists, or knuckles. Without jointed appendages, you could not walk or grasp any object. Arthropods use jointed appendages such as legs for walking, antennae to sense their environment, and mouthparts for feeding.

Exoskeleton

The arthropod body plan has a second major innovation: a rigid external skeleton, or **exoskeleton**, made of chitin and protein. In any animal, the skeleton functions to provide places for muscle attachment. In arthropods, the muscles attach to the interior surface of their hard exoskeleton, which also protects the animal from predators and impedes water loss. Chitin is chemically similar to cellulose, the dominant structural



component of plants, and shares similar properties of toughness and flexibility. Together, the chitin and protein provide an external covering that is both very strong and capable of flexing in response to the contraction of muscles attached to it. In most crustaceans, the exoskeleton is made even tougher, although less flexible, with deposits of calcium salts. However, there is a limitation. The exoskeleton must be much thicker to bear the pull of the muscles in large insects than in small ones. That is why you don't see beetles as big as birds, or crabs the size of a cow—the exoskeleton would be so thick the animal couldn't move its great weight. Because this size limitation is inherent in the body design of arthropods, there are no large arthropods—few are larger than your thumb.

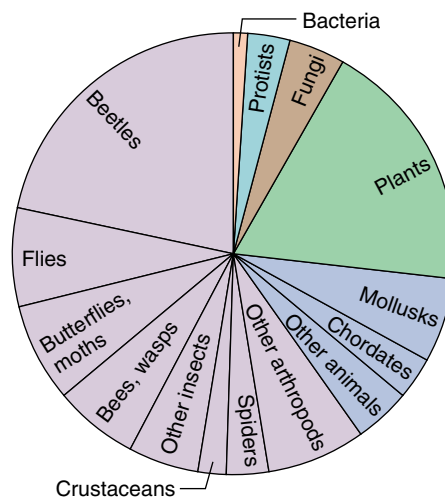


FIGURE 46.2

Arthropods are a successful group.

About two-thirds of all named species are arthropods. About 80% of all arthropods are insects, and about half of the named species of insects are beetles.

The Arthropods

Arthropods, especially the largest class—insects—are by far the most successful of all animals. Well over 1,000,000 species—about two-thirds of all the named species on earth—are members of this phylum (figure 46.2). One scientist recently estimated, based on the number and diversity of insects in tropical forests, that there might be as many as 30 million species in this one class alone. About 200 million insects are alive at any one time for each human! Insects and other arthropods (figure 46.3) abound in every habitat on the planet, but they especially dominate the land, along with flowering plants and vertebrates.

The majority of arthropod species consist of small animals, mostly about a millimeter in length. Members of

the phylum range in adult size from about 80 micrometers long (some parasitic mites) to 3.6 meters across (a gigantic crab found in the sea off Japan).

Arthropods, especially insects, are of enormous economic importance and affect all aspects of human life. They compete with humans for food of every kind, play a key role in the pollination of certain crops, and cause bil-

PHYLUM ARTHROPODA: Jointed appendages and exoskeleton

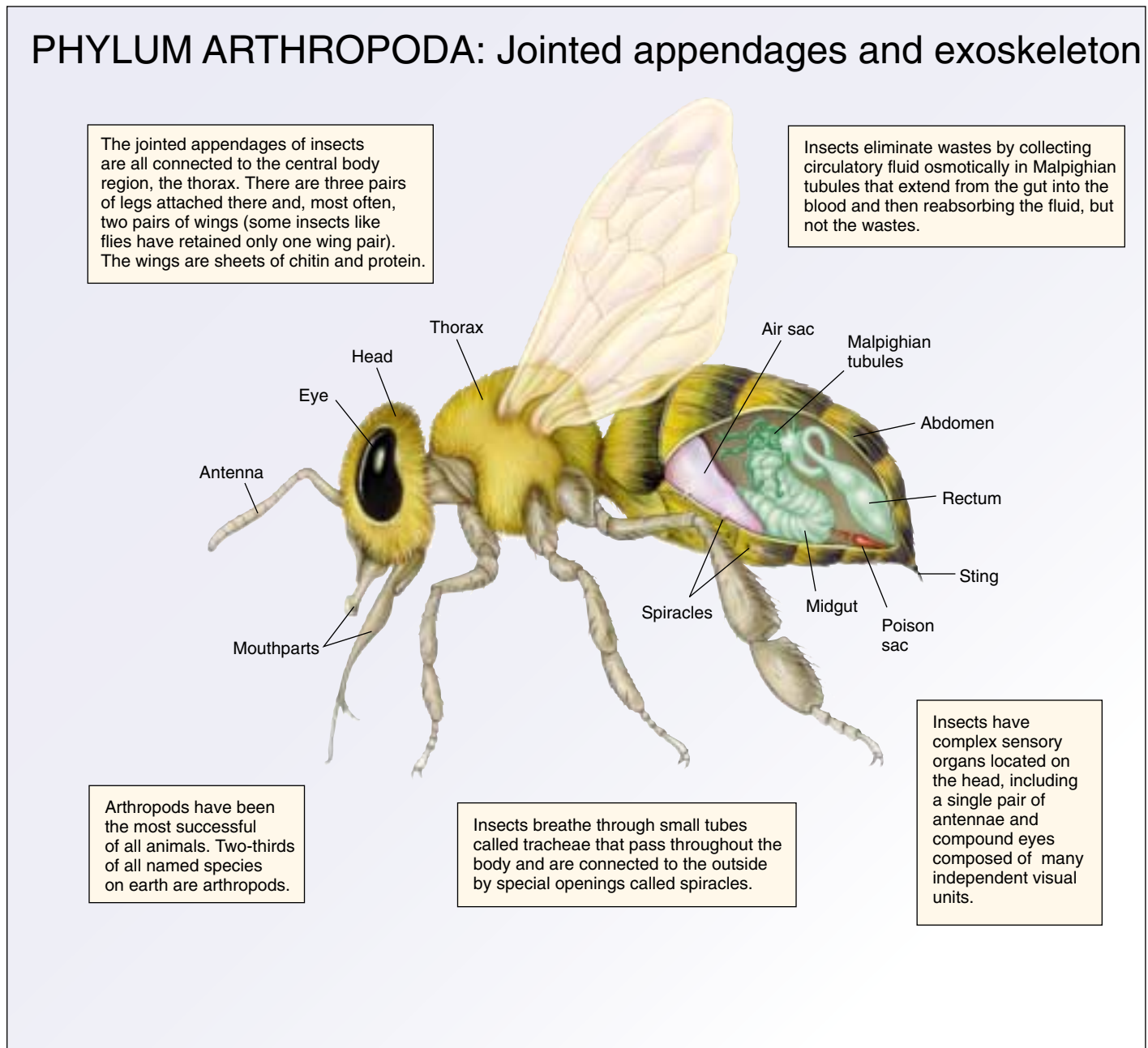


FIGURE 46.3

The evolution of jointed appendages and an exoskeleton. Insects and other arthropods (phylum Arthropoda) have a coelom, segmented bodies, and jointed appendages. The three body regions of an insect (head, thorax, and abdomen) are each actually composed of a number of segments that fuse during development. All arthropods have a strong exoskeleton made of chitin. One class, the insects, has evolved wings that permit them to fly rapidly through the air.

lions of dollars of damage to crops, before and after harvest. They are by far the most important herbivores in all terrestrial ecosystems and are a valuable food source as well. Virtually every kind of plant is eaten by one or more species of insect. Diseases spread by insects cause enormous financial damage each year and strike every

kind of domesticated animal and plant, as well as human beings.

Arthropods are segmented protostomes with jointed appendages. Arthropods are the most successful of all animal groups.

Classification of the Arthropods

Arthropods are among the oldest of animals, first appearing in the Precambrian over 600 million years ago. Ranging in size from enormous to microscopic, all arthropods share a common heritage of segmented bodies and jointed appendages, a powerful combination for generating novel evolutionary forms. Arthropods are the most diverse of all the animal phyla, with more species than all other animal phyla combined, most of them insects.

Origin of the Arthropods

Taxonomists have long held that there is a close relationship between the annelids and the arthropods, the two great segmented phyla. Velvet worms (phylum Onychophora), known from the Burgess Shale (where upside-down fossils were called *Hallucigenia*) and many other early Cambrian deposits, have many features in common with both annelids and arthropods. Some recent molecular studies have supported the close relationship between annelids and arthropods, others have not.

Traditional Classification

Members of the phylum Arthropoda have been traditionally divided into three subphyla, based largely on morphological characters.

1. Trilobites (the extinct trilobites). Trilobites, common in the seas 250 million years ago, were the first animals whose eyes were capable of a high degree of resolution.
2. Chelicerates (spiders, horseshoe crabs, sea spiders). These arthropods lack jaws. The foremost appendages of their bodies are mouthparts called **chelicerae** (figure 46.4a) that function in feeding, usually pinchers or fangs.
3. Mandibulates (crustaceans, insects, centipedes, millipedes). These arthropods have biting jaws, called **mandibles** (figure 46.4b). In mandibulates, the most anterior appendages are one or more pairs of sensory antennae, and the next appendages are the mandibles. Among the mandibulates, insects have traditionally been set apart from the crustaceans, grouped instead with the myriapods (centipedes and millipedes) in a taxon called Tracheata. This phylogeny, still widely employed, dates back to benchmark work by the great comparative biologist Robert Snodgrass in the 1930s. He pointed out that insects, centipedes, and millipedes are united by several seemingly powerful attributes:

A tracheal respiratory system. Trachea are small, branched air ducts that transmit oxygen from openings in the exoskeleton to every cell of the body.

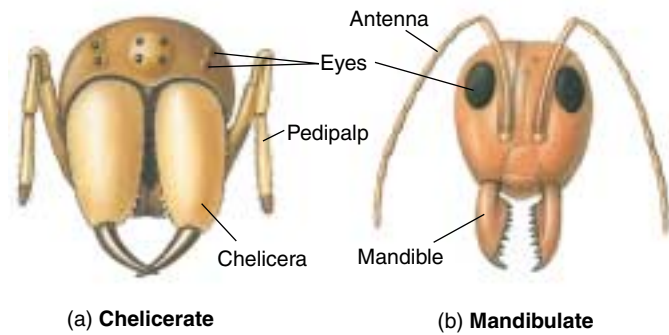


FIGURE 46.4

Chelicerates and mandibulates. In the chelicerates, such as a spider (a), the chelicerae are the foremost appendages of the body. In contrast, the foremost appendages in the mandibulates, such as an ant (b), are the antennae, followed by the mandibles.

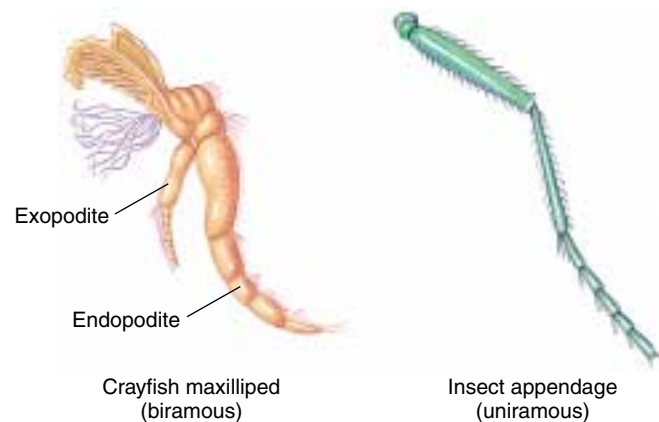


FIGURE 46.5

Mandibulate appendages. A biramous leg in a crustacean (crayfish) and a uniramous leg in an insect.

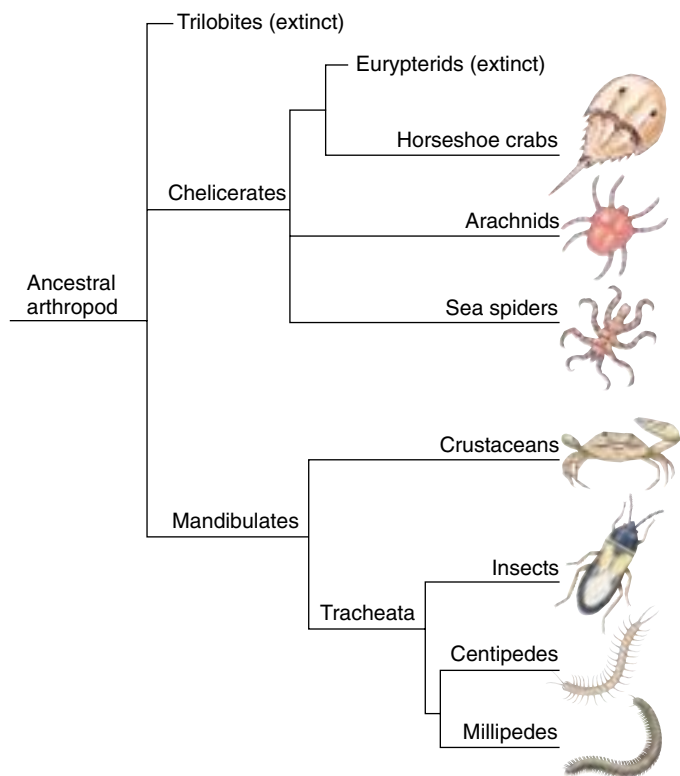
Use of Malpighian tubules for excretion. Malpighian tubules are slender projections from the digestive tract which collect and filter body fluids, emptying wastes into the hindgut.

Uniramous (single-branched) legs. All crustacean appendages are basically biramous, or “two-branched” (figure 46.5), although some of these appendages have become single-branched by reduction in the course of their evolution. Insects, by contrast, have uniramous, or single-branched, mandibles and other appendages.

Doubts about the Traditional Approach

Recent research is casting doubt on the wisdom of this taxonomic decision. The problem is that the key morphological traits used to define the Tracheata are not as powerful taxonomically as had been assumed. Taxonomists have traditionally assumed a character like branching ap-

Traditional Phylogeny



Revised Phylogeny

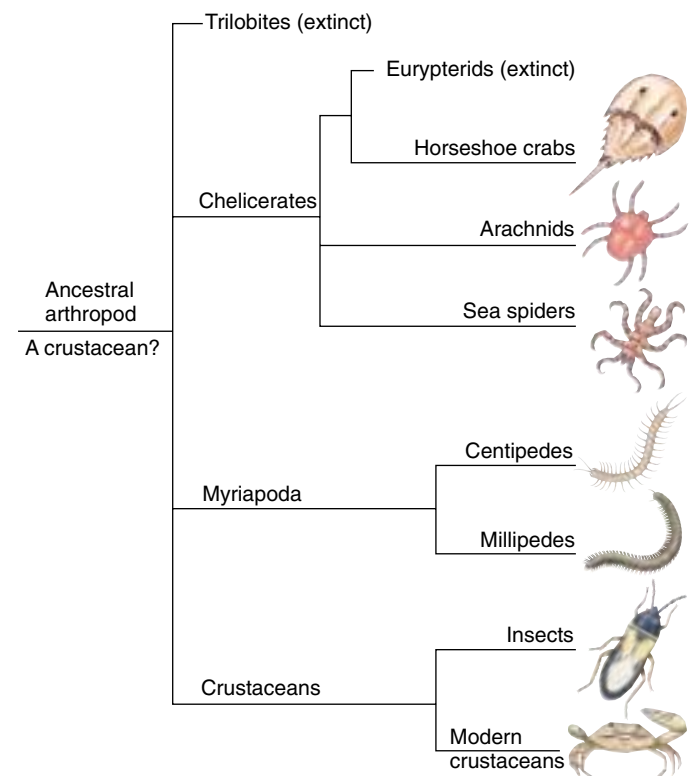


FIGURE 46.6

A proposed revision of arthropod phylogeny. Accumulating evidence supports the hypothesis that insects and modern crustaceans are sister groups, having evolved from the same ancient crustacean ancestor in the Precambrian. This implies that insects may be viewed as “flying crustaceans,” and that the traditional Tracheata taxon, which places centipedes, millipedes, and insects together, is in fact a polyphyletic group.

pendages to be a fundamental one, conserved over the course of evolution, and thus suitable for making taxonomic distinctions.

However, modern molecular biology now tells us that this is not a valid assumption. The branching of arthropod legs, for example, turns out to be controlled by a single gene. The pattern of appendages among arthropods is orchestrated by a family of genes called homeotic (*Hox*) genes, described in detail in chapter 17. A single one of these *Hox* genes, called *Distal-less*, has recently been shown to initiate development of unbranched limbs in insects and branched limbs in crustaceans. The same *Distal-less* gene is found in many animal phyla, including vertebrates.

A Revolutionary New Phylogeny

In recent years a mass of accumulating morphological and molecular data has led many taxonomists to suggest new arthropod taxonomies. The most revolutionary of these, championed by Richard Brusca of Columbia University, considers crustaceans to be the basic arthropod group, and insects a close sister group (figure 46.6).

Morphological Evidence. The most recent morphological study of arthropod phylogeny, reported in 1998, was based on 100 conserved anatomical features of the central nervous system. It concluded insects were more closely related to crustaceans than to any other arthropod group. They share a unique pattern of segmental neurons, and many other features.

Molecular Evidence. Molecular phylogenies based on 18S rRNA sequences, the 18S rDNA gene, the elongation factor EF-1a, and the RNA polymerase II gene, all place insects as a sister group to crustaceans, not myriapods, and arising from within the crustaceans. In conflict with 150 years of morphology-based thinking, these conclusions are certain to engender lively discussion.

Arthropods have traditionally been classified into arachnids and other chelicerates that lack jaws and have fang mouthparts, and mandibulates (crustaceans and tracheates) with biting jaws. A revised arthropod taxonomy considers Tracheata to be the products convergent evolution, with insects and crustaceans sister groups.

General Characteristics of Arthropods

Arthropod bodies are segmented like annelids, a phylum to which at least some arthropods are clearly related. Members of some classes of arthropods have many body segments. In others, the segments have become fused together into functional groups, or **tagmata** (singular, **tagma**), such as the head and thorax of an insect (figure 46.7). This fusing process, known as **tagmatization**, is of central importance in the evolution of arthropods. In most arthropods, the original segments can be distinguished during larval development. All arthropods have a distinct head, sometimes fused with the thorax to form a tagma called the **cephalothorax**.

Exoskeleton

The bodies of all arthropods are covered by an exoskeleton, or cuticle, that contains chitin. This tough outer covering, against which the muscles work, is secreted by the epidermis and fused with it. The exoskeleton remains fairly flexible at specific points, allowing the exoskeleton to bend and appendages to move. The exoskeleton protects arthropods from water loss and helps to protect them from predators, parasites, and injury.

Molting. Arthropods periodically undergo **ecdysis**, or molting, the shedding of the outer cuticular layer. When they outgrow their exoskeleton, they form a new one underneath. This process is controlled by hormones. When the new exoskeleton is complete, it becomes separated from the old one by fluid. This fluid dissolves the chitin and protein and, if it is present, calcium carbonate, from the old exoskeleton. The fluid increases in volume until, finally, the original exoskeleton cracks open, usually along the

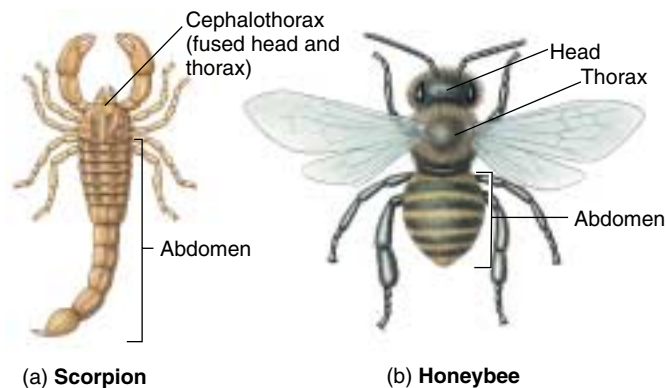


FIGURE 46.7
Arthropod evolution from many to few body segments. The (a) scorpion and the (b) honeybee are arthropods with different numbers of body segments.

back, and is shed. The arthropod emerges, clothed in a new, pale, and still somewhat soft exoskeleton. The arthropod then “puffs itself up,” ultimately expanding to full size. The blood circulation to all parts of the body aids them in this expansion, and many insects and spiders take in air to assist them. The expanded exoskeleton subsequently hardens. While the exoskeleton is soft, the animal is especially vulnerable. At this stage, arthropods often hide under stones, leaves, or branches.

Compound Eye

Another important structure in many arthropods is the **compound eye** (figure 46.8a). Compound eyes are composed of many independent visual units, often thousands of them, called **ommatidia**. Each ommatidium is covered with a lens and linked to a complex of eight reticular cells

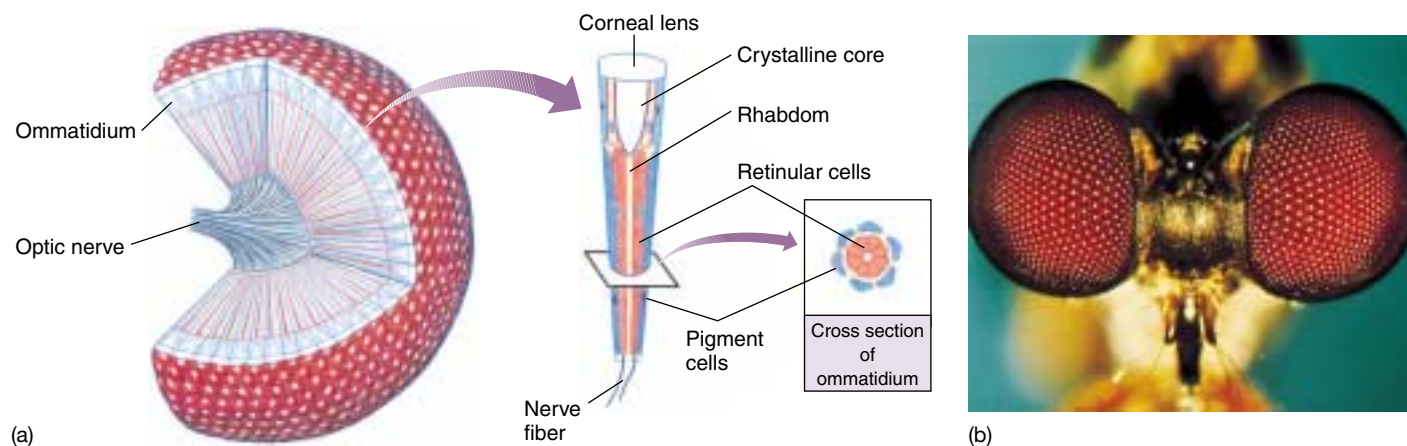


FIGURE 46.8
The compound eye. (a) The compound eyes found in insects are complex structures. (b) Three ocelli are visible between the compound eyes of the robberfly (order Diptera).

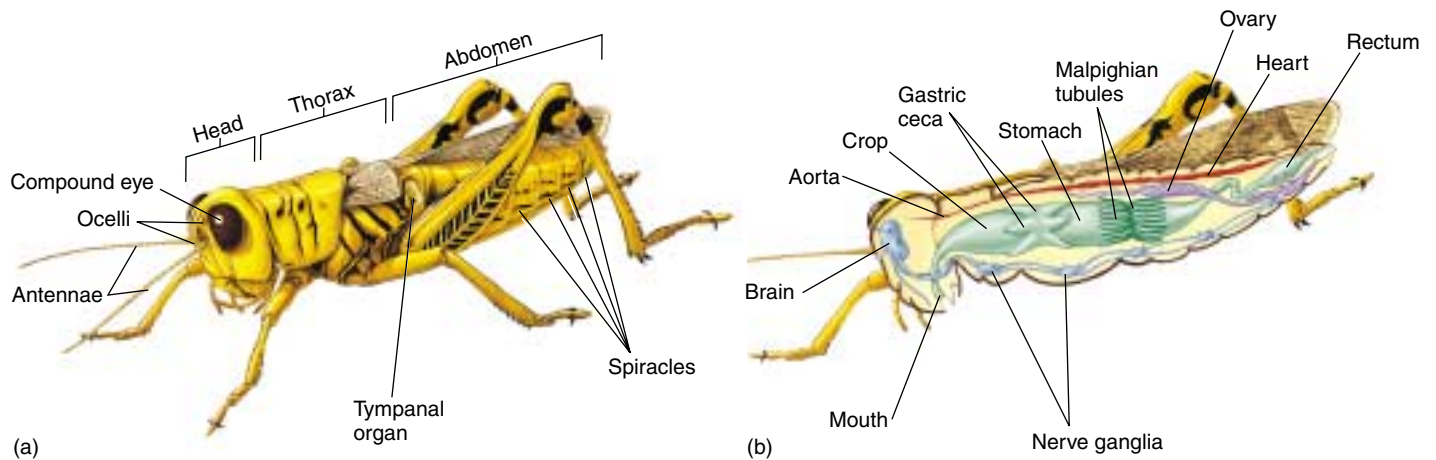


FIGURE 46.9

A grasshopper (order Orthoptera). This grasshopper illustrates the major structural features of the insects, the most numerous group of arthropods. (a) External anatomy. (b) Internal anatomy.

and a light-sensitive central core, or **rhabdom**. Compound eyes among insects are of two main types: **apposition eyes** and **superposition eyes**. Apposition eyes are found in bees and butterflies and other insects that are active during the day. Each ommatidium acts in isolation, surrounded by a curtain of pigment cells that blocks the passage of light from one to another. Superposition eyes, such as those found in moths and other insects that are active at night, are designed to maximize the amount of light that enters each ommatidium. At night, the pigment in the pigment cells is concentrated at the top of the cells so that the low levels of light can be received by many different ommatidia. During daylight, the pigment in the pigment cells is evenly dispersed throughout the cells, allowing the eye to function much like an apposition eye. The pigment in the pigment cells gives the arthropod eye its color, but it is not the critical pigment needed for vision. The visual pigment is located in an area called the rhabdom found in the center of the ommatidium. The individual images from each ommatidium are combined in the arthropod's brain to form its image of the external world.

Simple eyes, or ocelli, with single lenses are found in the other arthropod groups and sometimes occur together with compound eyes, as is often the case in insects (figure 46.8b). Ocelli function in distinguishing light from darkness. The ocelli of some flying insects, namely locusts and dragonflies, function as horizon detectors and help the insect visually stabilize its course in flight.

Circulatory System

In the course of arthropod evolution, the coelom has become greatly reduced, consisting only of cavities that house the reproductive organs and some glands. Arthropods completely lack cilia, both on the external surfaces of

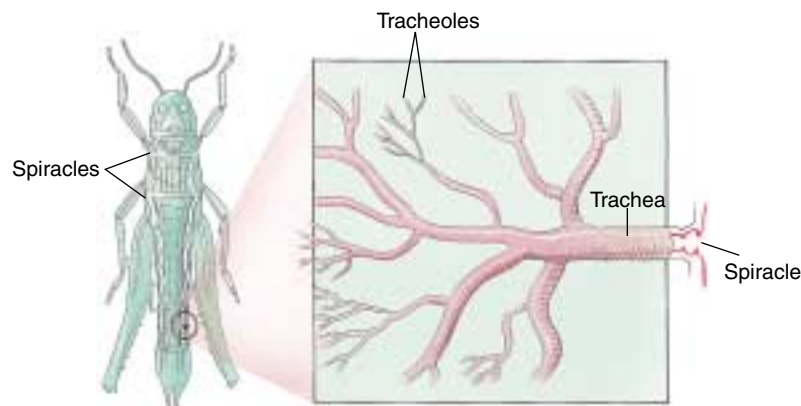
the body and on the internal organs. Like annelids, arthropods have a tubular gut that extends from the mouth to the anus. In the next paragraphs we will discuss the circulatory, respiratory, excretory, and nervous systems of the arthropods (figure 46.9).

The circulatory system of arthropods is open; their blood flows through cavities between the internal organs and not through closed vessels. The principal component of an insect's circulatory system is a longitudinal vessel called the heart. This vessel runs near the dorsal surface of the thorax and abdomen. When it contracts, blood flows into the head region of the insect.

When an insect's heart relaxes, blood returns to it through a series of valves. These valves are located in the posterior region of the heart and allow the blood to flow inward only. Thus, blood from the head and other anterior portions of the insect gradually flows through the spaces between the tissues toward the posterior end and then back through the one-way valves into the heart. Blood flows most rapidly when the insect is running, flying, or otherwise active. At such times, the blood efficiently delivers nutrients to the tissues and removes wastes from them.

Nervous System

The central feature of the arthropod nervous system is a double chain of segmented ganglia running along the animal's ventral surface. At the anterior end of the animal are three fused pairs of dorsal ganglia, which constitute the brain. However, much of the control of an arthropod's activities is relegated to ventral ganglia. Therefore, the animal can carry out many functions, including eating, movement, and copulation, even if the brain has been removed. The brain of arthropods seems to be a control point, or inhibitor, for various actions, rather than a stimulator, as it is in vertebrates.



(a)



(b)

FIGURE 46.10

Tracheae and tracheoles. Tracheae and tracheoles are connected to the exterior by specialized openings called spiracles and carry oxygen to all parts of a terrestrial insect's body. (a) The tracheal system of a grasshopper. (b) A portion of the tracheal system of a cockroach.

Respiratory System

Insects and other members of subphylum Uniramia, which are fundamentally terrestrial, depend on their respiratory rather than their circulatory system to carry oxygen to their tissues. In vertebrates, blood moves within a closed circulatory system to all parts of the body, carrying the oxygen with it. This is a much more efficient arrangement than exists in arthropods, in which all parts of the body need to be near a respiratory passage to obtain oxygen. As a result, the size of the arthropod body is much more limited than that of the vertebrates. Along with the brittleness of their chitin exoskeletons, this feature of arthropod design places severe limitations on size.

Unlike most animals, the arthropods have no single major respiratory organ. The respiratory system of most terrestrial arthropods consists of small, branched, cuticle-lined air ducts called **tracheae** (figure 46.10). These tracheae, which ultimately branch into very small **tracheoles**, are a series of tubes that transmit oxygen throughout the body. Tracheoles are in direct contact with individual cells, and oxygen diffuses directly across the cell membranes. Air passes into the tracheae by way of specialized openings in the exoskeleton called **spiracles**, which, in most insects, can be opened and closed by valves. The ability to prevent water loss by closing the spiracles was a key adaptation that facilitated the invasion of the land by arthropods. In many insects, especially larger ones, muscle contraction helps to increase the flow of gases in and out of the tracheae. In other terrestrial arthropods, the flow of gases is essentially a passive process.

Many spiders and some other chelicerates have a unique respiratory system that involves **book lungs**, a series of leaflike plates within a chamber. Air is drawn in and expelled out of this chamber by muscular contraction. Book lungs may exist alongside tracheae, or they may function

instead of tracheae. One small class of marine chelicerates, the horseshoe crabs, have book gills, which are analogous to book lungs but function in water. Tracheae, book lungs, and book gills are all structures found only in arthropods and in the phylum Onychophora, which have tracheae. Crustaceans lack such structures and have gills.

Excretory System

Though there are various kinds of excretory systems in different groups of arthropods, we will focus here on the unique excretory system consisting of **Malpighian tubules** that evolved in terrestrial uniramians. Malpighian tubules are slender projections from the digestive tract that are attached at the junction of the midgut and hindgut (see figure 46.3). Fluid passes through the walls of the Malpighian tubules to and from the blood in which the tubules are bathed. As this fluid passes through the tubules toward the hindgut, nitrogenous wastes are precipitated as concentrated uric acid or guanine. These substances are then emptied into the hindgut and eliminated. Most of the water and salts in the fluid are reabsorbed by the hindgut and rectum and returned to the arthropod's body. Malpighian tubules are an efficient mechanism for water conservation and were another key adaptation facilitating invasion of the land by arthropods.

All arthropods have a rigid chitin and protein exoskeleton that provides places for muscle attachment, protects the animal from predators and injury, and, most important, impedes water loss. Many arthropods have compound eyes. Arthropods have an open circulatory system. Many arthropods eliminate metabolic wastes by a unique system of Malpighian tubules. Most terrestrial insects have a network of tubes called tracheae that transmit oxygen from the outside to the organs.

46.2 The chelicerates all have fangs or pincers.

Class Arachnida: The Arachnids

Chelicerates (subphylum Chelicerata) are a distinct evolutionary line of arthropods in which the most anterior appendages have been modified into chelicerae, which often function as fangs or pincers. By far the largest of the three classes of chelicerates is the largely terrestrial Arachnida, with some 57,000 named species; it includes spiders, ticks, mites, scorpions, and daddy longlegs. Arachnids have a pair of chelicerae, a pair of pedipalps, and four pairs of walking legs. The chelicerae are the foremost appendages; they consist of a stout basal portion and a movable fang often connected to a poison gland.

The next pair of appendages, **pedipalps**, resemble legs but have one less segment and are not used for locomotion. In male spiders, they are specialized copulatory organs. In scorpions, the pedipalps are large pincers.

Most arachnids are carnivorous. The main exception is mites, which are largely herbivorous. Most arachnids can ingest only preliquified food, which they often digest externally by secreting enzymes into their prey. They can then suck up the digested material with their muscular, pumping pharynx. Arachnids are primarily, but not exclusively, terrestrial. Some 4000 known species of mites and one species of spider live in fresh water, and a few mites live in the sea. Arachnids breathe by means of tracheae, book lungs, or both.

Order Opiliones: The Daddy Longlegs

A familiar group of arachnids consists of the daddy longlegs, or harvestmen (order Opiliones). Members of this order are easily recognized by their oval, compact bodies and extremely long, slender legs (figure 46.11). They respire by means of a primary pair of tracheae and are unusual among the arachnids in that they engage in direct copulation. The males have a penis, and the females an **ovipositor**, or egg-laying organ which deposits their eggs in cracks and crevices. Most daddy longlegs are predators of insects and other arachnids, but some live on plant juices and many scavenge dead animal matter. The order includes about 5000 species.

Order Scorpiones: The Scorpions

Scorpions (order Scorpiones) are arachnids whose pedipalps are modified into pincers. Scorpions use these pincers to handle and tear apart their food (figure 46.12). The venomous stings of scorpions are used mainly to stun their prey and less commonly in self-defense. The stinging apparatus is located in the terminal segment of the abdomen. A scorpion holds its abdomen folded forward over its body



FIGURE 46.11
A harvestman, or daddy longlegs.



FIGURE 46.12
The scorpion, *Uroctonus mordax*. This photograph shows the characteristic pincers and segmented abdomen, ending in a stinging apparatus, raised over the animal's back. The white mass is comprised of the scorpion's young.

when it is moving about. The elongated, jointed abdomens of scorpions are distinctive; in most chelicerates, the abdominal segments are more or less fused together and appear as a single unit.

Scorpions are probably the most ancient group of terrestrial arthropods; they are known from the Silurian Period, some 425 million years ago. Adults of this order of arachnids range in size from 1 to 18 centimeters. There are some 1200 species of scorpions, all terrestrial, which occur throughout the world. They are most common in tropical, subtropical, and desert regions. The young are born alive, with 1 to 95 in a given brood.

Order Araneae: The Spiders

There are about 35,000 named species of spiders (order Araneae). These animals play a major role in virtually all terrestrial ecosystems. They are particularly important as predators of insects and other small animals. Spiders hunt their prey or catch it in silk webs of remarkable diversity. The silk is formed from a fluid protein that is forced out of spinnerets on the posterior portion of the spider's abdomen. The webs and habits of spiders are often distinctive. Some spiders can spin gossamer floats that allow them to drift away in the breeze to a new site.

Many kinds of spiders, like the familiar wolf spiders and tarantulas, do not spin webs but instead hunt their prey actively. Others, called trap-door spiders, construct silk-lined burrows with lids, seizing their prey as it passes by. One species of spider, *Argyroneta aquatica*, lives in fresh water, spending most of its time below the surface. Its body is surrounded by a bubble of air, while its legs, which are used both for underwater walking and for swimming, are not. Several other kinds of spiders walk about freely on the surface of water.

Spiders have poison glands leading through their chelicerae, which are pointed and used to bite and paralyze prey. Some members of this order, such as the black widow and brown recluse (figure 46.13), have bites that are poisonous to humans and other large mammals.

Order Acari: Mites and Ticks

The order Acari, the mites and ticks, is the largest in terms of number of species and the most diverse of the arachnids. Although only about 30,000 species of mites and ticks have been named, scientists that study the group estimate that there may be a million or more members of this order in existence.

Most mites are small, less than 1 millimeter long, but adults of different species range from 100 nanometers to 2 centimeters. In most mites, the cephalothorax and abdomen are fused into an unsegmented ovoid body. Respiration occurs either by means of tracheae or directly through the exoskeleton. Many mites pass through several distinct stages during their life cycle. In most, an inactive eight-legged prelarva gives rise to an active six-legged larva, which in turn produces a succession of three eight-legged stages and, finally, the adult males and females.

Mites and ticks are diverse in structure and habitat. They are found in virtually every terrestrial, freshwater, and marine habitat known and feed on fungi, plants, and animals. They act as predators and as internal and external parasites of both invertebrates and vertebrates.



(a)



(b)

FIGURE 46.13

Two common poisonous spiders. (a) The black widow spider, *Latrodectus mactans*. (b) The brown recluse spider, *Loxosceles reclusa*. Both species are common throughout temperate and subtropical North America, but bites are rare in humans.



FIGURE 46.14

Ticks (order Acari). Ticks (the large one is engorged) on the hide of a tapir in Peru. Many ticks spread diseases in humans and other vertebrates.

Many mites produce irritating bites and diseases in humans. Mites live in the hair follicles and wax glands of your forehead and nose, but usually cause no symptoms.

Ticks are blood-feeding **ectoparasites**, parasites that occur on the surface of their host (figure 46.14). They are larger than most other mites and cause discomfort by sucking the blood of humans and other animals. Ticks can carry many diseases, including some caused by viruses, bacteria, and protozoa. The spotted fevers (Rocky Mountain spotted fever is a familiar example) are caused by bacteria carried by ticks. Lyme disease is apparently caused by spirochaetes transmitted by ticks. Red-water fever, or Texas fever, is an important tick-borne protozoan disease of cattle, horses, sheep, and dogs.

Scorpions, spiders, and mites are all arachnids, the largest class of chelicerates.



FIGURE 46.15
Limulus. Horseshoe crabs, emerging from the sea to mate at the edge of Delaware Bay, New Jersey, in early May.

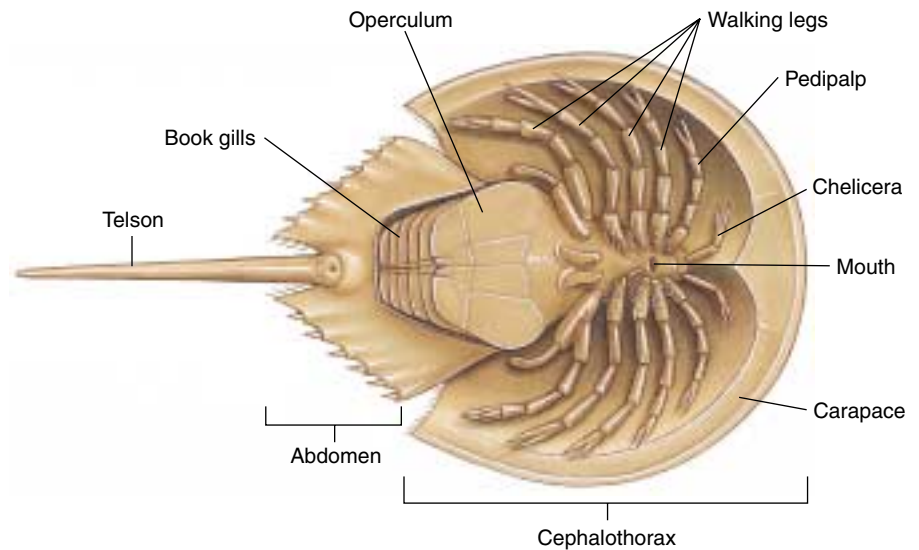


FIGURE 46.16
Diagram of a horseshoe crab, *Limulus*, from below. This diagram illustrates the principal features of this archaic animal.

Class Merostomata: Horseshoe Crabs

A second class of chelicerates is the horseshoe crabs (class Merostomata). There are three genera of horseshoe crabs. One, *Limulus* (figure 46.15), is common along the East Coast of North America. The other two genera live in the Asian tropics. Horseshoe crabs are an ancient group, with fossils virtually identical to *Limulus* dating back 220 million years to the Triassic Period. Other members of the class, the now-extinct eurypterans, are known from 400 million years ago. Horseshoe crabs may have been derived from trilobites, a relationship suggested by the appearance of their larvae. Individuals of *Limulus* grow up to 60 centimeters long. They mature in 9 to 12 years and have a life span of 14 to 19 years. *Limulus* individuals live in deep water, but they migrate to shallow coastal waters every spring, emerging from the sea to mate on moonlit nights when the tide is high.

Horseshoe crabs feed at night, primarily on mollusks and annelids. They swim on their backs by moving their abdominal plates. They can also walk on their four pairs of legs, protected along with chelicerae and pedipalps by their shell (figure 46.16).

Horseshoe crabs are a very ancient group.

Class Pycnogonida: The Sea Spiders

The third class of chelicerates is the sea spiders (class Pycnogonida). Sea spiders are common in coastal waters, with more than 1000 species in the class. These animals are not often observed because many are small, only about 1 to 3 centimeters long, and rather inconspicuous. They are found in oceans throughout the world but are most abundant in the far north and far south. Adult sea spiders are mostly external parasites or predators of other animals like sea anemones (figure 46.17).

Sea spiders have a sucking proboscis in a mouth located at its end. Their abdomen is much reduced, and their body appears to consist almost entirely of the cephalothorax, with no well-defined head. Sea spiders usually have four, or less commonly five or six, pairs of legs. Male sea spiders carry the eggs on their legs until they hatch, thus providing a measure of parental care. Sea spiders completely lack excretory and respiratory systems. They appear to carry out these functions by direct diffusion, with waste products flowing outward through the cells and oxygen flowing inward through them. Sea spiders are not closely related to either of the other two classes of chelicerates.



FIGURE 46.17
A marine pycnogonid. The sea spider, *Pycnogonum littorale* (yellow animal), crawling over a sea anemone.

Sea spiders are very common in marine habitats. They are not closely related to terrestrial spiders.

46.3 Crustaceans have branched appendages.

Crustaceans

The crustaceans (subphylum Crustacea) are a large group of primarily aquatic organisms, consisting of some 35,000 species of crabs, shrimps, lobsters, crayfish, barnacles, water fleas, pillbugs, and related groups (table 46.1). Most crustaceans have two pairs of antennae, three types of chewing appendages, and various numbers of pairs of legs. All crustacean appendages, with the possible exception of the first pair of antennae, are basically biramous. In some crustaceans, appendages appear to have only a single branch; in those cases, one of the branches has been lost during the course of evolutionary specialization. The **nauplius** larva stage through which all crustaceans pass (figure 46.18) provides evidence that all members of this diverse group are descended from a common ancestor. The nauplius hatches with three pairs of appendages and metamorphoses through several stages before reaching maturity. In many groups, this nauplius stage is passed in the egg, and development of the hatchling to the adult form is direct.

Crustaceans differ from insects but resemble centipedes and millipedes in that they have appendages on their abdomen as well as on their thorax. They are the only arthropods with two pairs of antennae. Their mandibles likely originated from a pair of limbs that took on a chewing function during the course of evolution, a process that apparently occurred independently in the common ancestor of the terrestrial mandibulates. Many crustaceans have compound eyes. In addition, they have delicate tactile hairs that project from the cuticle all over the body. Larger crustaceans have feathery gills near the bases of their legs. In smaller members of this class, gas exchange takes place directly through the thinner areas of the cuticle or the entire body. Most crustaceans have separate sexes. Many different kinds of specialized copulation occur among the crustaceans, and the members of some orders carry their eggs with them, either singly or in egg pouches, until they hatch.

Decapod Crustaceans

Large, primarily marine crustaceans such as shrimps, lobsters, and crabs, along with their freshwater relatives, the crayfish, are collectively called *decapod crustaceans* (figure 46.19). The term *decapod* means “ten-footed.” In these animals, the exoskeleton is usually reinforced with calcium carbonate. Most of their body segments are fused into a cephalothorax covered by a dorsal shield, or **carapace**, which arises from the head. The crushing pincers common in many decapod crustaceans are used in obtaining food, for example, by crushing mollusk shells.

Table 46.1 Traditional Classification of the Phylum Arthropoda

Subphylum	Characteristics	Members
Chelicerata	Mouthparts are chelicerae	The chelicerates: spiders, horseshoe crabs, mites
Crustacea	Mouthparts are mandibles; biramous appendages	The crustaceans: lobsters, crabs, shrimp, isopods, barnacles
Uniramia	Mouthparts are mandibles; uniramous appendages	Chilopods (centipedes), diplopods (millipedes), and insects

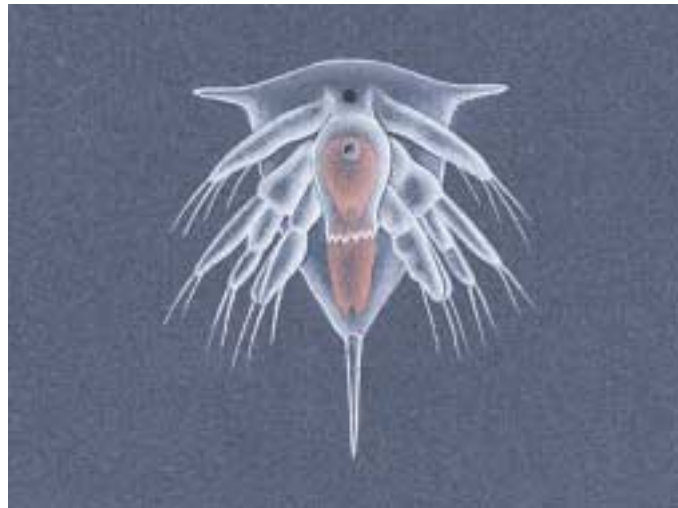


FIGURE 46.18 Although crustaceans are diverse, they have fundamentally similar larvae. The nauplius larva of a crustacean is an important unifying feature found in all members of this group.

In lobsters and crayfish, appendages called **swimmerets** occur in lines along the ventral surface of the abdomen and are used in reproduction and swimming. In addition, flattened appendages known as **uropods** form a kind of compound “paddle” at the end of the abdomen. These animals may also have a **telson**, or tail spine. By snapping its abdomen, the animal propels itself through the water rapidly and forcefully. Crabs differ from lobsters and crayfish in proportion; their carapace is much larger and broader and the abdomen is tucked under it.

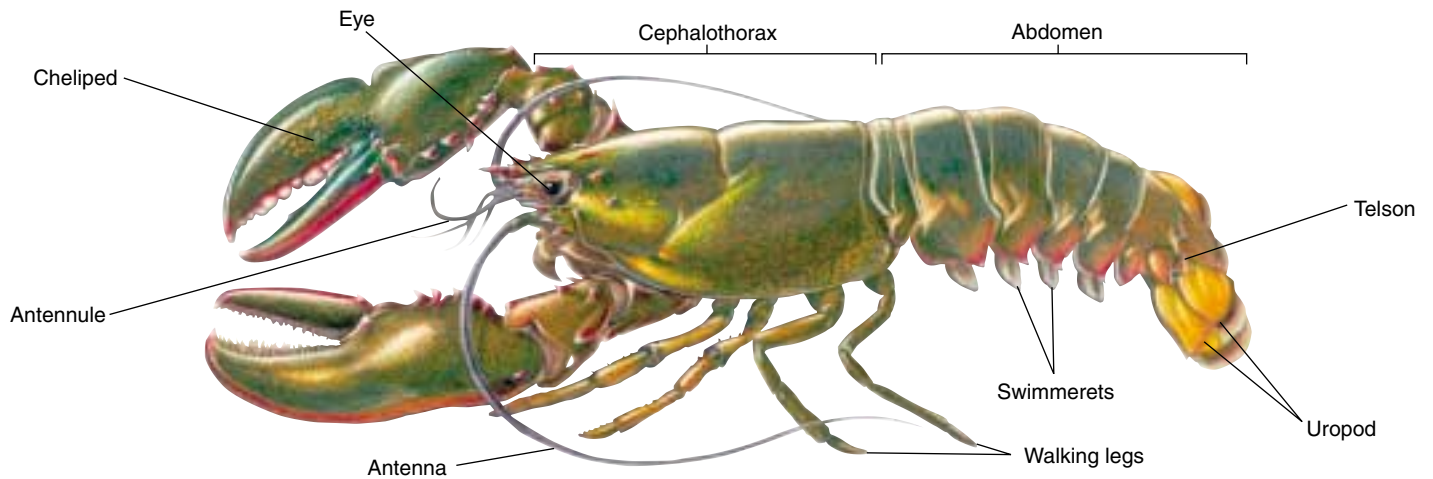


FIGURE 46.19
Decapod crustacean. A lobster, *Homarus americanus*. The principal features are labeled.

Terrestrial and Freshwater Crustaceans

Although most crustaceans are marine, many occur in fresh water and a few have become terrestrial. These include pillbugs and sowbugs, the terrestrial members of a large order of crustaceans known as the isopods (order Isopoda). About half of the estimated 4500 species of this order are terrestrial and live primarily in places that are moist, at least seasonally. Sand fleas or beach fleas (order Amphipoda) are other familiar crustaceans, many of which are semiterrestrial (intertidal) species.

Along with the larvae of larger species, minute crustaceans are abundant in the plankton. Especially significant are the tiny copepods (order Copepoda; figure 46.20), which are among the most abundant multicellular organisms on earth.

Sessile Crustaceans

Barnacles (order Cirripedia; figure 46.21) are a group of crustaceans that are sessile as adults. Barnacles have free-swimming larvae, which ultimately attach their heads to a piling, rock, or other submerged object and then stir food into their mouth with their feathery legs. Calcareous plates protect the barnacle's body, and these plates are usually attached directly and solidly to the substrate. Although most crustaceans have separate sexes, barnacles are hermaphroditic, but they generally cross-fertilize.

Crustaceans include marine, freshwater, and terrestrial forms. All possess a nauplius larval stage and branched appendages.

FIGURE 46.21
Gooseneck barnacles, *Lepas anatifera*, feeding.
 These are stalked barnacles; many others lack a stalk.



FIGURE 46.20
Freshwater crustacean. A copepod with attached eggs, a member of an abundant group of marine and freshwater crustaceans (order Copepoda), most of which are a few millimeters long. Copepods are important components of the plankton.



46.4 Insects are the most diverse of all animal groups.

Millipedes, centipedes, and insects, three distinct classes, are uniramian mandibulates. They respire by means of tracheae and excrete their waste products through Malpighian tubules. These groups were certainly derived from annelids, probably ones similar to the oligochaetes, which they resemble in their embryology.

Classes Chilopoda and Diplopoda: The Centipedes and Millipedes

The centipedes (class Chilopoda) and millipedes (class Diplopoda) both have bodies that consist of a head region followed by numerous segments, all more or less similar and nearly all bearing paired appendages. Although the name *centipede* would imply an animal with a hundred legs and the name *millipede* one with a thousand, adult centipedes usually have 30 or more legs, adult millipedes 60 or more. Centipedes have one pair of legs on each body segment (figure 46.22), millipedes two (figure 46.23). Each segment of a millipede is a tagma that originated during the group's evolution when two ancestral segments fused. This explains why millipedes have twice as many legs per segment as centipedes.

In both centipedes and millipedes, fertilization is internal and takes place by direct transfer of sperm. The sexes are separate, and all species lay eggs. Young millipedes usually hatch with three pairs of legs; they experience a number of growth stages, adding segments and legs as they mature, but do not change in general appearance.

Centipedes, of which some 2500 species are known, are all carnivorous and feed mainly on insects. The appendages of the first trunk segment are modified into a pair of poison fangs. The poison is often quite toxic to human beings, and many centipede bites are extremely painful, sometimes even dangerous.

In contrast, most millipedes are herbivores, feeding mainly on decaying vegetation. A few millipedes are carnivorous. Many millipedes can roll their bodies into a flat coil or sphere because the dorsal area of each of their body segments is much longer than the ventral one. More than 10,000 species of millipedes have been named, but this is estimated to be no more than one-sixth of the actual number of species that exists. In each segment of their body, most millipedes have a pair of complex glands that produces a bad-smelling fluid. This fluid is ex-



FIGURE 46.22

A centipede. Centipedes, like this member of the genus *Scolopendra*, are active predators.

uded for defensive purposes through openings along the sides of the body. The chemistry of the secretions of different millipedes has become a subject of considerable interest because of the diversity of the compounds involved and their effectiveness in protecting millipedes from attack. Some produce cyanide gas from segments near their head end. Millipedes live primarily in damp, protected places, such as under leaf litter, in rotting logs, under bark or stones, or in the soil.

Centipedes are segmented hunters with one pair of legs on each segment. Millipedes are segmented herbivores with two pairs of legs on each segment.



FIGURE 46.23

A millipede. Millipedes, such as this *Sigmoria* individual, are herbivores.

Class Insecta: The Insects

The insects, class Insecta, are by far the largest group of organisms on earth, whether measured in terms of numbers of species or numbers of individuals. Insects live in every conceivable habitat on land and in fresh water, and a few have even invaded the sea. More than half of all the named animal species are insects, and the actual proportion is doubtless much higher because millions of additional forms await detection, classification, and naming. Approximately 90,000 described species occur in the United States and Canada, and the actual number of species in this area probably approaches 125,000. A hectare of lowland tropical forest is estimated to be inhabited by as many as 41,000 species of insects, and many suburban gardens may have 1500 or more species. It has been estimated that approximately a billion billion (10^{18}) individual insects are alive at any one time. A glimpse at the enormous diversity of insects is presented in figure 46.24 and later in table 46.2.



(a)



(b)



(c)



(d)



(e)



(f)

FIGURE 46.24

Insect diversity. (a) Luna moth, *Actias luna*. Luna moths and their relatives are among the most spectacular insects (order Lepidoptera). (b) Soldier fly, *Ptericus trivittatus* (order Diptera). (c) Boll weevil, *Anthonomus grandis*. Weevils are one of the largest groups of beetles (order Coleoptera). (d) A thorn-shaped leafhopper, *Umbonica crassicornis* (order Hemiptera). (e) Copulating grasshoppers (order Orthoptera). (f) Termite, *Macrotermes bellicosus* (order Isoptera). The large, sausage-shaped individual is a queen, specialized for laying eggs; most of the smaller individuals around the queen are nonreproductive workers, but the larger individual at the lower left is a reproductive male.

External Features

Insects are primarily a terrestrial group, and most, if not all, of the aquatic insects probably had terrestrial ancestors. Most insects are relatively small, ranging in size from 0.1 millimeter to about 30 centimeters in length or wingspan. Insects have three body sections, the head, thorax, and abdomen; three pairs of legs, all attached to the thorax; and one pair of antennae. In addition, they may have one or two pairs of wings. Insect mouthparts all have the same basic structure but are modified in different groups in relation to their feeding habits (figure 46.25). Most insects have compound eyes, and many have ocelli as well.

The insect thorax consists of three segments, each with a pair of legs. Legs are completely absent in the larvae of certain groups, for example, in most members of the order Diptera (flies) (figure 46.26). If two pairs of wings are present, they attach to the middle and posterior segments of the thorax. If only one pair of wings is present, it usually attaches to the middle segment. The thorax is almost entirely filled with muscles that operate the legs and wings.

The wings of insects arise as saclike outgrowths of the body wall. In adult insects, the wings are solid except for the veins. Insect wings are not homologous to the other appendages. Basically, insects have two pairs of wings, but in some groups, like flies, the second set has been reduced to a pair of balancing knobs called halteres during the course of evolution. Most insects can fold their wings over their abdomen when they are at rest; but a few, such as the dragonflies and damselflies (order Odonata), keep their wings erect or outstretched at all times.

Insect forewings may be tough and hard, as in beetles. If they are, they form a cover for the hindwings and usually open during flight. The tough forewings also serve a protective function in the order Orthoptera, which includes grasshoppers and crickets. The wings of insects are made of sheets of chitin and protein; their strengthening veins are tubules of chitin and protein. Moths and butterflies have wings that are covered with detachable scales that provide most of their bright colors (figure 46.27). In some wingless insects, such as the springtails or silverfish, wings never evolved. Other wingless groups, such as fleas and lice, are derived from ancestral groups of insects that had wings.

Internal Organization

The internal features of insects resemble those of the other arthropods in many ways. The digestive tract is a tube, usually somewhat coiled. It is often about the same length as the body. However, in the order Hemiptera, which consists of the leafhoppers, cicadas, and related groups, and in many flies (order Diptera), the digestive tube may be greatly coiled and several times longer than the body. Such long digestive tracts are generally found in

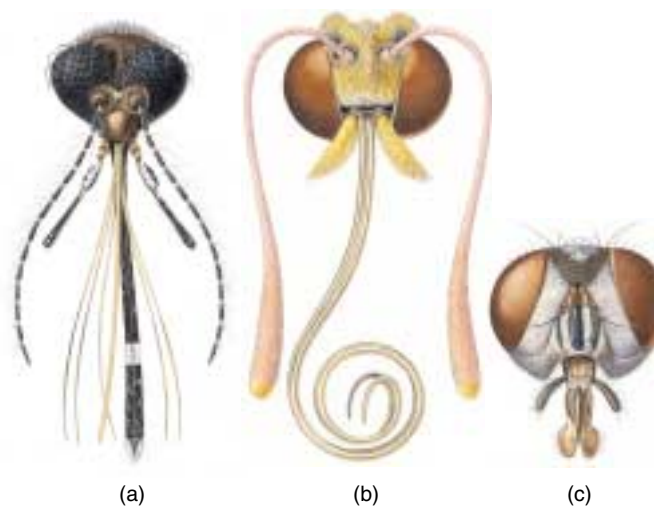


FIGURE 46.25
Modified mouthparts in three kinds of insects. Mouthparts are modified for (a) piercing in the mosquito, *Culex*, (b) sucking nectar from flowers in the alfalfa butterfly, *Colias*, and (c) sipping up liquids in the housefly, *Musca domestica*.



FIGURE 46.26
Larvae of a mosquito, *Culex pipiens*. The aquatic larvae of mosquitoes are quite active. They breathe through tubes from the surface of the water, as shown here. Covering the water with a thin film of oil causes them to drown.

insects that have sucking mouthparts and feed on juices rather than on protein-rich solid foods because they offer a greater opportunity to absorb fluids and their dissolved nutrients. The digestive enzymes of the insect also are more dilute and thus less effective in a highly liquid medium than in a more solid one. Longer digestive tracts give these enzymes more time to work while food is passing through.

The anterior and posterior regions of an insect's digestive tract are lined with cuticle. Digestion takes place primarily in the stomach, or midgut; and excretion takes place through Malpighian tubules. Digestive enzymes are mainly secreted from the cells that line the midgut, although some are contributed by the salivary glands near the mouth.

The tracheae of insects extend throughout the body and permeate its different tissues. In many winged insects, the tracheae are dilated in various parts of the body, forming air sacs. These air sacs are surrounded by muscles and form a kind of bellows system to force air deep into the tracheal system. The spiracles, a maximum of 10 on each side of the insect, are paired and located on or between the segments along the sides of the thorax and abdomen. In most insects, the spiracles can be opened by muscular action. Closing the spiracles at times may be important in retarding water loss. In some parasitic and aquatic groups of insects, the spiracles are permanently closed. In these groups, the tracheae run just below the surface of the insect, and gas exchange takes place by diffusion.

The **fat body** is a group of cells located in the insect body cavity. This structure may be quite large in relation to the size of the insect, and it serves as a food-storage reservoir, also having some of the functions of a vertebrate liver. It is often more prominent in immature insects than in adults, and it may be completely depleted when metamorphosis is finished. Insects that do not feed as adults retain their fat bodies and live on the food stored in them throughout their adult lives (which may be very short).

Sense Receptors

In addition to their eyes, insects have several characteristic kinds of sense receptors. These include **sensory hairs**, which are usually widely distributed over their bodies. The



FIGURE 46.27
Scales on the wing of *Parnassius imperator*, a butterfly from China. Scales of this sort account for most of the colored patterns on the wings of butterflies and moths.

sensory hairs are linked to nerve cells and are sensitive to mechanical and chemical stimulation. They are particularly abundant on the antennae and legs—the parts of the insect most likely to come into contact with other objects.

Sound, which is of vital importance to insects, is detected by tympanal organs in groups such as grasshoppers and crickets, cicadas, and some moths. These organs are paired structures composed of a thin membrane, the **tympanum**, associated with the tracheal air sacs. In many other groups of insects, sound waves are detected by sensory hairs. Male mosquitoes use thousands of sensory hairs on their antennae to detect the sounds made by the vibrating wings of female mosquitoes.

Sound detection in insects is important not only for protection but also for communication. Many insects communicate by making sounds, most of which are quite soft, very high-pitched, or both, and thus inaudible to humans. Only a few groups of insects, especially grasshoppers, crickets, and cicadas, make sounds that people can hear. Male crickets and longhorned grasshoppers produce sounds by rubbing their two front wings together. Shorthorned grasshoppers do so by

rubbing their hind legs over specialized areas on their wings. Male cicadas vibrate the membranes of air sacs located on the lower side of the most anterior abdominal segment.

In addition to using sound, nearly all insects communicate by means of chemicals or mixtures of chemicals known as **pheromones**. These compounds, extremely diverse in their chemical structure, are sent forth into the environment, where they are active in very small amounts and convey a variety of messages to other individuals. These messages not only convey the attraction and recognition of members of the same species for mating, but they also mark trails for members of the same species, as in the ants.

All insects possess three body segments (tagmata): the head, the thorax, and the abdomen. The three pairs of legs are attached to the thorax. Most insects have compound eyes, and many have one or two pairs of wings. Insects possess sophisticated means of sensing their environment, including sensory hairs, tympanal organs, and chemoreceptors.

Insect Life Histories

Most young insects hatch from fertilized eggs laid outside their mother's body. The zygote develops within the egg into a young insect, which escapes by chewing through or bursting the shell. Some immature insects have specialized projections on the head that assist in this process. In a few insects, eggs hatch within the mother's body.

During the course of their development, young insects undergo ecdysis a number of times before they become adults. Most insects molt four to eight times during the course of their development, but some may molt as many as 30 times. The stages between the molts are called **instars**. When an insect first emerges following ecdysis, it is pale, soft, and especially susceptible to predators. Its exoskeleton generally hardens in an hour or two. It must grow to its new size, usually by taking in air or water, during this brief period.

There are two principal kinds of metamorphosis in insects: **simple metamorphosis** and **complete metamorphosis** (figure 46.28). In insects with simple metamorphosis, immature stages are often called **nymphs**. Nymphs are usually quite similar to adults, differing mainly in their smaller size, less well-developed wings, and sometimes color. In insect orders with simple metamorphosis, such as mayflies and dragonflies, nymphs are aquatic and extract oxygen from the water through gills. The adult stages are terrestrial and look very different from the nymphs. In other groups, such as grasshoppers and their relatives, nymphs and adults live in the same habitat. Such insects usually change gradually during their life cycles with respect to wing development, body proportions, the appearance of ocelli, and other features.

In complete metamorphosis, the wings develop internally during the juvenile stages and appear externally only during the resting stage that immediately precedes the final molt (figure 46.28*b*). During this stage, the insect is called a **pupa** or **chrysalis**, depending on the group to which it belongs. A pupa or chrysalis does not normally move around much, although mosquito pupae do move around freely. A large amount of internal body reorganization takes place while the insect is a pupa or chrysalis.

More than 90% of the insects, including the members of all of the largest and most successful orders, display complete metamorphosis. The juvenile stages and adults often live in distinct habitats, have different habits, and are usually extremely different in form. In these insects, development is indirect. The immature stages, called **larvae**, are often wormlike, differing greatly in appearance from the adults. Larvae do not have compound eyes. They may be legless or have legs or leg-like appendages on the abdomen. They usually have chewing mouthparts, even in those orders in which the adults have sucking mouthparts; chewing mouthparts are the primitive condition in these groups. When larvae and adults play different ecological roles, they

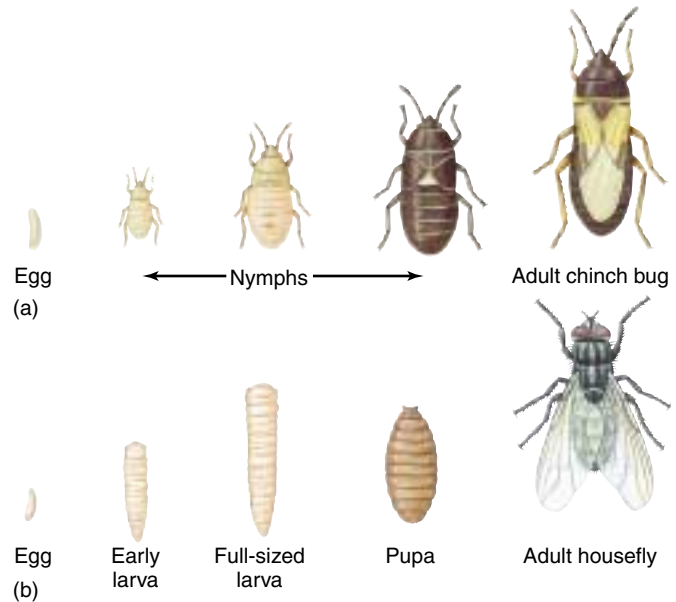


FIGURE 46.28

Metamorphosis. (a) Simple metamorphosis in a chinch bug (order Hemiptera), and (b) complete metamorphosis in a housefly, *Musca domestica* (order Diptera).

do not compete directly for the same resources, an advantage to the species.

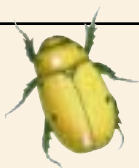








Pupae do not feed and are usually relatively inactive. As pupae, insects are extremely vulnerable to predators and parasites, but they are often covered by a cocoon or some other protective structure. Groups of insects with complete metamorphosis include moths and butterflies; beetles; bees, wasps, and ants; flies; and fleas.

Some species of insects exhibit no dramatic change in form from immature stages to adult. This type of development is called **ametabolus** (meaning without change) and is seen in the most primitive orders of insects such as the silverfish and springtails.

Hormones control both ecdysis and metamorphosis. **Molting hormone**, or **ecdysone**, is released from a gland in the thorax when that gland has been stimulated by brain hormone, which in turn is produced by neurosecretory cells and released into the blood. The effects of the molting induced by ecdysone are determined by juvenile hormone, which is present during the immature stages but declines in quantity as the insect passes through successive molts. When the level of juvenile hormone is relatively high, the molt produces another larva; when it is lower, it produces the pupa and then the final development of the adult.

Insects undergo either simple or complete metamorphosis.

Table 46.2 Major Orders of Insects

Order	Typical Examples		Key Characteristics	Approximate Number of Named Species
Coleoptera	Beetles		The most diverse animal order; two pairs of wings; front pair of wings is a hard cover that partially protects the transparent rear pair of flying wings; heavily armored exoskeleton; biting and chewing mouthparts; complete metamorphosis	350,000
Diptera	Flies		Some that bite people and other mammals are considered pests; front flying wings are transparent; hind wings are reduced to knobby balancing organs; sucking, piercing, and lapping mouthparts; complete metamorphosis	120,000
Lepidoptera	Butterflies, moths		Often collected for their beauty; two pairs of broad, scaly, flying wings, often brightly colored; hairy body; tubelike, sucking mouthparts; complete metamorphosis	120,000
Hymenoptera	Bees, wasps, ants		Often social, known to many by their sting; two pairs of transparent flying wings; mobile head and well-developed eyes; often possess stingers; chewing and sucking mouthparts; complete metamorphosis	100,000
Hemiptera	True bugs, bedbugs, leafhoppers		Often live on blood; two pairs of wings, or wingless; piercing, sucking mouthparts; simple metamorphosis	60,000
Orthoptera	Grasshoppers, crickets, roaches		Known for their jumping; two pairs of wings or wingless; among the largest insects; biting and chewing mouthparts in adults; simple metamorphosis	20,000
Odonata	Dragonflies		Among the most primitive of the insect order; two pairs of transparent flying wings; large, long, and slender body; chewing mouthparts; simple metamorphosis	5,000
Isoptera	Termites		One of the few types of animals able to eat wood; two pairs of wings, but some stages are wingless; social insects; there are several body types with division of labor; chewing mouthparts; simple metamorphosis	2,000
Siphonaptera	Fleas		Small, known for their irritating bites; wingless; small flattened body with jumping legs; piercing and sucking mouthparts; complete metamorphosis	1,200

**Summary****Questions****Media Resources****46.1 The evolution of jointed appendages has made arthropods very successful.**

- Jointed appendages and an exoskeleton greatly expanded locomotive and manipulative capabilities for the arthropod phyla, the most successful of all animals in terms of numbers of individuals, species, and ecological diversification.
- Traditionally, arthropods have been grouped into three subphyla based on morphological characters but new research is calling this classification of the arthropods into question.
- Like annelids, arthropods have segmented bodies, but some of their segments have become fused into tagmata during the course of evolution. All possess a rigid external skeleton, or exoskeleton.

1. What are the advantages of an exoskeleton? What occurs during ecdysis? What controls this process?
2. What type of circulatory system do arthropods have? Describe the direction of blood flow. What helps to maintain this one-way flow?
3. What are Malpighian tubules? How do they work? What other system are they connected to? How does this system process wastes? How does it regulate water loss?



- Arthropods



- Enhancement
Chapter: Arthropod
Taxonomy,
Sections 1 and 2

46.2 The chelicerates all have fangs or pincers.

- Chelicerates consist of three classes: Arachnida (spiders, ticks, mites, and scorpions); Merostomata (horseshoe crabs); and Pycnogonida (sea spiders).
- Spiders, the best known arachnids, have a pair of chelicerae, a pair of pedipalps, and four pairs of walking legs. Spiders secrete digestive enzymes into their prey, then suck the contents out.

4. Into what two groups are arthropods traditionally divided? Describe each group in terms of its mouthparts and appendages, and give several examples of each.

46.3 Crustaceans have branched appendages.

- Crustaceans comprise some 35,000 species of crabs, shrimps, lobsters, barnacles, sowbugs, beach fleas, and many other groups. Their appendages are basically biramous, and their embryology is distinctive.

5. On which parts of the body do crustaceans possess legs?
6. How do biramous and uniramous appendages differ?



- Enhancement
Chapter: Arthropod
Taxonomy, Section 3

46.4 Insects are the most diverse of all animal groups.

- Centipedes and millipedes are segmented uniramia. Centipedes are hunters with one pair of legs per segment, and millipedes are herbivores with two pairs of legs per segment.
- Insects have three body segments, three pairs of legs, and often one or two pairs of wings. Many have complex eyes and other specialized sensory structures.
- Insects exhibit either simple metamorphosis, moving through a succession of forms relatively similar to the adult, or complete metamorphosis, in which an often wormlike larva becomes a usually sedentary pupa, and then an adult.

7. How are millipedes and centipedes similar to each other? How do they differ?
8. What type of digestive system do most insects possess? What digestive adaptations occur in insects that feed on juices low in protein? Why?
9. What is an instar as it relates to insect metamorphosis? What are the two different kinds of metamorphosis in insects? How do they differ?



- Enhancement
Chapter: Arthropod
Taxonomy, Section 4
- Student Research:
Insect Behavior