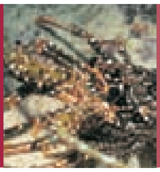
12



chapter twelve

Arthropods

Spotted spiny lobster, *Panulirus guttatus*.

A Winning Combination

> Tunis, Algeria—Treating it as an invading army, Tunisia, Algeria, and Morocco have mobilized to fight the most serious infestation of locusts in over 30 years. Billions of the insects have already caused extensive damage to crops and are threatening to inflict great harm to the delicate economies of North Africa.
> Source: *New York Times,* April 20, 1988

Humans suffer staggering economic losses due to insects, of which outbreaks of billions of locusts in Africa are only one example. In the western United States and Canada, an outbreak of mountain pine beetles in the 1980s and 1990s killed pines on huge acreages, and the 1973 to 1985 outbreak of spruce budworm in fir/spruce forests killed millions of conifer trees. These examples serve to remind us of our ceaseless struggle with the dominant group of animals on earth today: insects. Insects far outnumber all other species of animals in the world combined, and numbers of individuals are equally enormous. Some scientists have estimated that there are 200 million insects for every human alive today! Insects have an unmatched ability to adapt to all land environments and to virtually all climates. Having originally evolved as land animals, insects developed wings and invaded the air 150 million years before flying reptiles, birds, or mammals. Many have exploited freshwater and saltwater (shoreline) habitats, where they are now widely prevalent; only in the seas are insects almost nonexistent, but there are vast numbers of crustaceans in marine habitats.

How can we account for the enormous success of these creatures? Arthropods have a combination of valuable structural and physiological adaptations, including a versatile exoskeleton, metamerism, an efficient respiratory system, and highly developed sensory organs. In addition, many have a waterproofed cuticle and have extraordinary abilities to survive adverse environmental conditions. We describe these adaptations and others in this chapter.

Phylum Arthropoda (ar-throp´o-da) (Gr. *arthron,* joint, + *pous, podos,* foot) embraces the largest assemblage of living animals on earth. It includes spiders, scorpions, ticks, mites, crustaceans, millipedes, centipedes, insects, and some smaller groups. In addition there is a rich fossil record extending back to the mid-Cambrian period (figure 12.1).

Arthropods are eucoelomate protostomes with well-developed organ systems, and their cuticular exoskeleton containing chitin is a prominent characteristic. Like annelids, they are conspicuously segmented; their primitive body pattern is a linear series of similar somites, each with a pair of jointed appendages. However, unlike annelids, arthropods have embellished the segmentation theme: variation occurs in the pattern of somites and appendages in the phylum. Often somites are combined or fused into functional groups, called **tagmata,** for specialized purposes. Appendages, too, are frequently differentiated and specialized for walking, swimming, flying, or eating.

Few arthropods exceed 60 cm in length, and most are far below this size. The largest is a Japanese crab (*Macrocheira kaempferi*), which has approximately a 3.7 m span; the smallest is a parasitic mite, which is less than 0.1 mm long.

Arthropods are usually active, energetic animals. However we judge them, whether by their great diversity or their wide ecological distribution or their vast numbers of species, the answer is the same: they are the most abundant and diverse of all animals.

Although arthropods compete with us for food supplies and spread serious diseases, they are essential in pollination of many food plants, and they also serve as food, yield drugs and dyes, and create such products as silk, honey, and beeswax.

Ecological Relationships

Arthropods are found in all types of environment from low ocean depths to very high altitudes and from the tropics far into both north and south polar regions. Some species are adapted for life on land or in fresh, brackish, and marine waters; others live in or on plants and other animals. Most species use flight to varying degrees to move among their favored habitats. Some live in places where no other animal could survive.

Although all types—carnivorous, omnivorous, and herbivorous—occur in this vast group, the majority are herbivorous. Most aquatic arthropods depend on algae for their nourishment, and most land forms live chiefly on plants. There are many parasites. In diversity of ecological distribution arthropods have no rivals.

Why Have Arthropods Achieved Such Great Diversity and Abundance?

Arthropods have achieved a great diversity, number of species, wide distribution, variety of habitats and feeding habits, and power of adaptation to changing conditions. These are some of the structural and physiological patterns that have been helpful to them:

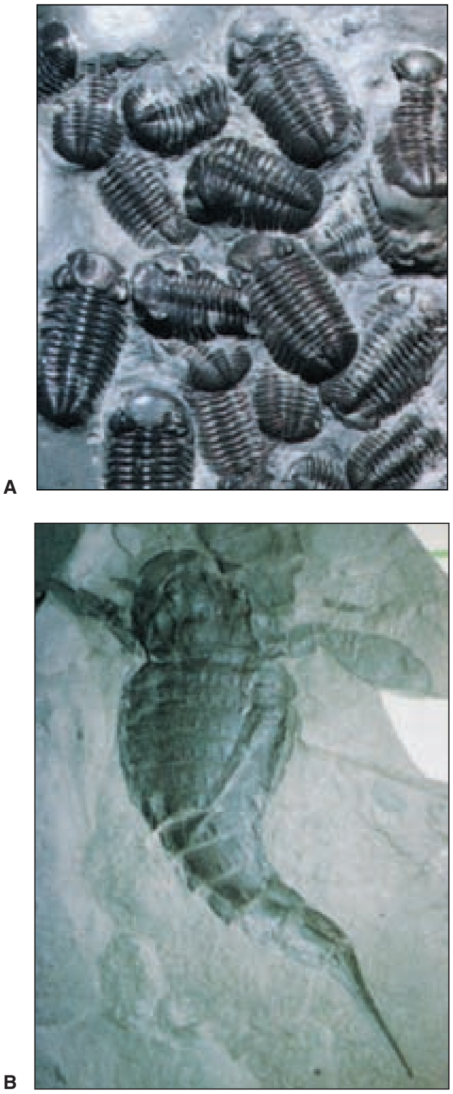


figure 12.1
Fossils of early arthropods. **A,** Trilobite fossils, dorsal view. These animals were abundant in the mid-Cambrian period. **B,** Eurypterid fossil; eurypterids flourished in Europe and North America from Ordovician to Permian periods.

1. **A versatile exoskeleton.** Arthropods possess an exoskeleton that is highly protective without sacrificing mobility. The skeleton is the cuticle, an outer covering secreted by underlying epidermis.

   The cuticle consists of an inner and thicker **procuticle** and an outer, relatively thin **epicuticle.** The procuticle is divided into **exocuticle,** which is secreted before a molt, and **endocuticle,** which is secreted after molting. Both layers of the procuticle contain **chitin** bound with protein. Chitin is a tough,

characteristics of phylum arthropoda

1. Bilateral symmetry; metameric body, **tagmata** of head and trunk; head, thorax, and abdomen; or cephalothorax and abdomen
2. **Appendages jointed;** primitively, one pair to each somite (metamere), but number often reduced; appendages often modified for specialized functions
3. **Exoskeleton of cuticle** containing protein, lipid, chitin, and often calcium carbonate secreted by underlying epidermis and shed (molted) at intervals
4. Muscular system complex, with exoskeleton for attachment; striated muscles for rapid action; smooth muscles for visceral organs; **no cilia**
5. Coelom reduced; most of body cavity consisting of **hemocoel** (sinuses, or spaces, in the tissues) filled with blood
6. Complete digestive system; mouthparts modified from appendages and adapted for different methods of feeding
7. **Circulatory system open,** with dorsal contractile heart, arteries, and hemocoel
8. Respiration by body surface, gills, tracheae (air tubes), or book lungs
9. Paired excretory glands called coxal, antennal, or maxillary glands present in some; some with other excretory organs, called Malpighian tubules
10. Nervous system similar to annelid plan, with dorsal brain connected by a ring around the gullet to a double nerve chain of ventral ganglia; fusion of ganglia in some species; well-developed sensory organs
11. Sexes usually separate, with paired reproductive organs and ducts; usually internal fertilization; oviparous or ovoviviparous; often with metamorphosis; parthenogenesis in a few forms; **growth with ecdysis**

resistant, nitrogenous polysaccharide that is insoluble in water, alkalis, and weak acids. Thus the procuticle not only is flexible and lightweight but also affords protection, particularly against dehydration. In most crustaceans, the procuticle in some areas is also impregnated with **calcium salts,** which reduce its flexibility. In the hard shells of lobsters and crabs, for instance, this calcification is extreme. The outer epicuticle is composed of protein and often lipids. The protein is stabilized and hardened by a chemical process called tanning, adding further protection. Both the procuticle and the epicuticle are composed of several layers each.

The cuticle may be soft and permeable or may form a veritable coat of armor. Between body segments and between segments of appendages it is thin and flexible, permitting free movement of joints. In crustaceans and insects the cuticle forms ingrowths for muscle attachment. It may also line the foregut and hindgut, line and support the trachea, and be adapted for a variety of purposes.

The nonexpansible cuticular exoskeleton does, however, impose important conditions on growth. To grow, an arthropod must shed its outer covering at intervals and grow a larger one—a process called **ecdysis,** or **molting.** Arthropods molt from four to seven times before reaching adulthood, and some continue to molt after that. Much of an arthropod's physiology centers on molting, particularly in young animals—preparation, molting itself, and then all processes that must be completed in the postmolt period.

An exoskeleton is also relatively heavy and becomes proportionately heavier with increasing size. Weight of the exoskeleton tends to limit ultimate body size.

2. **Segmentation and appendages for more efficient locomotion.** Typically each somite has a pair of jointed appendages, but this arrangement is often modified, with both segments and appendages specialized for adaptive functions. Limb segments are essentially hollow levers that are moved by muscles, most of which are striated for rapid action. The jointed appendages are equipped with sensory hairs and are variously modified for sensory functions, food handling, and swift and efficient walking or swimming.
3. **Air piped directly to cells.** Most land arthropods have a highly efficient tracheal system of air tubes, which delivers oxygen directly to tissues and cells and makes a high metabolic rate possible. Aquatic arthropods breathe mainly by some form of gill.
4. **Highly developed sensory organs.** Sensory organs are found in great variety, from compound (mosaic) eyes to senses of touch, smell, hearing, balancing, and chemical reception. Arthropods are keenly alert to what goes on in their environment.
5. **Complex behavior patterns.** Arthropods exceed most other invertebrates in complexity and organization of their activities. Innate (unlearned) behavior unquestionably controls much of what they do, but learning also plays an important part in the lives of many arthropods.
6. **Reduced competition through metamorphosis.** Many arthropods pass through metamorphic changes, including a larval form quite different from adults in structure. Larval forms are often adapted for eating a different kind of food from that of adults and occupy a different space, resulting in less competition within a species.

Subphylum Trilobita

Trilobites (figure 12.1A) probably had their beginnings a million or more years before the Cambrian period in which they flourished. They have been extinct some 200 million years, but were abundant during the Cambrian and Ordovician periods.

Their name refers to the trilobed shape of the body, caused by a pair of longitudinal grooves. They were bottom dwellers, probably scavengers. Most of them could roll up like pill bugs.

Subphylum Chelicerata

Chelicerate arthropods are a very ancient group that includes eurypterids (extinct), horseshoe crabs, spiders, ticks and mites, scorpions, sea spiders, and others. They are characterized by having six pairs of appendages that include a pair of **chelicerae,** a pair of **pedipalps,** and **four pairs of walking legs** (a pair of chelicerae and five pairs of walking legs in horseshoe crabs). They have **no mandibles** and **no antennae.** Most chelicerates suck liquid food from their prey.

Class Merostomata

Subclass Eurypterida

Eurypterids, or giant water scorpions (figure 12.1B), lived 200 to 500 million years ago and some were perhaps the largest of all arthropods, reaching a length of 3 m. They had some resemblances to marine horseshoe crabs (figure 12.2) and to scorpions, their terrestrial counterparts.

Subclass Xiphosurida: Horseshoe Crabs

Xiphosurids are an ancient marine group that dates from the Cambrian period. There are only three genera (five species) living today. *Limulus* (L. *limus,* sidelong, askew) (figure 12.2), which lives in shallow water along the North American Atlantic coast, goes back practically unchanged to the Triassic period. Horseshoe crabs have an unsegmented, horseshoe-shaped **carapace** (hard dorsal shield) and a broad abdomen, which has a long spinelike **telson,** or tailpiece. On some abdominal appendages **book gills** (flat leaflike gills) are exposed. Horseshoe crabs can swim awkwardly by means of their abdominal plates and can walk on their walking legs. They feed at night on worms and small molluscs and are harmless to humans.

Class Pycnogonida: Sea Spiders

Pycnogonids are curious little marine animals that are much more common than most of us realize. They stalk about on their four pairs of long, thin walking legs, sucking juices from hydroids and soft-bodied animals with their large suctorial proboscis (figure 12.3). They often have a pair of ovigerous legs **(ovigers)** with which males carry the egg masses. Their odd appearance is enhanced by the much reduced abdomen attached to an elongated cephalothorax. Most are only a few millimeters long, although some are much larger. They are common in all oceans.

Class Arachnida

Arachnids (Gr. *arachnē*, spider) are a numerous and diverse group, with over 50,000 species described so far. They include spiders, scorpions, pseudoscorpions, whip scorpions, ticks, mites, harvestmen (daddy longlegs), and others. The arachnid tagmata are a cephalothorax and an abdomen.

Order Araneae: Spiders

Spiders are a large group of 35,000 recognized species, distributed all over the world. The cephalothorax and abdomen show no external segmentation, and the tagmata are joined by a narrow, waistlike **pedicel** (figure 12.4).

All spiders are predaceous and feed largely on insects (figure 12.5). Their chelicerae function as fangs and bear ducts

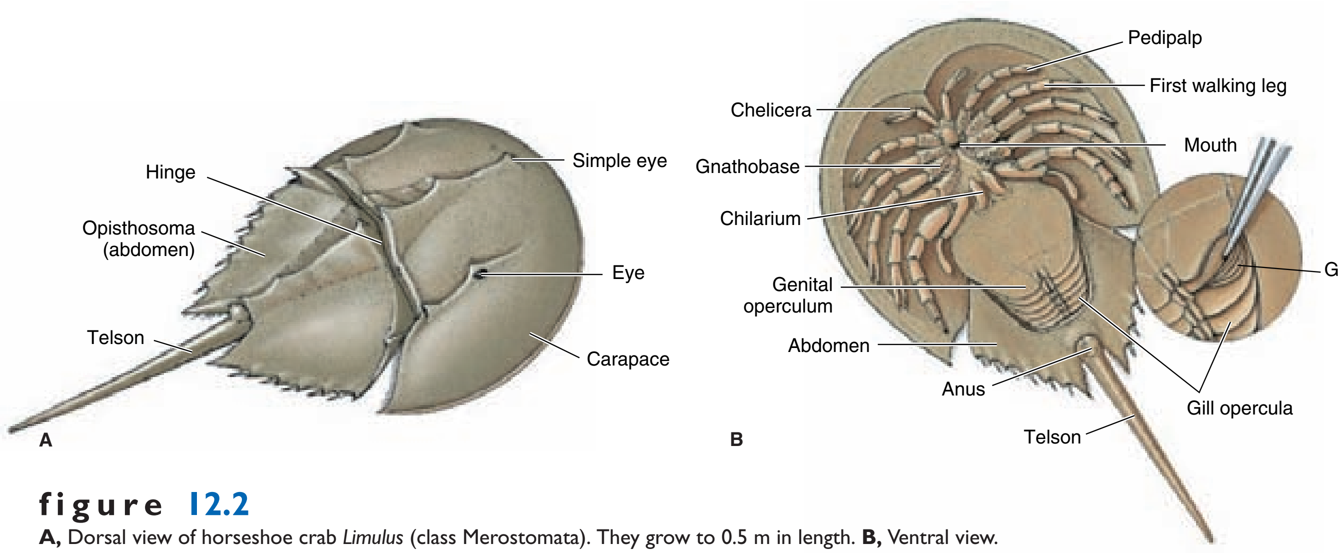


figure 12.2
A, Dorsal view of horseshoe crab *Limulus* (class Merostomata). They grow to 0.5 m in length. **B,** Ventral view.

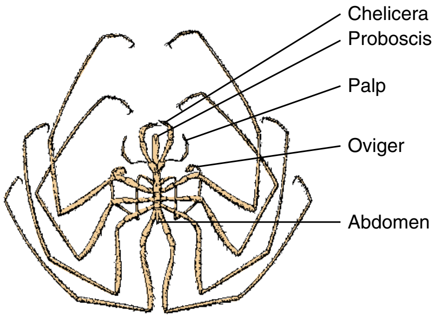


figure 12.3
Pycnogonid, *Nymphon* sp. In this genus all anterior appendages (chelicerae, palps, and ovigers) are present in both sexes, although ovigers are often not present in females of other genera.

from their poison glands, with which they effectively dispatch their prey. Some spiders chase their prey, others ambush them, and many trap them in a net of silk. After a spider seizes its prey with its chelicerae and injects venom, it liquefies tissues with a digestive fluid and sucks up the resulting broth into the stomach. Spiders with teeth at the bases of their chelicerae crush or chew up prey, aiding digestion by enzymes from their mouth. Many spiders provision their young with previously captured prey.

Spiders breathe by **book lungs** or **tracheae** or both. Book lungs, which are unique to spiders, consist of many parallel air pockets extending into a blood-filled chamber (see figure 12.4). Air enters the chamber by a slit in the body wall. Tracheae are a system of air tubes that carry air directly to tissues from openings called **spiracles.** Tracheae are similar to those in insects (p. 236), but are much less extensive.

Spiders and insects have a unique excretory system of **Malpighian tubules** (see figure 12.4), which work in conjunction with specialized rectal glands. Potassium and other solutes and waste materials are secreted into the tubules, which drain the fluid, or "urine," into the intestine. Rectal glands reabsorb most of the potassium and water, leaving behind such wastes as uric acid. By this cycling of water and potassium, species living in dry environments conserve body fluids, producing a nearly dry mixture of urine and feces. Many spiders also have **coxal glands,** which are modified nephridia that open at the coxa, or base, of the first and third walking legs

Spiders usually have eight **simple eyes,** each provided with a lens, optic rods, and a retina (see figure 12.4B). Chiefly they perceive moving objects, but some, such as those of the

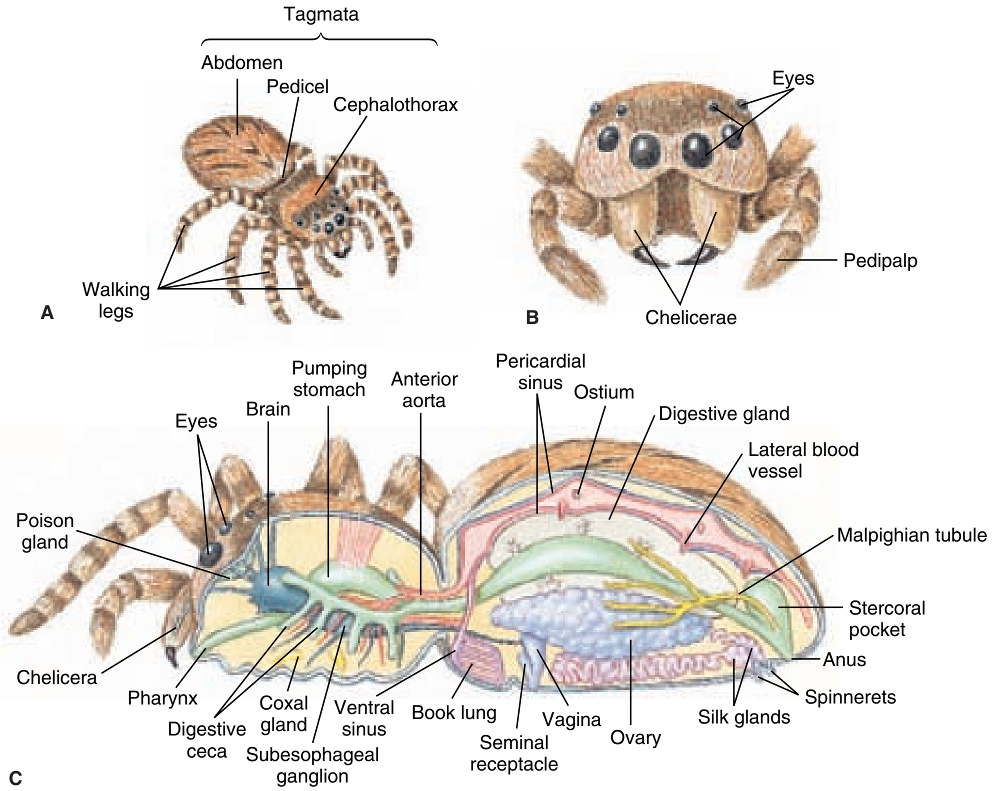


figure 12.4
A, External anatomy of a jumping spider. **B,** Anterior view of head. **C,** Internal anatomy of a spider.

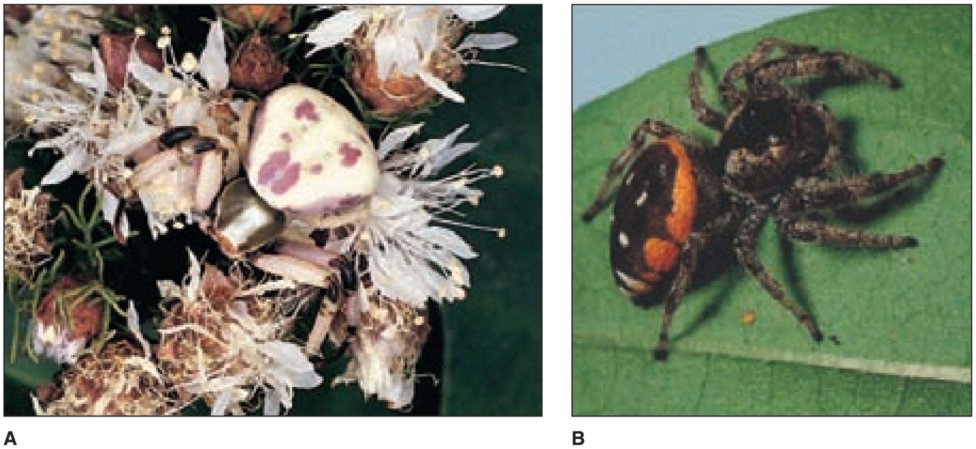


figure 12.5
A, A camouflaged crab spider, *Misumenoides* sp., awaits its insect prey. Its coloration matches the petals among which it lies, thus deceiving insects that visit the flowers in search of pollen or nectar. **B,** A jumping spider, *Eris aurantius*. This species has excellent vision and stalks an insect until it is close enough to leap with unerring precision, fixing its chelicerae into its prey.

hunting and jumping spiders, may form images. Because vision is usually poor, a spider's awareness of its environment depends especially on its hairlike **sensory setae.** Every seta on its surface is useful in communicating some information about its surroundings, air currents, or changing tensions in the spider's web. By sensing vibrations of its web, a spider can judge the size and activity of its entangled prey or can receive a message tapped out on a silk thread by a prospective mate.

Web-Spinning Habits The ability to spin silk is an important factor in the lives of spiders, as it is in some other arachnids. Two or three pairs of spinnerets containing hundreds of microscopic tubes connect to special abdominal **silk glands** (see figure 12.4C). A protein secretion emitted as a liquid hardens on contact with air to form a silk thread. Spiders' silk threads are stronger than steel threads of the same diameter and are said to be second in tensional strength only to fused quartz fibers. The threads will stretch one-fifth of their length before breaking.

The spider web used for trapping insects is familiar to most people. Webs of some species consist merely of a few strands of silk radiating out from a spider's burrow or place of retreat. Other species spin beautiful, geometric orb webs. However, spiders use silk threads for many purposes besides web making. They use silk threads to line their nests; form sperm webs or egg sacs; build draglines; make bridge lines, warning threads, molting threads, attachment discs, or nursery webs; or to wrap up prey securely (figure 12.6). Not all spiders spin webs for traps. Some, such as the wolf spiders, jumping spiders (see figure 12.5B), and fisher spiders (figure 12.7), simply chase and catch their prey.

Reproduction Before mating, a male spins a small web, deposits a drop of sperm on it, and then picks the package up and stores it in special cavities of his pedipalps. When he mates, he inserts his pedipalps into a female's genital opening to store the sperm in his mate's seminal receptacles. A courtship ritual usually precedes mating. A female lays her fertilized eggs in a silken cocoon, which she may carry about or may attach to a web or plant. A cocoon may contain hundreds of eggs, which hatch in approximately two weeks. Young usually remain in their egg sac for a few weeks and molt once before leaving it. Several molts occur before adulthood.

Are Spiders Really Dangerous? It is truly amazing that such small and helpless creatures as spiders have generated so much unreasoned fear in humans. Spiders are timid creatures, which, rather than being dangerous enemies to humans, are actually allies in our continuing conflict with insects. The venom produced to kill prey is usually harmless to humans. Even the most poisonous spiders bite only when threatened or when defending their eggs or young. American tarantulas (figure 12.8), despite their fearsome appearance, are not dangerous. They rarely bite, and their bite is not considered serious.

figure 12.6
Grasshopper, snared and helpless in the web of a golden garden spider (*Argiope aurantia*), is wrapped in silk while still alive. If the spider is not hungry, its prize will be saved for a later meal.

figure 12.7
A fisher spider, *Dolomedes triton,* feeds on a minnow. This handsome spider feeds mostly on aquatic and terrestrial insects but occasionally captures small fishes and tadpoles. It pulls its paralyzed victim from the water, pumps in digestive enzymes, then sucks out the predigested contents.

figure 12.8
A tarantula, *Brachypelma vagans*.

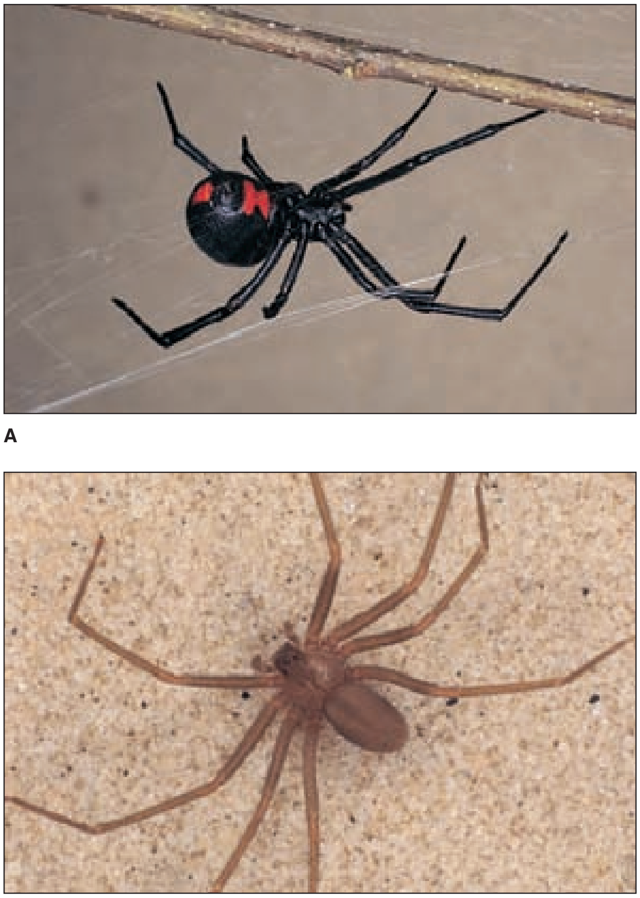


figure 12.9
A, A black widow spider, *Latrodectus mactans,* suspended on her web. Note the orange "hourglass" on the ventral side of her abdomen.
B, The brown recluse spider, *Loxosceles reclusa,* is a small venomous spider. Note the small violin-shaped marking on its cephalothorax. The venom is hemolytic and dangerous.

Two genera in the United States can give severe or even fatal bites: *Latrodectus* (L. *latro,* robber, + *dektes,* biter), and *Loxosceles* (Gr. *loxos,* crooked, + *skelos,* leg). The most important species are *Latrodectus mactans,* or **black widows,** and *Loxosceles reclusa,* or **brown recluse.** Black widows are moderate to small in size and shiny black, with a bright orange or red "hourglass" on the underside of their abdomen (figure 12.9). Their venom is neurotoxic; that is, it acts on the nervous system. About four or five out of each 1000 bites reported are fatal.

Brown recluse spiders, which are smaller than black widows, are brown, and bear a violin-shaped dorsal stripe on their cephalothorax (figure 12.9). Their venom is hemolytic rather than neurotoxic, destroying tissues and skin surrounding a bite. Their bite can be mild to serious and occasionally fatal.

Some spiders in other parts of the world are dangerous, for example, funnel-web spiders *Atrax robustus* in Australia. Most dangerous of all are certain ctenid spiders in South America, for example, *Phoneutria fera.* In contrast to most spiders, these are quite aggressive.

Order Scorpionida: Scorpions

Although scorpions are more common in tropical and subtropical regions, some occur in temperate zones. Scorpions are generally secretive, hiding in burrows or under objects by day and feeding at night. They feed largely on insects and spiders, which they seize with clawlike pedipalps and tear up with jawlike chelicerae.

A scorpion's body consists of a rather short cephalothorax, which bears appendages and from one to six pairs of eyes,

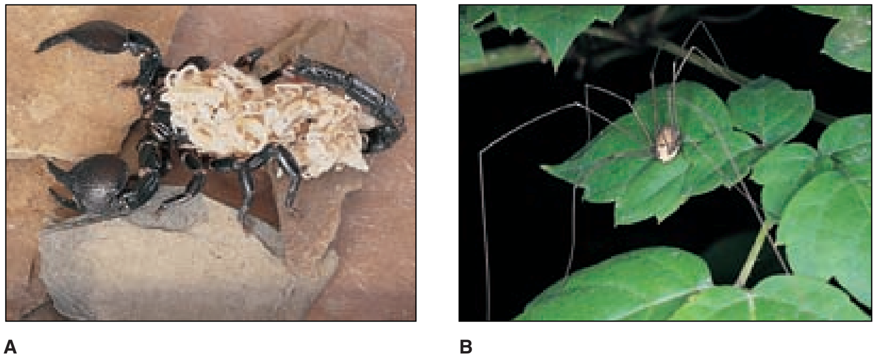


figure 12.10
A, An emperor scorpion (order Scorpionida), *Paninus imperator,* with young, which stay with their mother until their first molt. **B,** A harvestman (order Opiliones). Harvestmen run rapidly on their stiltlike legs. They are especially noticeable during the harvesting season, hence the common name.

and a clearly segmented abdomen without appendages. The abdomen is divided into a broader **preabdomen** and tail-like **postabdomen,** which ends in a stinging apparatus used to inject venom (figure 12.10). Venom of most species is not harmful to humans, although that of certain species of *Androctonus* in Africa and *Centruroides* in Mexico, Arizona, and New Mexico can be fatal unless antivenom is available.

Scorpions bear living young, which their mother carries on her back until after the first molt.

Order Opiliones: Harvestmen

Harvestmen, often known as "daddy longlegs," are common in the United States and other parts of the world (figure 12.10). These curious creatures are easily distinguished from spiders by a broad joining of their abdomen and cephalothorax without constriction of a pedicel, and by presence of external segmentation of their abdomen. They have four pairs of long, spindly legs, and without apparent ill effect, they can cast off one or more legs if they are grasped by a predator (or human hand). The ends of their chelicerae are pincerlike, and they feed much more as scavengers than do most arachnids.

Order Acari: Ticks and Mites

Acarines differ from all other arachnids in having their cephalothorax and abdomen completely fused, with no sign of external division or segmentation (figure 12.11). Their mouthparts are carried on a little anterior projection, or **capitulum.** They are found almost everywhere—in both fresh and salt water, on vegetation, on the ground, and parasitic on vertebrates and invertebrates. Over 25,000 species have been described, many of which are important to humans, but this is probably only a fraction of the species that exist.

Many species of mites are entirely free living. *Dermatophagoides farinae* (Gr. *dermatos,* skin, + *phago,* to eat, + *eidos,* likeness of form) (figure 12.12) and related species are denizens of house dust all over the world, sometimes causing allergies and dermatoses. Some mites are marine, but most aquatic species are found in fresh water. They have long, hairlike setae on their legs for swimming, and their larvae may be parasitic on aquatic invertebrates. Such abundant organisms have to be important ecologically, but many acarines have more direct effects on our food supply and health. Spider mites (family Tetranychidae) are serious agricultural pests on fruit trees, cotton, clover, and many other plants. Larvae of genus *Trombicula* are called chiggers or redbugs. They feed on dermal tissues of terrestrial vertebrates, including humans, and cause an irritating dermatitis; some species of chiggers transmit a disease called Asiatic scrub typhus. Hair-follicle mites, *Demodex* (figure 12.13), are apparently nonpathogenic in humans; they infect most of us although we are unaware of them. Other species of *Demodex* and other genera of mites cause mange in domestic animals.

figure 12.11
A wood tick, *Dermacentor variabilis* (order Acarina).

The inflamed welt and intense itching that follows a chigger bite is not the result of a chigger burrowing into the skin, as is popularly believed. Rather the chigger bites through skin with its chelicerae and injects a salivary secretion containing powerful enzymes that liquefy skin cells. Human skin responds defensively by forming a hardened tube that the larva uses as a sort of drinking straw and through which it gorges itself with host cells and fluid. Scratching usually removes the chigger but leaves the tube, which is a source of irritation for several days.

figure 12.12
Scanning electron micrograph of house dust mite, *Dermatophagoides farinae.*

figure 12.13
Demodex follicuorum, human follicle mite. This tiny mite (100 to 400 μm) lives in follicles, particularly around the nose and eyes. Its prevalence ranges from about 20% in persons 20 years of age or younger to nearly 100% in the aged.

Ticks are usually larger than mites. They pierce the skin of vertebrates and suck blood until enormously distended; then they drop off and digest their meal. After molting, they are ready for another meal. In addition to disease conditions that they themselves cause, ticks are among the world's premier disease vectors, ranking second only to mosquitos. They carry a greater variety of infectious agents than any other arthropods; such agents include protozoan, rickettsial, viral, bacterial, and fungal organisms. Species of *Ixodes* carry the most common arthropod-borne infection in the United States, Lyme disease (see accompanying note). Species of *Dermacentor* (see figure 12.11) and other ticks transmit Rocky Mountain spotted fever, a poorly named disease because most cases occur in the eastern United States. *Dermacentor* also transmits tularemia and agents of several other diseases. Texas cattle fever, also called red-water fever, is caused by a protozoan parasite transmitted by the cattle tick *Boophilus annulatus.* Many more examples could be cited.

In the 1970s people in the town of Lyme, Connecticut, experienced an epidemic of arthritis. Subsequently known as Lyme disease, it is caused by a bacterium and carried by ticks of the genus *Ixodes*. Now thousands of cases are reported each year in Europe and North America, and other cases have been reported from Japan, Australia, and South Africa. Many people bitten by infected ticks recover spontaneously or do not suffer any ill effects. Others, if not treated at an early stage, develop a chronic, disabling disease. Lyme disease is now the leading arthropod-borne disease in the United States.

Subphylum Crustacea

Crustaceans traditionally have been included as a class in subphylum Mandibulata, along with insects and myriapods. Members of all of these groups have, at least, a pair of antennae, mandibles, and maxillae on the head. Whether Mandibulata constitutes a monophyletic grouping has been debated, and we discuss this question further on page 248.

The 30,000 or more species of Crustacea (L. *crusta,* shell) include lobsters, crayfishes, shrimp, crabs, water fleas, copepods, and barnacles. It is the only arthropod class that is primarily aquatic; they are mainly marine, but many freshwater and a few terrestrial species are known. The majority are free living, but many are sessile, commensal, or parasitic. Crustaceans are often very important components of aquatic ecosystems, and several have considerable economic importance.

Crustaceans are the only arthropods with **two pairs of antennae** (figure 12.14). In addition to antennae and **mandibles,** they have **two pairs of maxillae** on the head, followed by a pair of appendages on each body segment (although appendages on some somites are absent in some groups). All appendages, except perhaps the first antennae (antennules), are primitively **biramous** (two main branches), and at least some appendages of all present-day adults show that condition. Organs specialized for respiration, if present, are in the form of gills. Crustaceans lack Malpighian tubules.

Crustaceans primitively have 60 segments or more, but most tend to have between 16 and 20 somites and increased tagmatization. The major tagmata are **head, thorax,** and **abdomen,** but these are not homologous throughout the subphylum (or even within some classes) because of varying degrees of fusion of somites, for example, as in the cephalothorax.

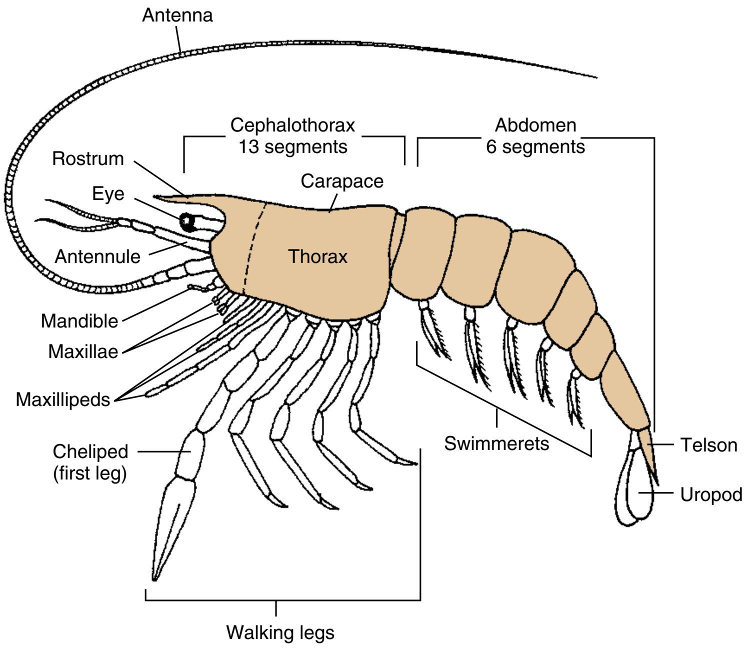


figure 12.14

Archetypical plan of Malacostraca. Note that maxillae and maxillipeds have been separated diagrammatically to illustrate general plan. Typically in living animals only the third maxilliped is visible externally. In order Decapoda the carapace covers the cephalothorax, as shown here.

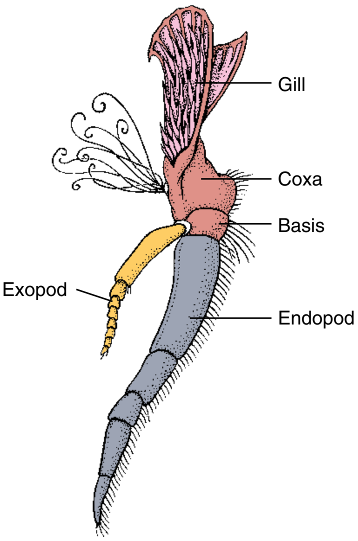


figure 12.15

Parts of a biramous crustacean appendage (third maxilliped of a crayfish).

In many crustaceans, the dorsal cuticle of the head extends posteriorly and around the sides of the animal to cover or fuse with some or all thoracic and abdominal somites. This covering is called a **carapace.** In some groups the carapace forms clamshell-like valves that cover most or all of the body. In decapods (including lobsters, shrimp, crabs, and others) the carapace covers the entire cephalothorax but not the abdomen.

Form and Function

Appendages

Some modifications of crustacean appendages may be illustrated by those of crayfishes and lobsters (class Malacostraca, order Decapoda, p. 228). **Swimmerets,** or abdominal appendages, retain the primitive biramous condition. Such an appendage consists of inner and outer branches, called the **endopod** and **exopod,** which are attached to one or more basal segments collectively called a **protopod** (figure 12.15).

There are many modifications of this plan. In the primitive character state for crustaceans, all trunk appendages are rather similar in structure and adapted for swimming. The evolutionary trend, shown in crayfishes, has been toward reduction in number of appendages and toward a variety of modifications that fit them for many functions. Some are foliaceous (flat and leaflike), as are the maxillae; some are biramous, as are the swimmerets, maxillipeds, uropods, and antennae; some have lost one branch and are **uniramous,** as are the walking legs.

In crayfishes we find the first three pairs of thoracic appendages, called **maxillipeds,** serving along with the two pairs of maxillae as food handlers; the other five pairs of appendages are lengthened and strengthened for walking and defense (figure 12.16). The first pair of walking legs, called **chelipeds,** are enlarged with a strong claw, or chela, for defense. Abdominal swimmerets serve not only for locomotion, but in males the first pair is modified for copulation, and in females they all serve as a nursery for attached eggs and young. The last pair of appendages, or **uropods,** are wide and serve as paddles for swift backward movements, and, with the telson, they form a protective device for eggs or young on the swimmerets.

Terminology applied by various workers to crustacean appendages has not been blessed with uniformity. At least two systems are in wide use. Alternative terms to those we use, for example, are protopodite, exopodite, endopodite, basipodite, coxopodite, and epipodite. The first and second pairs of antennae may be called antennules and antennae, and the first and second maxillae are often called maxillules and maxillae. A rose by any other name . . .

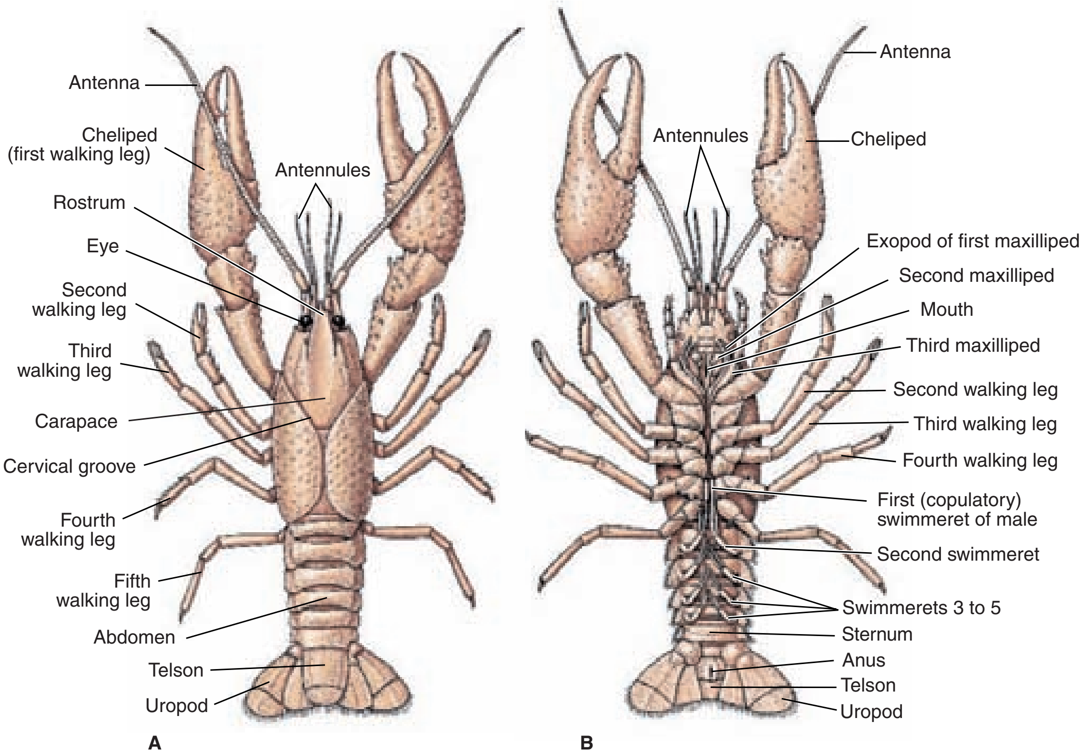


figure 12.16
External structure of crayfishes. **A,** Dorsal view. **B,** Ventral view.

Ecdysis

The problem of growth despite a restrictive exoskeleton is solved in crustaceans, as in other arthropods, by ecdysis (Gr. *ekdysis,* to strip off), a periodic shedding of old cuticle and formation of a larger new one. Molting occurs most frequently during larval stages and less often as an animal reaches adulthood. Although actual shedding of the cuticle is periodic, the molting process and preparations for it, involving a storage of reserves and changes in the integument, are a continuous process going on during most of an animal's life.

During each **premolt** period the old cuticle becomes thinner as inorganic salts are withdrawn from it and stored in tissues. Other reserves, both organic and inorganic, also accumulate and are stored. The underlying epidermis begins to grow by cell division; it secretes first a new inner layer of epicuticle and then enzymes that digest away the inner layers of old endocuticle (figure 12.17). Gradually a new cuticle forms inside the degenerating old one. Finally actual ecdysis occurs as the old cuticle ruptures, usually along the middorsal line, and the animal backs out (figure 12.18). By taking in air or water the animal swells to stretch the new larger cuticle to its full size. During the **postmolt** period the cuticle thickens, its outer layer hardens by tanning, and its inner layer is strengthened as salvaged inorganic salts and other constituents are redeposited. Usually an animal is very secretive during its postmolt period when its defenseless condition makes it particularly vulnerable to predation.

That ecdysis is under hormonal control has been demonstrated in both crustaceans and insects, but the process is often initiated by a stimulus perceived by the central nervous system. The action of the stimulus in decapods is to decrease production of a **molt-inhibiting hormone** from neurosecretory cells in the **X-organ** of the eyestalk. The sinus gland, also in the eyestalk, releases the hormone. When the level of molt-inhibiting hormone drops, **Y-organs** near the mandibles produce **molting hormone.** This hormone initiates processes leading to premolt. Y-organs are homologous to prothoracic glands of insects, which produce ecdysone.

> Neurosecretory cells are modified nerve cells that secrete hormones. They are widespread in invertebrates and also occur in vertebrates. Cells in the vertebrate hypothalamus and in the posterior pituitary are good examples.

Other Endocrine Functions

Body color of crustaceans is largely a result of pigments in special branched cells **(chromatophores)** in the epidermis. Chromatophores change color by concentrating pigment granules in

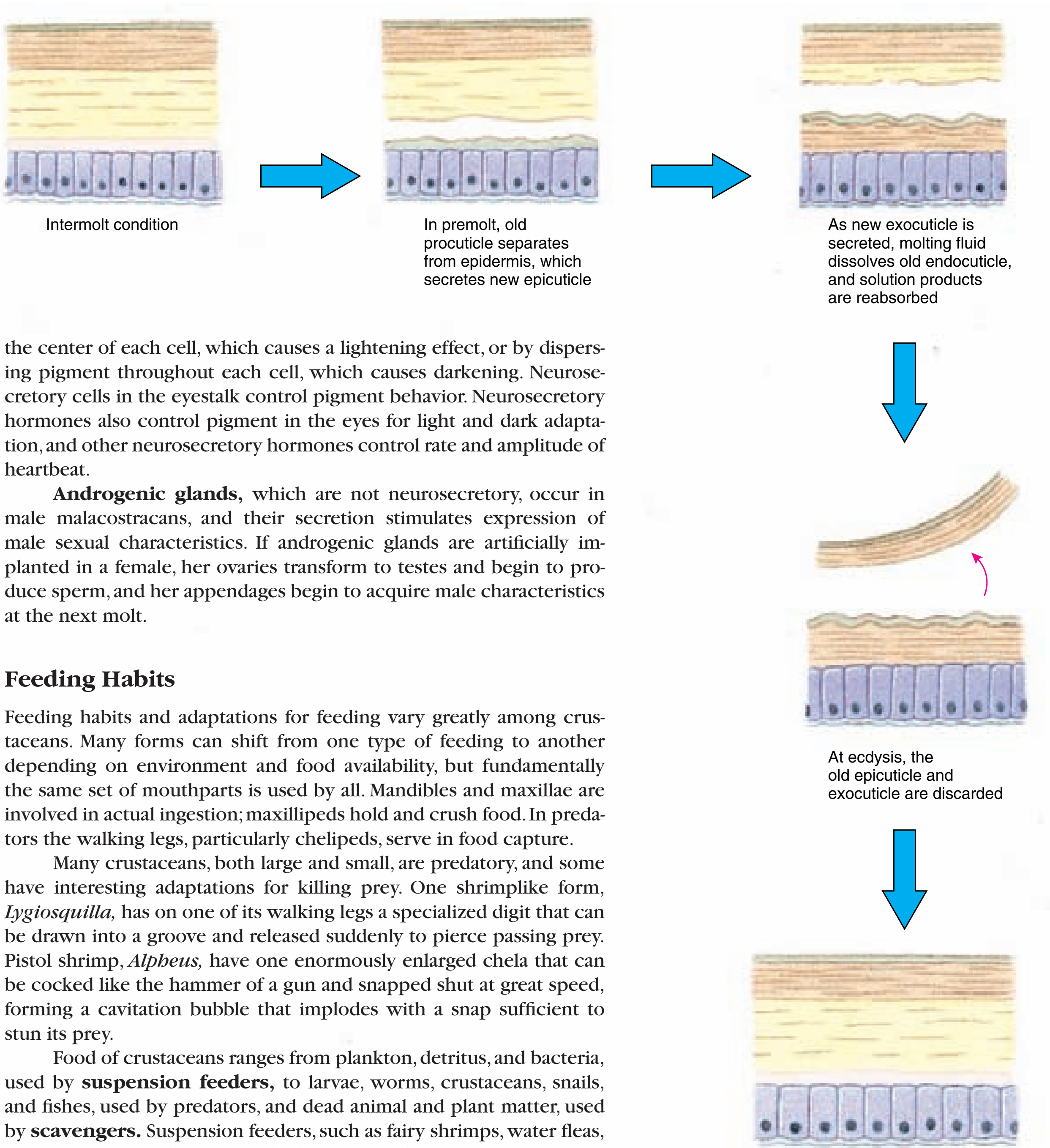


figure 12.17
Cuticle secretion and reabsorption in ecdysis.

the center of each cell, which causes a lightening effect, or by dispersing pigment throughout each cell, which causes darkening. Neurosecretory cells in the eyestalk control pigment behavior. Neurosecretory hormones also control pigment in the eyes for light and dark adaptation, and other neurosecretory hormones control rate and amplitude of heartbeat.

Androgenic glands, which are not neurosecretory, occur in male malacostracans, and their secretion stimulates expression of male sexual characteristics. If androgenic glands are artificially implanted in a female, her ovaries transform to testes and begin to produce sperm, and her appendages begin to acquire male characteristics at the next molt.

Feeding Habits

Feeding habits and adaptations for feeding vary greatly among crustaceans. Many forms can shift from one type of feeding to another depending on environment and food availability, but fundamentally the same set of mouthparts is used by all. Mandibles and maxillae are involved in actual ingestion; maxillipeds hold and crush food. In predators the walking legs, particularly chelipeds, serve in food capture.

Many crustaceans, both large and small, are predatory, and some have interesting adaptations for killing prey. One shrimplike form, *Lygiosquilla,* has on one of its walking legs a specialized digit that can be drawn into a groove and released suddenly to pierce passing prey. Pistol shrimp, *Alpheus,* have one enormously enlarged chela that can be cocked like the hammer of a gun and snapped shut at great speed, forming a cavitation bubble that implodes with a snap sufficient to stun its prey.

Food of crustaceans ranges from plankton, detritus, and bacteria, used by **suspension feeders,** to larvae, worms, crustaceans, snails, and fishes, used by predators, and dead animal and plant matter, used by **scavengers.** Suspension feeders, such as fairy shrimps, water fleas, and barnacles, use their legs, which bear a thick fringe of setae, to create water currents that sweep food particles through the setae. Mud shrimps, *Upogebia,* use long setae on their first two pairs of thoracic appendages to strain food material from water circulated through their burrow by movements of their swimmerets.

Crayfishes have a two-part stomach. The first contains a **gastric mill** in which food, already torn up by the mandibles, can be ground up further by three calcareous teeth into particles fine enough to pass through a filter of setae in the second part of the stomach; food particles then pass into the intestine for chemical digestion.

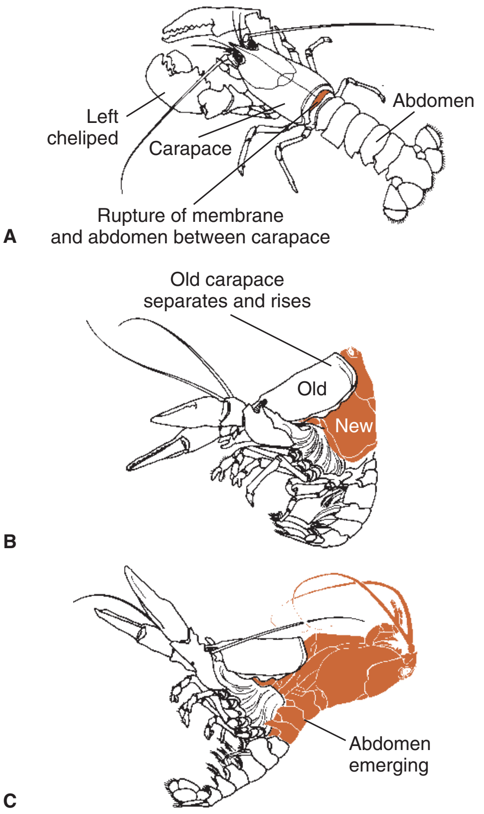


figure 12.18

Molting sequence in a lobster, *Homarus americanus.* **A,** Membrane between carapace and abdomen ruptures, and carapace begins a slow elevation. This step may take up to two hours. **B** and **C,** Head, thorax, and finally abdomen are withdrawn. This process usually takes no more than 15 minutes. Immediately after ecdysis, chelipeds are desiccated and the body is very soft. The lobster now begins rapid absorption of water so that within 12 hours its body increases about 20% in length and 50% in weight. Tissue water will be replaced by protein in succeeding weeks.

Respiration, Excretion, and Circulation

Gills of crustaceans vary in shape—treelike, leaflike, or filamentous—all provided with blood vessels or sinuses. They usually are attached to appendages and kept ventilated by movement of appendages through water. The overlapping carapace usually protects the **branchial chambers.** Some smaller crustaceans breathe through their general body surface.

Excretory and **osmoregulatory** organs in crustaceans are paired glands located in their head, with excretory pores opening at the base of either antennae or maxillae, thus called **antennal glands** or **maxillary glands,** respectively (figure 12.19). Antennal glands of decapods are also called **green glands.** They resemble coxal glands of chelicerates. Waste products are mostly ammonia with some urea and uric acid. Some wastes diffuse through the gills as well as through the excretory glands.

Circulation, as in other arthropods, is an **open system** consisting of a heart, either compact or tubular, and arteries, which transport blood to different areas of the hemocoel. Some smaller crustaceans lack a heart. An open circulatory system depends less on heartbeats for circulation because movement of organs and limbs circulates blood more effectively in open sinuses than in capillaries. Blood may contain as respiratory pigments either hemocyanin or hemoglobin (hemocyanin in decapods), and it has the property of clotting to prevent loss of blood in minor injuries.

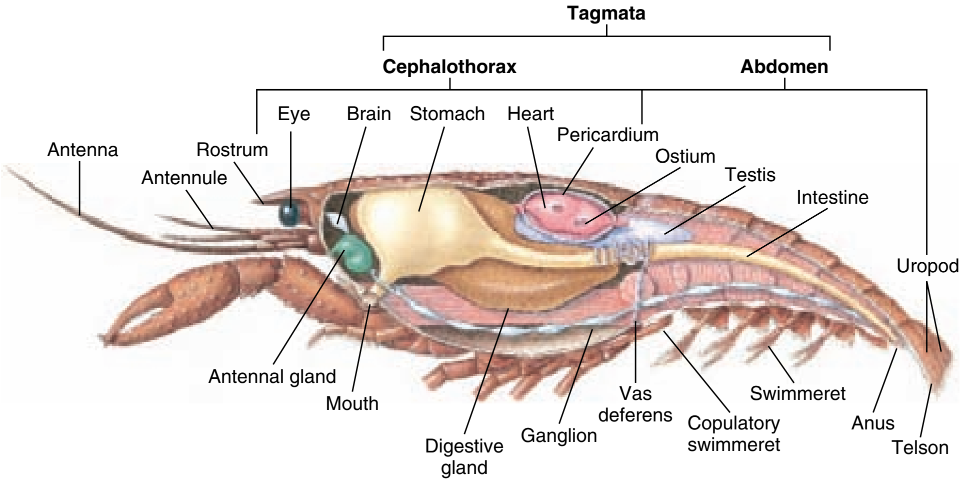
Nervous and Sensory Systems

A cerebral ganglion above the esophagus sends nerves to the anterior sense organs and connects to a subesophageal ganglion by a pair of connectives around the esophagus. A double ventral nerve cord has a ganglion in each segment that sends nerves to viscera, appendages, and muscles (figure 12.19). Giant fiber systems are common among crustaceans.

Sensory organs are well developed. There are two types of eyes—a median, or nauplius, eye and compound eyes. A

figure 12.19

Internal structure of a male crayfish.



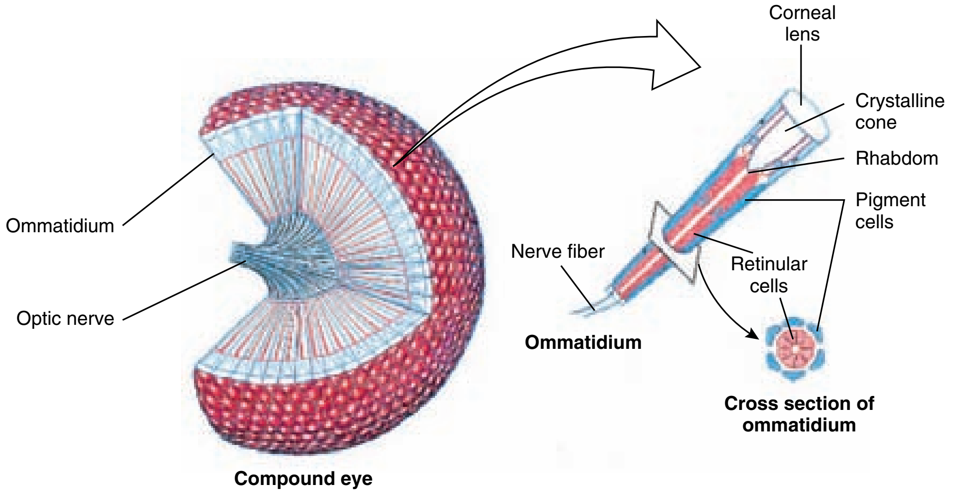


figure 12.20
Compound eye of an insect. A single ommatidium is shown enlarged to the right.

median eye consists usually of a group of three pigment cups containing retinal cells, and it may or may not have a lens. Median eyes are found in nauplius larvae and in some adult forms, and they may be an adult's only eye, as in copepods.

Most crustaceans have **compound eyes** similar to insect eyes. In crabs and crayfishes they are on the ends of movable eyestalks (figure 12.19). Compound eyes are precise instruments, different from vertebrate eyes, yet especially adept at detecting motion; they can analyze polarized light. The convex corneal surface gives a wide visual field, particularly in stalked eyes where the surface may cover an arc of 200 degrees or more.

Compound eyes are composed of many tapering units called **ommatidia** set close together (figure 12.20). Facets, or corneal surfaces, of ommatidia give the surface of the eye an appearance of a fine mosaic. Most crustacean eyes are adapted either to bright or to dim light, depending on their diurnal or nocturnal habits, but some are able, by means of screening pigments, to adapt, to some extent at least, to both bright and dim light. The number of ommatidia varies from a dozen or two in some small crustaceans to 15,000 or more in a large lobster. Some insects have approximately 30,000.

Other sensory organs include statocysts, tactile setae on the cuticle of most of the body, and chemosensitive setae, especially on antennae, antennules, and mouthparts.

Reproduction and Life Cycles

Most crustaceans have separate sexes, and numerous specializations for copulation occur among different groups. Barnacles are monoecious but generally practice cross-fertilization. In some ostracods males are scarce, and reproduction is usually parthenogenetic. Most crustaceans brood their eggs in some manner—branchiopods and barnacles have special brood chambers, copepods have egg sacs attached to the sides of their abdomen (see figure 12.24), and malacostracans usually carry eggs and young attached to their appendages.

A hatchling of a crayfish is a tiny juvenile similar in form to the adult and has a complete set of appendages and somites. However, most crustaceans produce larvae that must go through a series of changes, either gradual or abrupt over a series of molts, to assume adult form (metamorphosis). The primitive larva of crustaceans is **nauplius** (figure 12.21). It has an unsegmented body, a frontal eye, and three pairs of appendages, representing the two pairs of antennae and the mandibles. Developmental stages and postlarvae of different groups of Crustacea are varied and have special names.

Class Branchiopoda

Members of class Branchiopoda (bran´kee-op´o-da) (Gr. *branchia,* gills, + *pous, podos,* foot) have several primitive characteristics. Four orders are recognized: **Anostraca** (fairy shrimp and brine shrimp), which lack a carapace; **Notostraca** (tadpole shrimp such as *Triops*), whose carapace forms a large dorsal shield covering most trunk somites; **Conchostraca** (clam shrimp such as *Lynceus*), whose carapace is bivalved and usually encloses the entire body; and **Cladocera** (water fleas such as *Daphnia,* figure 12.22), with a carapace typically covering the entire body but not the head. Branchiopods have reduced first antennae and second maxillae. Their legs are flattened and leaflike **(phyllopodia)** and are the chief respiratory organs (hence, the name branchiopods). Legs also are used in suspension feeding in most branchiopods, and in groups other than cladocerans, they are used for locomotion as well. The most important and diverse order is Cladocera, which often forms a large segment of freshwater zooplankton.

Class Maxillopoda

Class Maxillopoda includes a number of crustacean groups traditionally considered classes themselves. Specialists have recognized evidence that these groups descended from a

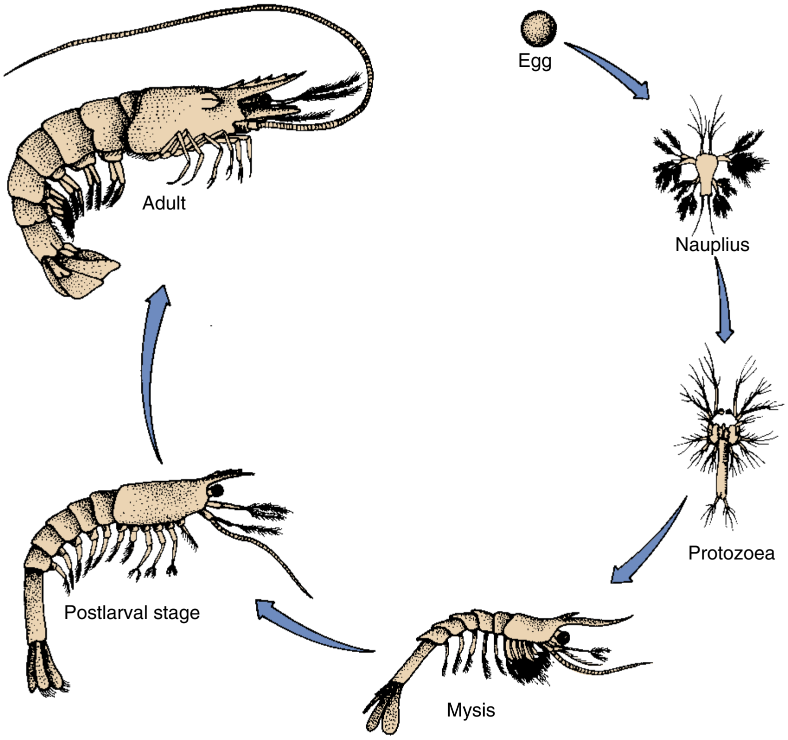


figure 12.21
Life cycle of a Gulf shrimp *Penaeus*. Penaeids spawn at depths of 40 to 90 m. Young larval forms are planktonic and move inshore to water of lower salinity to develop as juveniles. Older shrimp return to deeper water offshore.

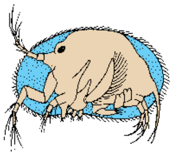


figure 12.23
An ostracod (subclass Ostracoda, class Maxillopoda).

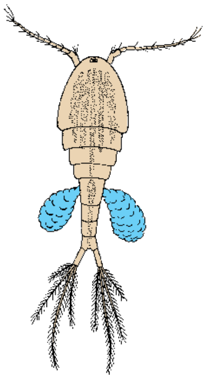


figure 12.24
A copepod with attached ovisacs (subclass Copepoda, class Maxillopoda).

figure 12.22
A water flea, *Daphnia* (order Cladocera), photographed with polarized light. These tiny forms occur in great numbers in northern lakes and are an important component of the food chain leading to fishes.

common ancestor and thus form a clade within Crustacea. They basically have five cephalic, six thoracic, and usually four abdominal somites plus a telson, but reductions are common. No typical appendages occur on the abdomen. Eye of nauplii (when present) have a unique structure termed a **maxillopodan eye.**

Members of subclass **Ostracoda** (os-trak´o-da) (Gr. *ostrakodes,* testaceous, that is, having a shell) are, like conchostracans, enclosed in a bivalved carapace and resemble tiny clams, 0.25 to 8 mm long (figure 12.23). Ostracods show considerable fusion of trunk somites, and numbers of thoracic appendages are reduced to two or none.

Subclass **Copepoda** (ko-pep´o-da) (Gr. *kōpē,* oar, + *pous, podos,* foot) is an important group of Crustacea, second only to Malacostraca in number of species. Copepods are small (usually a few millimeters or less in length), rather elongate, tapering toward the posterior end, lacking a carapace, and retaining a simple, median, nauplius eye in adults (figure 12.24). They have four pairs of rather flattened, biramous, thoracic swimming appendages, and a fifth, reduced pair. Their abdomen bears no legs. Many symbiotic as well as free-living species are known. Many parasites may be so highly modified as adults (and may depart so far from the description just given) that they can hardly be recognized as arthropods. Ecologically, free-living copepods are of extreme importance, often dominating the primary consumer level (herbivore) in aquatic communities.

Subclass **Branchiura** (bran-kee-u´ra) (Gr. *branchia,* gills, + *ura,* tail) is a small group of primarily fish parasites, which, despite its name, has no gills (figure 12.25). Members of this

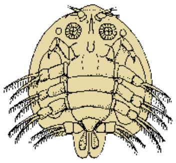


figure 12.25
Fish louse (subclass Branchiura, class Maxillopoda).

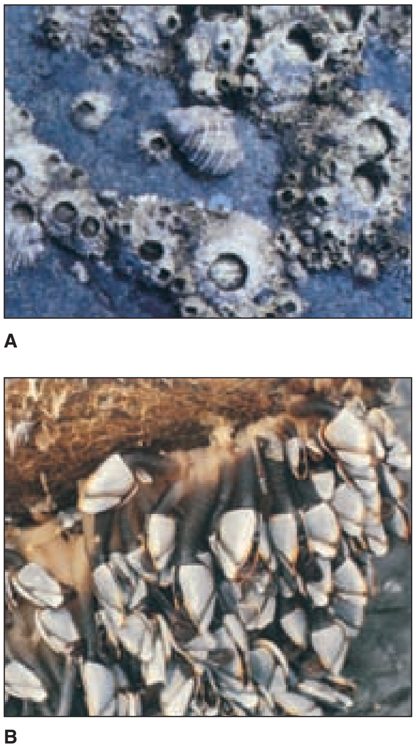


figure 12.26
A, Acorn barnacles, *Semibalanus cariosus* (subclass Cirripedia) are found on rocks along the Pacific Coast of North America. **B,** Common gooseneck barnacles, *Lepas anatifera.* Note the feeding legs, or cirri, on *Lepas*. Barnacles attach themselves to a variety of firm substrates, including rocks, pilings, and boat bottoms.

group are usually between 5 and 10 mm long and may be found on marine or freshwater fish. They typically have a broad, shieldlike carapace, compound eyes, four biramous thoracic appendages for swimming, and a short, unsegmented abdomen. The second maxillae have become modified as suction cups.

Subclass **Cirripedia** (sir-i-ped´i-a) (L. *cirrus,* curl of hair, + *pes, pedis,* foot) includes barnacles, individuals of which are usually enclosed in a shell of calcareous plates, as well as three smaller orders of burrowing or parasitic forms. Barnacles are sessile as adults and may be attached to their substrate by a stalk (gooseneck barnacles) (figure 12.26B) or directly (acorn barnacles) (figure 12.26A). Typically, a carapace (mantle) surrounds their body and secretes a shell of calcareous plates. Their head is reduced, their abdomen absent, and their thoracic legs are long, many-jointed cirri with hairlike setae. Cirri are extended through an opening between the calcareous plates to filter from water small particles on which the animal feeds (figure 12.26B).

Barnacles frequently foul ship bottoms by settling and growing there. So great may be their number that the speed of a ship may be reduced 30% to 40%, requiring expensive drydocking of the ship to clean them off.

Class Malacostraca

Class Malacostraca (mal´a-kos´tra-ka) (Gr. *malakos,* soft, + *ostrakon*, shell) is the largest class of Crustacea and shows great diversity. We will mention only 4 of its 12 to 13 orders. The trunk of malacostracans usually has eight thoracic and six abdominal somites, each with a pair of appendages. There are many marine and freshwater species.

Isopoda (i-sop´o-da) (Gr. *isos,* equal, + *pous, podos,* foot) are commonly dorsoventrally flattened, lack a carapace, and have sessile compound eyes. Their abdominal appendages bear gills. Common land forms are sow bugs or pill bugs (*Porcellio* and *Armadillidium,* figure 12.27A), which live under stones and in damp places. *Asellus* is common in fresh water, and *Ligia* is abundant on sea beaches and rocky shores. Some isopods are parasites of other crustaceans or of fish (figure 12.28).

Amphipoda (am-fip´o-da) (Gr. *amphis,* on both sides, + *pous, podos,* foot) resemble isopods in that members have no carapace and have sessile compound eyes. However, they are usually compressed laterally, and their gills are in the thoracic

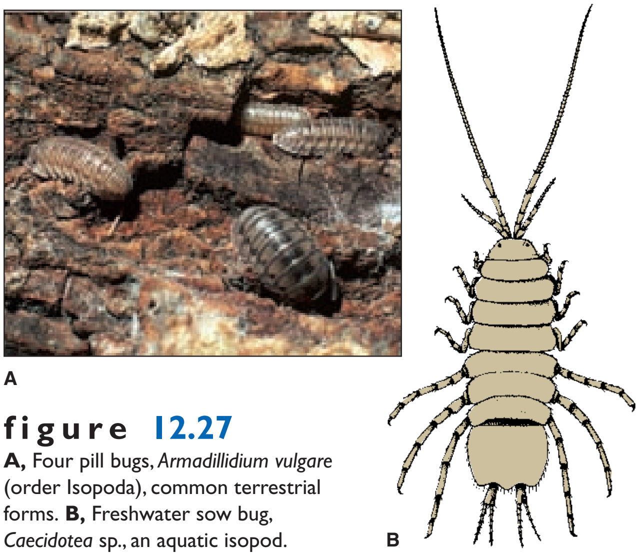


figure 12.27
A, Four pill bugs, *Armadillidium vulgare* (order Isopoda), common terrestrial forms. **B,** Freshwater sow bug, *Caecidotea* sp., an aquatic isopod.

figure 12.28
An isopod parasite (*Anilocra* sp.) on a coney (*Cephalopholis fulvus*) inhabiting a Caribbean coral reef (order Isopoda, class Malacostraca).

position, as in other malacostracans. There are many marine amphipods (figure 12.29), such as beach fleas, *Orchestia,* and numerous freshwater species.

Euphausiacea (yu-faws´i-a´se-a) (Gr. *eu,* well, + *phausi,* shining bright, + *acea,* L. suffix, pertaining to) is a group of only about 90 species, important as oceanic plankton known as "krill." They are about 3 to 6 cm long (figure 12.30) and commonly occur in great oceanic swarms, where they are eaten by baleen whales and many fishes.

Decapoda (de-cap´o-da) (Gr. *deka,* ten, + *pous, podos,* foot) have five pairs of walking legs of which the first is often modified to form pincers **(chelae)** (see figures 12.14 and 12.16). These are lobsters, crayfishes (see figure 12.14), shrimps (see figure 12.21), and crabs, the largest of the crustaceans (figure 12.31). True crabs differ from others in having a broader carapace and a much reduced abdomen (figure 12.31A and C). Familiar examples are fiddler crabs, *Uca,* which burrow in sand just below high-tide level (figure 12.31C), decorator crabs, which cover their carapaces with sponges and sea anemones for camouflage, and spider crabs, such as *Libinia.* Hermit crabs (figure 12.31B) have become adapted to live in snail shells; their abdomen, which lacks a hard exoskeleton, is protected by the snail shell.

Subphylum Uniramia

Appendages of members of Uniramia (yu´ni-ra´me-a) (L. *unus,* one, + *ramus,* a branch) are unbranched, as the name implies. This subphylum includes insects and myriapods. The term **myriapod** (Gr. *myrias,* a myriad, + *podos,* foot) refers to several classes that have evolved a pattern of two tagmata—head and trunk—with paired appendages on most or all trunk somites.

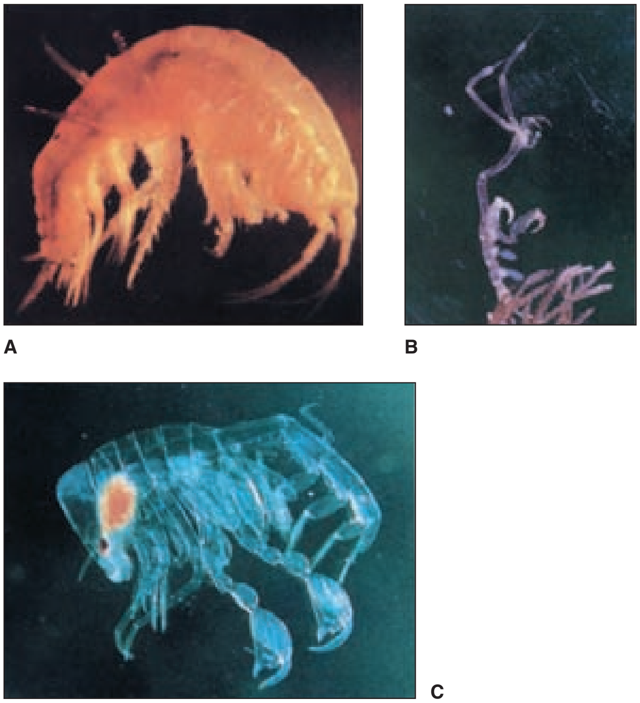


figure 12.29
Marine amphipods. **A,** Free-swimming amphipod, *Anisogammarus* sp. **B,** Skeleton shrimp, *Caprella* sp., shown on a bryozoan colony, resemble praying mantids. **C,** *Phronima,* a marine pelagic amphipod, takes over the tunic of a salp (subphylum Urochordata, Chapter 15). Swimming by means of its abdominal swimmerets, which protude from the opening of the barrel-shaped tunic, the amphipod maneuvers to catch its prey. The tunic is not seen (order Amphipoda, class Malacostraca).

Myriapods include Chilopoda (centipedes), Diplopoda (millipedes), Pauropoda (pauropods), and Symphyla (symphylans).

Insects have evolved a pattern of three tagmata—head, thorax, and abdomen—with appendages on the head and thorax but greatly reduced or absent from the abdomen. The common ancestor of insects probably resembled myriapods in general body form.

The head of myriapods and insects resembles the crustacean head but has only **one pair of antennae,** instead of two. It also has **mandibles** and two pairs of **maxillae** (one pair of maxillae in millipedes). The legs are all **uniramous.**

Respiratory exchange is by body surface and tracheal systems, although juveniles, if aquatic, may have gills.

Class Chilopoda: Centipedes

Centipedes are active predators with a preference for moist places such as under logs or stones, where they feed on earthworms, insects, etc. Their bodies are somewhat flattened dorsoventrally, and they may contain from a few to 177 somites (figure 12.32). Each somite, except the one behind the

figure 12.30
Meganyctiphanes, order Euphausiacea, "northern krill."

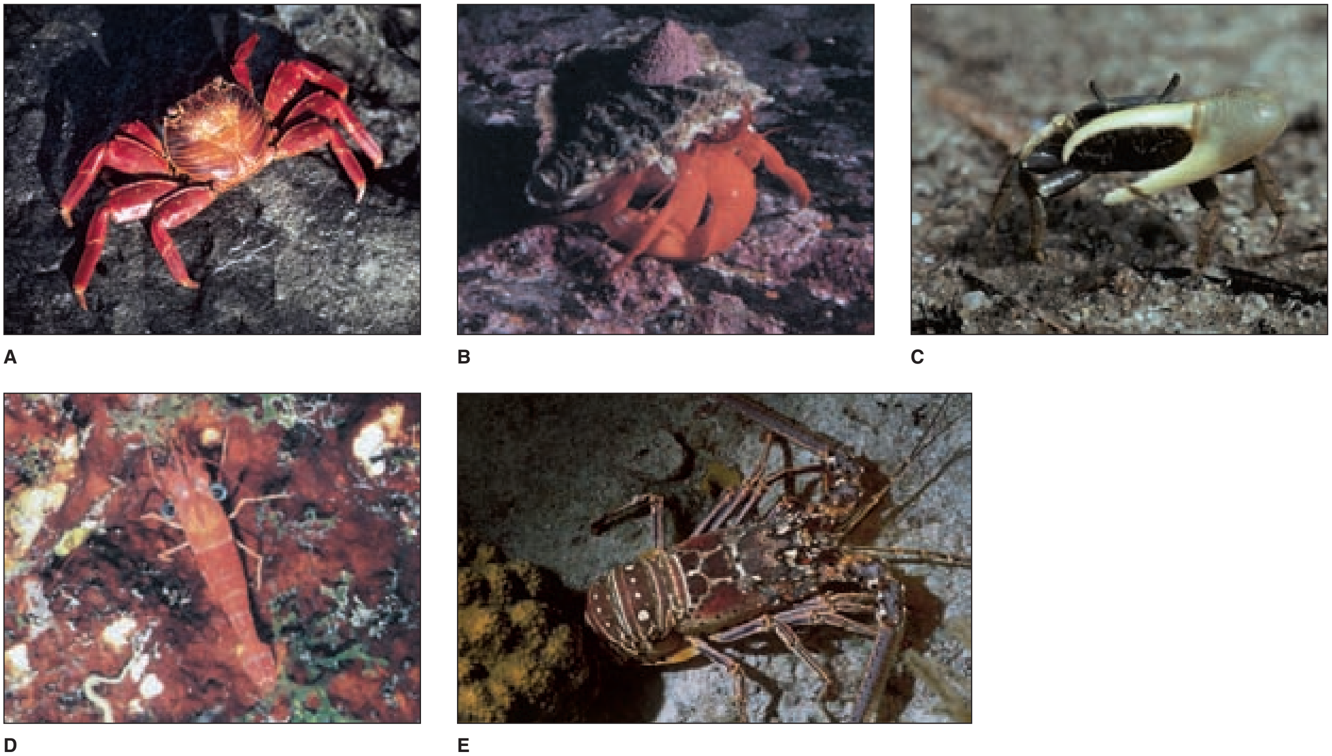


figure 12.31
Decapod crustaceans. **A,** A bright orange tropical rock crab, *Grapsus grapsus,* is a conspicuous exception to the rule that most crabs bear cryptic coloration. **B,** A hermit crab, *Elassochirus gilli,* which has a soft abdominal exoskeleton, lives in a snail shell that it carries about and into which it can withdraw for protection. **C,** A male fiddler crab, *Uca* sp., uses its enlarged cheliped to wave territorial displays and in threat and combat. **D,** A red night shrimp, *Rhynchocinetes rigens,* prowls caves and overhangs of coral reefs, but only at night. **E,** Spiny lobster *Panulirus argus* (order Decapoda, class Malacostraca).

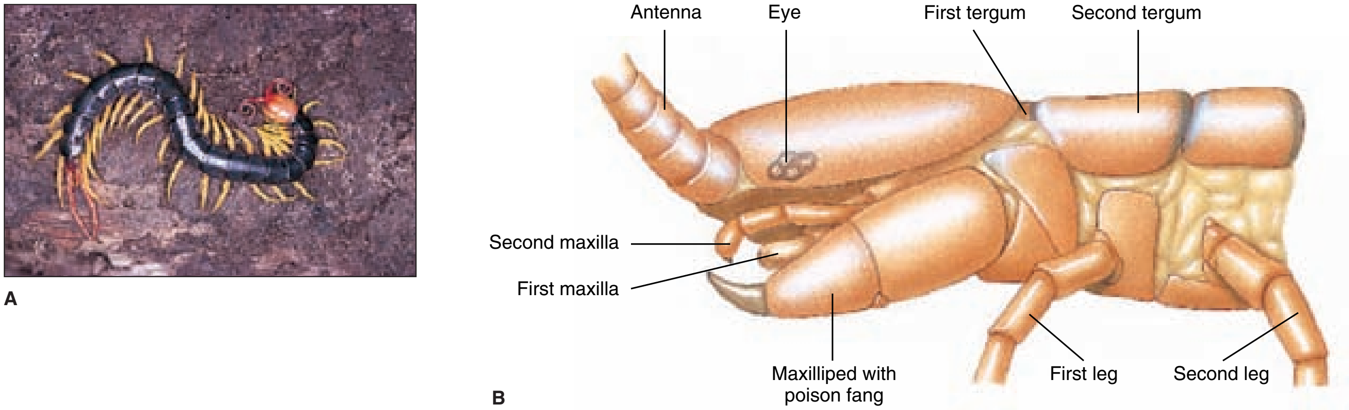


figure 12.32
A, A centipede, *Scolopendra* (class Chilopoda) from the Amazon Basin, Peru. Most segments have one pair of appendages each. First segment bears a pair of poison claws, which in some species can inflict serious wounds. Centipedes are carnivorous. **B,** Head of centipede.

head and the last two, bears one pair of appendages. Those of the first body segment are modified to form poison claws, which they use to kill their prey. Most species are harmless to humans.

Their head bears a pair of eyes, each consisting of a group of ocelli (simple eyes). Respiration is by tracheal tubes with a pair of spiracles in each somite. Sexes are separate, and all species are oviparous. Young are similar to adultS. Common house centipedes *Scutigera,* with 15 pairs of legs, and *Scolopendra* (figure 12.32), with 21 pairs of legs, are familiar genera.

Class Diplopoda: Millipedes

Diplopods, or "double-footed" arthropods, are commonly called millipedes, which literally means "thousand feet" (figure 12.33). Although they do not have a thousand legs, they do have a great many. Their cylindrical bodies are made up of 25 to 100 segments. The four thoracic segments bear only one pair of legs each, but abdominal segments each have two pairs, a condition that may have evolved from fusion of somites. Two pairs of spiracles occur on each abdominal somite, each opening into an air chamber that gives rise to tracheal tubes.

Millipedes are less active than centipedes and are generally herbivorous, living on decayed plant and animal matter and sometimes living plants. They prefer dark moist places under stones and logs. Females lay eggs in a nest and guard them carefully. Larval forms have only one pair of legs per somite.

Class Insecta: Insects

Insects are the most numerous and diverse of all groups of arthropods (figure 12.34). There are more species of insects than species in all the other classes of animals combined. The number of insect species named has been estimated at close to

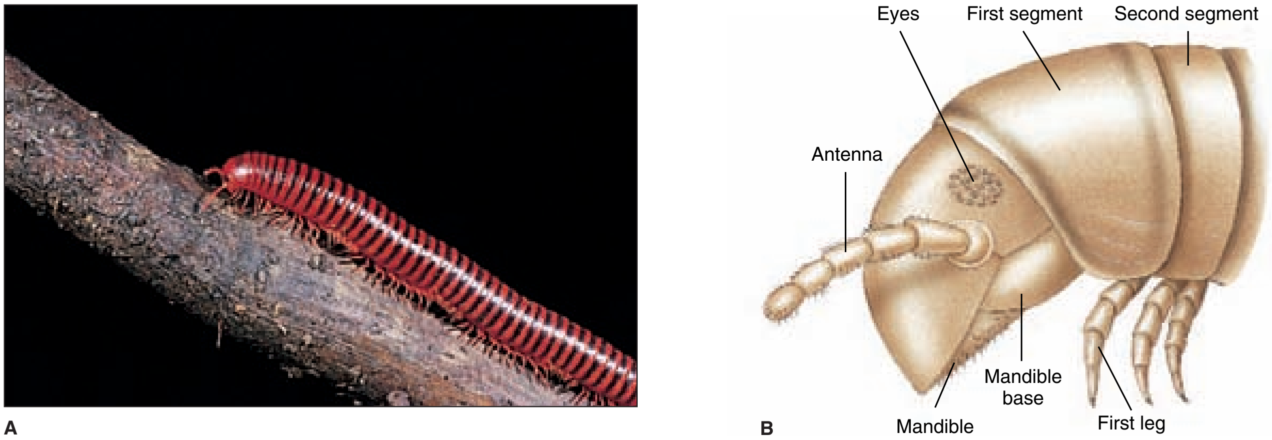


figure 12.33
A, A tropical millipede with warning coloration. Note the typical doubling of appendages on most segments, hence diplosegments. **B,** Head of millipede.

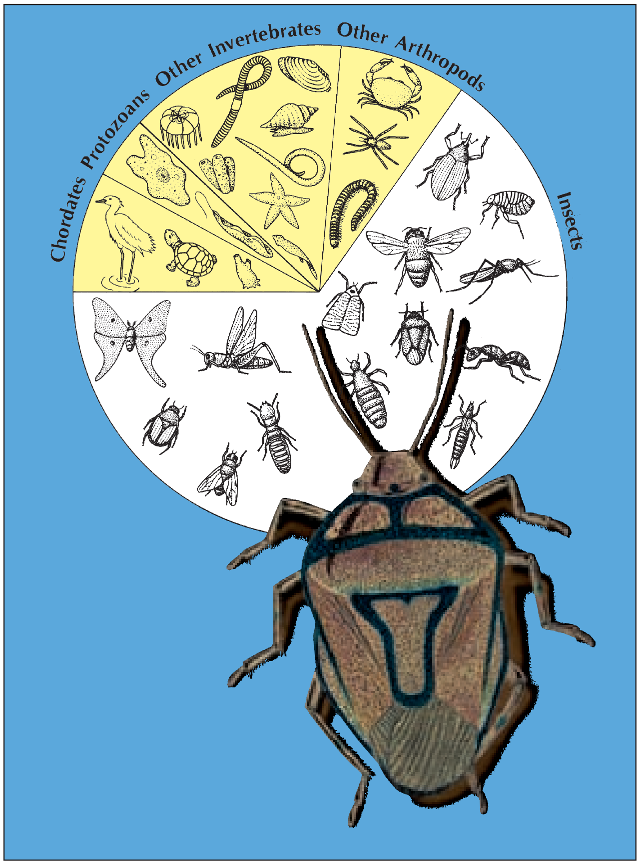


figure 12.34
Pie diagram indicating relative numbers of species of insects to the rest of the animal kingdom and protozoan groups.

1 million, with thousands, perhaps millions, of other species yet to be discovered and classified.

It is difficult to appreciate fully the significance of this extensive group and its role in the biological pattern of animal life. The study of insects **(entomology)** occupies the time and resources of thousands of skilled men and women all over the world. The struggle between humans and insect pests seems to be endless, yet paradoxically, insects are so interwoven into the economy of nature in so many roles that we would have a difficult time without them.

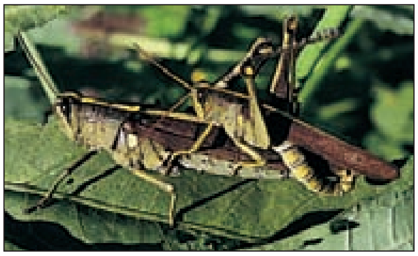
Insects differ from other arthropods in having **three pairs of legs** and usually **two pairs of wings** on the thoracic region of the body (figure 12.35), although some have one pair of wings or none. In size insects range from less than 1 mm to 20 cm in length, the majority being less than 2.5 cm long.

Distribution and Adaptability

Insects have spread into practically all habitats that can support life, but only a relatively few are marine. They are common in brackish water, in salt marshes, and on sandy beaches. They are abundant in fresh water, soils, forests, and plants, and they are found even in deserts and wastelands, on mountaintops, and as parasites in and on the bodies of plants and animals, including other insects.

Their wide distribution is made possible by their powers of flight and their highly adaptable nature. In many cases they can easily surmount barriers that are impassable to many other animals. Their small size and well-protected eggs allow them to be carried great distances by wind, water, and other animals.

The amazing adaptability of insects is evidenced by their wide distribution and enormous diversity of species. Such diversity enables this vigorous group to take advantage of all available resources of food and shelter.



A

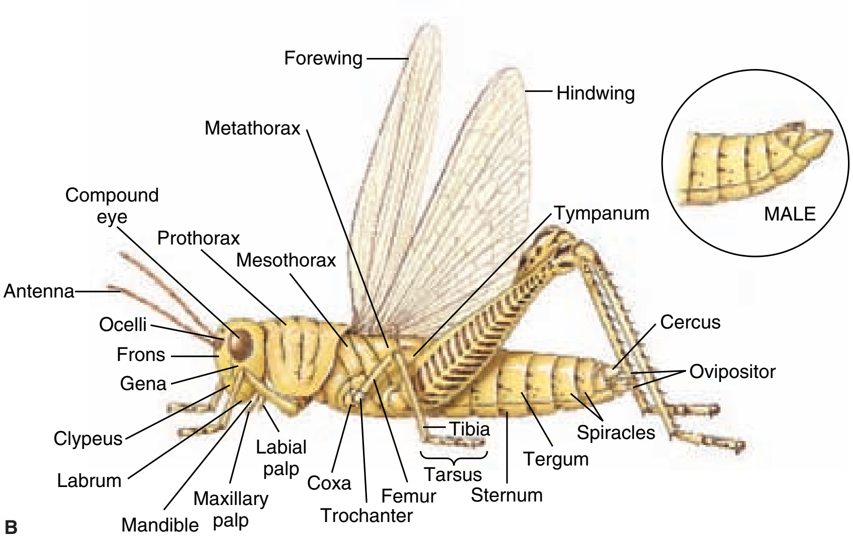


figure 12.35
A, A pair of grasshoppers, *Schistocerca obscura* (order Orthoptera), copulating. The African desert locust mentioned in the chapter prologue (p. 212) is *Schistocerca gregaria.* **B,** External features of a female grasshopper. The terminal segment of a male with external genitalia is shown in inset.

Much success of insects is due to adaptive qualities of their cuticular exoskeleton, as is the case in other arthropods. However, the great exploitation of terrestrial environments by insects has been made possible by an array of adaptations they possess to withstand its rigors. For example, their epicuticle has a waxy and a varnish layer and they can close their spiracles; both characteristics minimize evaporative water loss. They extract maximal fluid from food and fecal material, and many can retain water produced in oxidative metabolism. Many can enter a resting stage (diapause) and lie dormant during inhospitable conditions.

External Features

Insect tagmata are **head, thorax,** and **abdomen.** The cuticle of each body segment is typically composed of four plates **(sclerites),** a dorsal notum **(tergum),** a ventral **sternum,** and a pair of lateral **pleura.** Pleura of abdominal segments are membranous rather than sclerotized.

The head usually bears a pair of relatively large compound eyes, a pair of antennae, and usually three ocelli. Mouthparts typically consist of a **labrum,** a pair each of **mandibles** and **maxillae,** a **labium,** and a tonguelike **hypopharynx.** The type of mouthparts an insect possesses determines how it feeds. We discuss some of these modifications in a later section.

The thorax is composed of three somites: **prothorax, mesothorax,** and **metathorax,** each bearing a pair of legs (figure 12.35). In most insects the mesothorax and metathorax each bear a pair of wings. Wings consist of a double membrane that contains veins of thicker cuticle, which serve to strengthen the wing. Although these veins vary in their patterns among different species, they are constant within a species and serve as one means of classification and identification.

Legs of insects are often modified for special purposes. Terrestrial forms have walking legs with terminal pads and claws as in beetles. These pads may be sticky for walking upside down, as in house flies. Hindlegs of grasshoppers and crickets are adapted for jumping (figure 12.35B). Mole crickets have the first pair of legs modified for burrowing in the ground. Water bugs and many beetles have paddle-shaped appendages for swimming. For grasping prey, the forelegs of a praying mantis are long and strong (figure 12.36).

Wings and the Flight Mechanism

Insects share the power of flight with birds and flying mammals. However, their wings have evolved in a different manner from that of the limb buds of birds and mammals and are not homologous with them. Insect wings are formed by outgrowth from the body wall of the mesothoracic and metathoracic segments and are composed of cuticle.

Most insects have two pairs of wings, but Diptera (true flies) have only one pair (figure 12.37), the hindwings being represented by a pair of small **halteres** (balancers) that vibrate and are responsible for equilibrium during flight. Males in order Strepsiptera have only a hind pair of wings and an anterior pair of halteres. Males of scale insects also have one pair of wings but no halteres. Some insects are wingless. Ants and termites, for example, have wings only on males, and on females during certain periods; workers are always wingless. Lice and fleas are always wingless.

Wings may be thin and membranous, as in flies and many others (figure 12.37); thick and horny, as in forewings of beetles (see figure 12.51); parchmentlike, as in forewings of grasshoppers; covered with fine scales, as in butterflies and moths; or with hairs, as in caddis flies.

Wing movements are controlled by a complex of thoracic muscles. **Direct flight muscles** are attached to a part of the wing itself. **Indirect flight muscles** are not attached to the wing and cause wing movement by altering the shape of the thorax. The wing is hinged at the thoracic tergum and also slightly laterally on a pleural process, which acts as a fulcrum (figure 12.38). In all insects, the upstroke of a wing is effected by contracting indirect muscles that pull the tergum down toward the sternum (figure 12.38A). Dragonflies and cockroaches accomplish the downstroke by contracting direct muscles attached to the wings lateral to the pleural fulcrum. In Hymenoptera and Diptera all flight muscles are indirect. The downstroke occurs when sternotergal muscles relax and longitudinal muscles of the thorax arch the tergum (figure 12.38B), pulling the tergal articulations upward relative to the pleura. The downstroke in beetles and grasshoppers involves both direct and indirect muscles.

Contraction of flight muscles has two basic types of neural control: **synchronous** and **asynchronous.** Larger

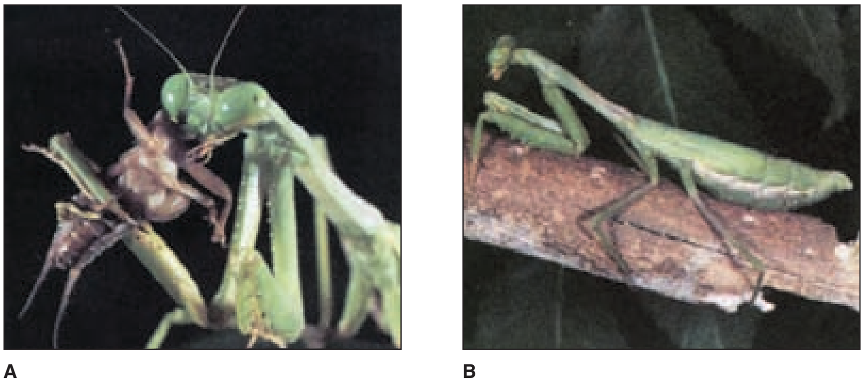


figure 12.36
A, Praying mantis (order Orthoptera), feeding on an insect. **B,** Praying mantis laying eggs.

figure 12.37
House fly *Musca domestica* (order Diptera). House flies can become contaminated with over 100 human pathogens, and there is strong circumstantial evidence for mechanical transmission of many of them.

insects such as dragonflies and butterflies have synchronous muscles, in which a single volley of nerve impulses stimulates a muscle contraction and thus one wing stroke. Asynchronous muscles are found in more specialized insects. Their mechanism of action is complex and depends on storage of potential energy in resilient parts of the thoracic cuticle. As one set of muscles contracts (moving the wing in one direction), they stretch the antagonistic set of muscles, causing them to contract (and move the wing in the other direction). Because the muscle contractions are not phase-related to nervous stimulation, only occasional nerve impulses are necessary to keep the muscles responsive to alternating stretch activation. Thus extremely rapid wing beats are possible. For example, butterflies (with synchronous muscles) may beat as few as four times per second. Insects with asynchronous muscles, such as flies and bees, may vibrate at 100 beats per second or more. Fruit flies, *Drosophila* (Gr. *drosos,* dew, + *philos,* loving), can fly at 300 beats per second, and midges have been clocked at more than 1000 beats per second!

Obviously flying entails more than a simple flapping of wings; a forward thrust is necessary. As the indirect flight muscles alternate rhythmically to raise and lower the wings, the direct flight muscles alter the angle of the wings so that they act as lifting airfoils during both upstroke and downstroke, twisting the leading edge of the wings downward during downstroke and upward during upstroke. This modulation produces a figure-eight movement (figure 12.38C) that aids in spilling air from the trailing edges of the wings. The quality of the forward thrust depends, of course, on several factors, such as variations in wing venation, how much the wings are tilted, and how they are feathered.

Flight speeds vary. The fastest flyers usually have narrow, fast-moving wings with a strong tilt and a strong figure-eight component. Sphinx moths and horse flies are said to achieve approximately 48 km (30 miles) per hour and dragonflies approximately 40 km (25 miles) per hour. Some insects are capable of long continuous flights. Migrating monarch butterflies, *Danaus plexippus* (Gr. after Danaus, mythical king of Arabia) (see figure 12.46) travel south for hundreds of miles in the fall, flying at a speed of approximately 10 km (6 miles) per hour.

Internal Form and Function

Nutrition The digestive system (figure 12.39) consists of a **foregut** (mouth with salivary glands, **esophagus, crop** for storage, and **proventriculus** for grinding), **midgut** (stomach and gastric ceca), and **hindgut** (intestine, rectum, and anus). The foregut and hindgut are lined with cuticle, so absorption of food is confined largely to the midgut, although some

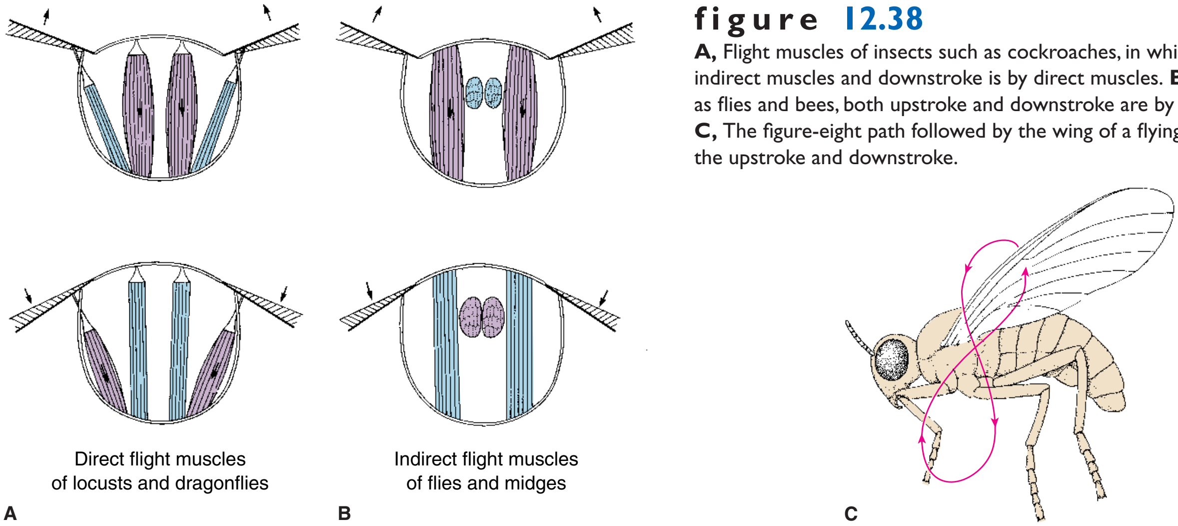

Direct flight muscles of locusts and dragonflies
Indirect flight muscles of flies and midges

figure 12.38
A, Flight muscles of insects such as cockroaches, in which upstroke is by indirect muscles and downstroke is by direct muscles. **B,** In insects such as flies and bees, both upstroke and downstroke are by indirect muscles. **C,** The figure-eight path followed by the wing of a flying insect during the upstroke and downstroke.

figure 12.39
Internal structure of female grasshopper.

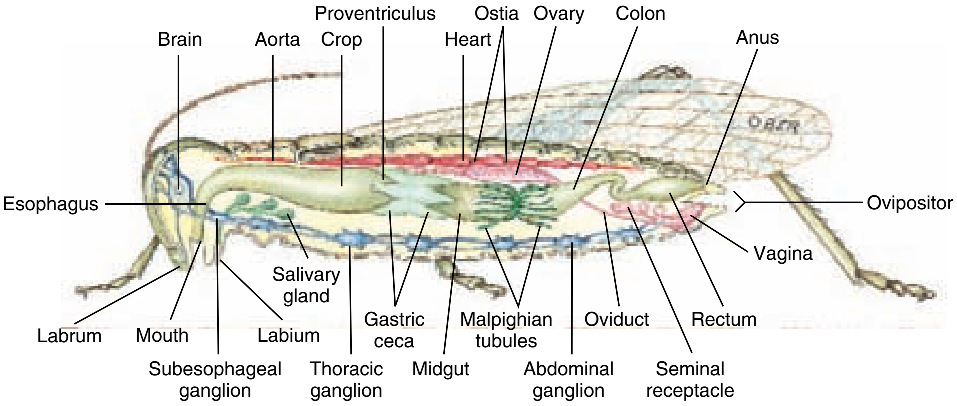


figure 12.40
Female human flea, *Pulex irritans* (order Siphonaptera).

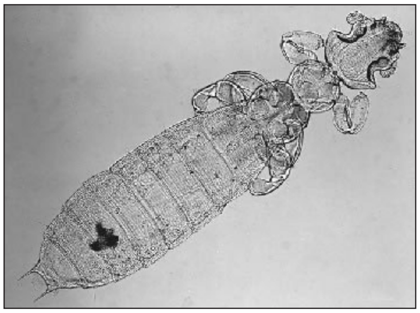


figure 12.41
Gliricola porcelli (order Mallophaga), a chewing louse of guinea pigs. Antennae are normally held in deep grooves on the sides of the head.

figure 12.42
The head and body louse of humans *Pediculus humanus* (order Anoplura) feeding.

absorption may take place in all sections. Most insects feed on plant juices and plant tissues. Such a food habit is called **phytophagous.** Some insects feed on specific plants; others, such as grasshoppers, can eat almost any plant. Caterpillars of many moths and butterflies eat foliage of only certain plants. Certain species of ants and termites cultivate fungus gardens as a source of food.

Many beetles and larvae of many insects live on dead animals **(saprophagous).** A number of insects are **predaceous,** catching and eating other insects as well as other types of animals.

Many insects are parasitic as adults, as larvae, or, in some cases, both juveniles and adults are parasites. For example, fleas (figure 12.40) live on blood of mammals as adults, but their larvae are free-living scavengers. Lice (figures 12.41 and 12.42) are parasitic throughout their life cycle. Many parasitic insects are themselves parasitized by other insects, a condition known as **hyperparasitism.** Larvae of many varieties of wasps live inside the bodies of spiders or other insects (figure 12.43B), consuming their hosts and eventually killing them. Because they always destroy their hosts, they are known as **parasitoids** (considered a particular type of parasite); typical parasites normally do not kill their hosts. Parasitoid insects are enormously important in controlling populations of other insects.

Feeding habits of insects are determined to some extent by their mouthparts, which are highly specialized for each type of feeding.

Biting and **chewing mouthparts,** such as those of grasshoppers and many herbivorous insects, are adapted for seizing and crushing food (figure 12.44). Mandibles of chewing insects are strong, toothed plates whose edges can bite or tear while the maxillae hold the food and pass it toward the mouth. Enzymes secreted by the salivary glands add chemical action to the chewing process.

Sucking mouthparts are greatly varied. House flies and fruit flies have no mandibles; their labium is modified into two soft lobes containing many small tubules that sponge up liquids with a capillary action much as the holes of a commercial sponge do (figure 12.44). Horse flies, however, are fitted not only to sponge up surface liquids but to bite into skin with slender, tapering mandibles and then sponge up blood. Mosquitos combine **piercing** by means of needlelike stylets and sucking through a food channel (figure 12.44). In honey bees the labium forms a flexible and contractile "tongue" covered

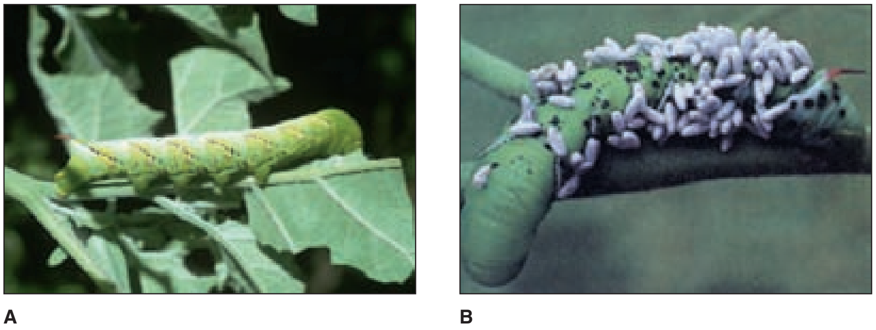
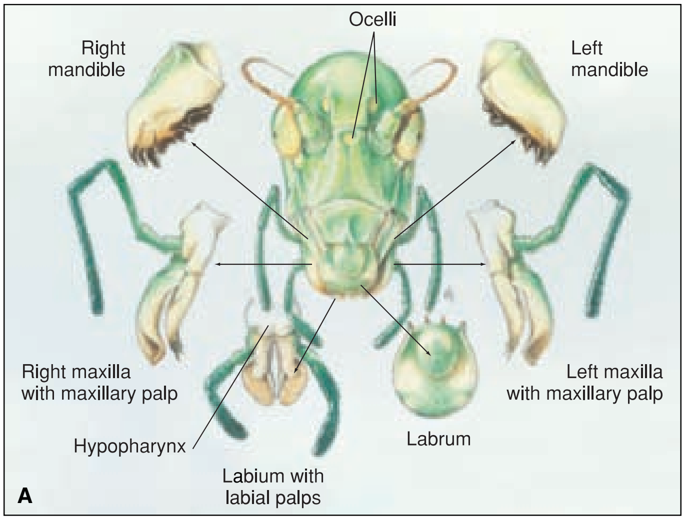


figure 12.43
A, Hornworm, larval stage of a sphinx moth (order Lepidoptera). The more than 100 species of North American sphinx moths are strong fliers and mostly nocturnal feeders. Their larvae, called hornworms because of the large fleshy posterior spine, are often pests of tomatoes, tobacco, and other plants. **B,** Hornworm parasitized by a tiny wasp, *Apanteles,* which laid its eggs inside the caterpillar. The wasp larvae have emerged, and their pupae are on the caterpillar's skin. Young wasps emerge in 5 to 10 days, and the caterpillar usually dies.

with many hairs. When a bee plunges its proboscis into nectar, the tip of the tongue bends upward and moves back and forth rapidly. Liquid enters the tube by capillarity and is drawn up the tube continuously by a pumping pharynx. In butterflies and moths mandibles are usually absent, and maxillae are modified into a long sucking proboscis (figure 12.44) for drawing nectar from flowers. At rest, the proboscis is coiled up into a flat spiral. In feeding it extends, and pharyngeal muscles pump up fluid.

Circulation A tubular heart in the pericardial cavity (see figure 12.39) moves **hemolymph** (blood) forward through the only blood vessel, a dorsal aorta. The heartbeat is a peristaltic wave. Accessory pulsatory organs help move hemolymph into wings and legs, and flow is also facilitated by various body movements. Hemolymph consists of plasma and amebocytes and apparently has little to do with oxygen transport.

Gas Exchange Terrestrial animals require efficient respiratory systems that permit rapid oxygen–carbon dioxide exchange but also restrict water loss. In insects this is the function of the **tracheal system,** an extensive network of thin-walled tubes that branch into every part of the body (figure 12.45). Tracheal trunks open to the outside by paired **spiracles,** usually two on the thorax and seven or eight on the abdomen. A spiracle may be merely a hole in the integument, as in primatively wingless insects, but it is usually provided with a valve or other closing mechanism that cuts down water loss. Evolution of such a device must have been very important in enabling insects to move into drier habitats.



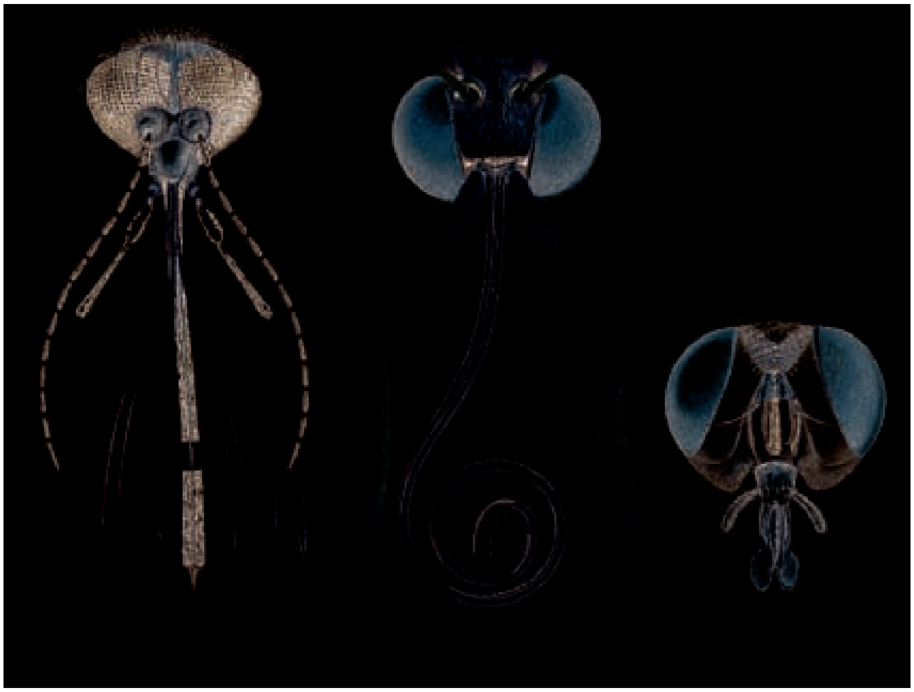


figure 12.44
Four types of insect mouthparts.

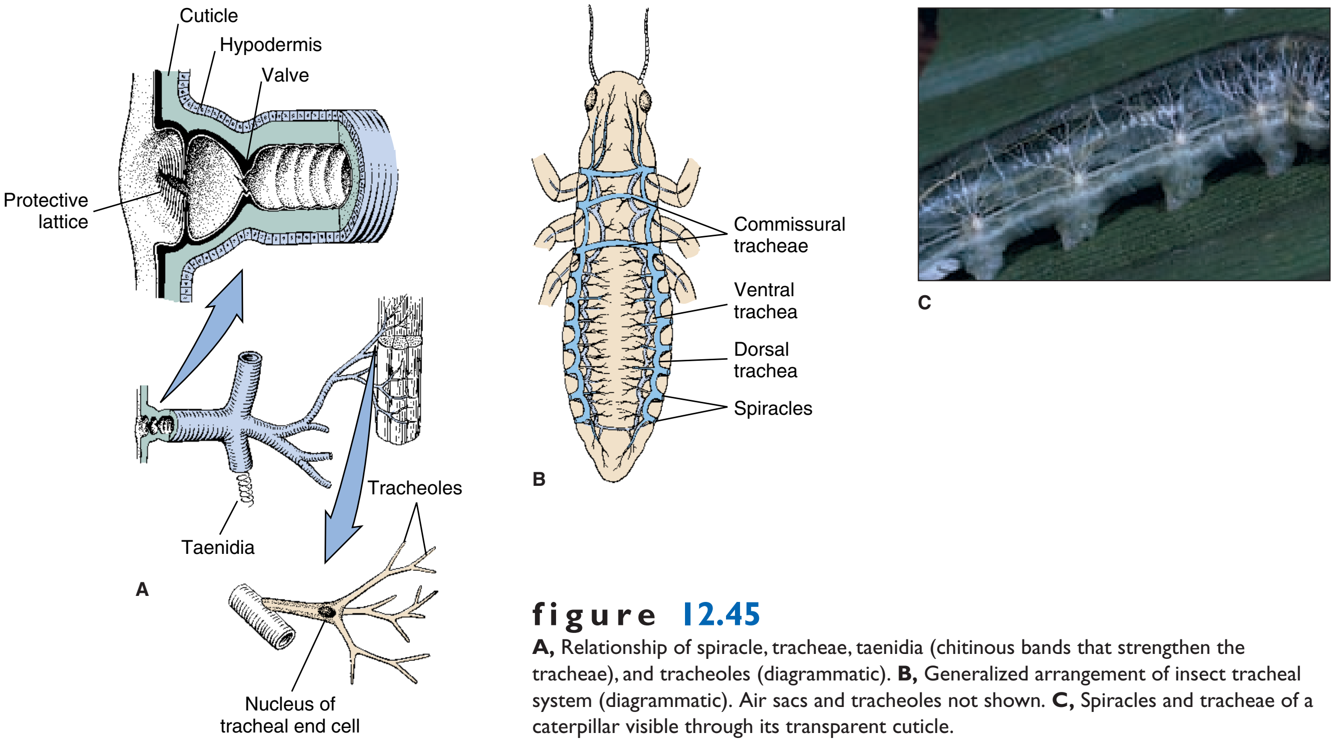


figure 12.45

A, Relationship of spiracle, tracheae, taenidia (chitinous bands that strengthen the tracheae), and tracheoles (diagrammatic). **B,** Generalized arrangement of insect tracheal system (diagrammatic). Air sacs and tracheoles not shown. **C,** Spiracles and tracheae of a caterpillar visible through its transparent cuticle.

Tracheae are composed of a single layer of cells and are lined with cuticle that is shed, along with the outer cuticle, during molts. Spiral thickenings of the cuticle, called **taenidia,** support the tracheae and prevent their collapse. Tracheae branch out into smaller tubes, ending in very fine, fluid-filled tubules called **tracheoles** (not lined with cuticle), which branch into a fine network over the cells. Scarcely any living cell is located more than a few micrometers away from a tracheole. In fact, the ends of some tracheoles actually indent the membranes of cells they supply, so that they terminate close to mitochondria. The tracheal system affords an efficient system of transport without use of oxygen-carrying pigments in hemolymph.

In some very small insects gas transport occurs entirely by diffusion along a concentration gradient. As oxygen is used, a partial vacuum develops in the tracheae, and air is sucked in through the spiracles. Larger or more active insects employ some ventilation device for moving air in and out of the tubes. Usually muscular movements in the abdomen perform the pumping action that draws air in or expels it.

The tracheal system is primarily adapted for breathing air, but many insects (nymphs, larvae, and adults) live in water. In small, soft-bodied aquatic nymphs, gaseous exchange may occur by diffusion through the body wall, usually into and out of a tracheal network just under the integument. Aquatic nymphs of stoneflies and mayflies are equipped with **tracheal gills,** which are thin extensions of the body wall containing a rich tracheal supply. Gills of dragonfly nymphs are ridges in the rectum (rectal gills) where gas exchange occurs as water enters and leaves.

Although diving beetles, *Dytiscus* (G. *dytikos,* able to swim), can fly, they spend most of their life in water as excellent swimmers. They use an "artificial gill" in the form of a bubble of air held under the first pair of wings. The bubble is kept stable by a layer of hairs on top of the abdomen and is in contact with the spiracles on the abdomen. Oxygen from the bubble diffuses into the tracheae and is replaced by diffusion of oxygen from the surrounding water. However, nitrogen from the bubble diffuses into the water, slowly decreasing the size of the bubble; therefore, diving beetles must surface every few hours to replace the air. Mosquito larvae are not good swimmers but live just below the surface, putting out short breathing tubes like snorkels to the surface for air. Spreading oil on the water, a favorite method of mosquito control, clogs the tracheae with oil and so suffocates the larvae. "Rattailed maggots" of syrphid flies have an extensible tail that can stretch as much as 15 cm to the water surface.

Excretion and Water Balance Malpighian tubules (see figure 12.39) are typical of most insects. As in spiders (p. 216), Malpighian tubules are very efficient, both as excretory organs and as a means of conserving body fluids—an important factor in the success of terrestrial animals.

Since water requirements vary among different types of insects, this ability to cycle water and salts is very important. Insects living in dry environments may resorb nearly all water from the rectum, producing a nearly dry mixture of urine and feces. Leaf-feeding insects take in and excrete large quantities of fluid. Freshwater larvae need to excrete water and conserve salts. Insects that feed on dry grains need to conserve water and excrete salt.

Nervous System The nervous system in general resembles that of larger crustaceans, with a similar tendency toward fusion of ganglia (see figure 12.39). Some insects have a giant fiber system. There is also a visceral nervous system that corresponds in function with the autonomic nervous system of vertebrates. Neurosecretory cells located in various parts of the brain have an endocrine function, but, except for their role in molting and metamorphosis, little is known of their activity.

Sense Organs Sensory perceptions of insects are usually keen. Organs receptive to mechanical, auditory, chemical, visual, and other stimuli are well developed. They are scattered over the body but are especially numerous on appendages.

Photoreceptors include both ocelli and compound eyes. Compound eyes are large and constructed of ommatidia, like those of crustaceans (p. 225). Apparently, visual acuity in insect eyes is much lower than that of human eyes, but most flying insects rate much higher than humans in flicker-fusion tests. Flickers of light become fused in human eyes at a frequency of 45 to 55 per second, but in bees and blow flies they do not fuse until 200 to 300 per second. This would be an advantage in analyzing a fast-changing landscape.

Most insects have three ocelli on their head, and they also have dermal light receptors on their body surface, but not much is known about them.

Sounds may be detected by sensitive hairlike **sensilla** or by tympanic organs sensitive to sonic or ultrasonic sound. Sensilla are modifications in the cuticular surface for reception of sensory stimuli other than light and are supplied with one or more neurons. Tympanic organs, found in grasshoppers (figure 12.35B), crickets, cicadas, butterflies, and moths, involve a number of sensory cells extending to a thin tympanic membrane that encloses an air space in which vibrations can be detected.

Chemoreceptive sensilla, which are peglike or setae, are especially abundant on the antennae, mouthparts, or legs. Mechanical stimuli, such as contact pressure, vibrations, and tension changes in the cuticle, are picked up by sensilla or by sensory cells in the epidermis. Insects also sense temperature, humidity, body position (proprioception), gravity, etc.

Reproduction Sexes are separate in insects, and fertilization is usually internal. Insects have various means of attracting mates. Female moths give off a chemical (pheromone) that can be detected for a great distance by males—several miles from females. Fireflies use flashes of light; some insects find each other by means of sounds or color signals and by various kinds of courtship behavior.

Sperm are usually deposited in the vagina of females at the time of copulation (see figure 12.35A). In some orders sperm are encased in spermatophores that may be transferred at copulation or deposited on the substratum to be picked up by a female. A male silverfish deposits a spermatophore on the ground, then spins signal threads to guide a female to it. During the evolutionary transition of mandibulates from aquatic to terrestrial life, spermatophores were widely used, with copulation evolving much later.

Usually sperm are stored in the seminal receptacle of a female in numbers sufficient to fertilize more than one batch of eggs. Many insects mate only once during their lifetime, and none mates more than a few times.

Insects usually lay a great many eggs. A queen honey bee, for example, may lay more than 1 million eggs during her lifetime. On the other hand, some flies are ovoviviparous and bring forth only a single offspring at a time. Forms that make no provision for care of young usually lay many more eggs than those that provide for young or those that have a very short life cycle.

Most species lay their eggs in a particular type of place to which they are guided by visual, chemical, or other clues. Butterflies and moths lay their eggs on the specific kind of plant on which their caterpillars must feed. A tiger moth may look for a pigweed, a sphinx moth for a tomato or tobacco plant, and a monarch butterfly for a milkweed plant (figure 12.46). Insects whose immature stages are aquatic lay their eggs in water. A tiny braconid wasp lays her eggs on a caterpillar of the sphinx moth where they will feed and pupate in tiny white cocoons (see figure 12.43B). An ichneumon wasp, with unerring accuracy, seeks out a certain kind of larva in which her young will live as internal parasites. Her long ovipositors may have to penetrate 1 to 2 cm of wood to find and deposit her eggs in the larva of a wood wasp or a wood-boring beetle (figure 12.47).

Metamorphosis and Growth

Although many animals undergo a metamorphosis, insects illustrate it more dramatically than any other group. The transformation of a caterpillar into a beautiful moth or butterfly is indeed an astonishing morphological change.

Early development occurs within the eggshell, and hatching young escape from the capsule in various ways. During postembryonic development most insects change in form; that is, they undergo **metamorphosis.** A number of molts are necessary during the growth period, and each stage between molts is called an **instar.**

Approximately 88% of insects go through **holometabolous (complete) metamorphosis** (Gr. *holo,* complete, + *metabolē,* change) (see figure 12.46), which separates physiological processes of growth **(larva)** from those of differentiation **(pupa)** and reproduction **(adult).** Each stage functions efficiently without competition with other stages, because the larvae often live in entirely different surroundings and eat

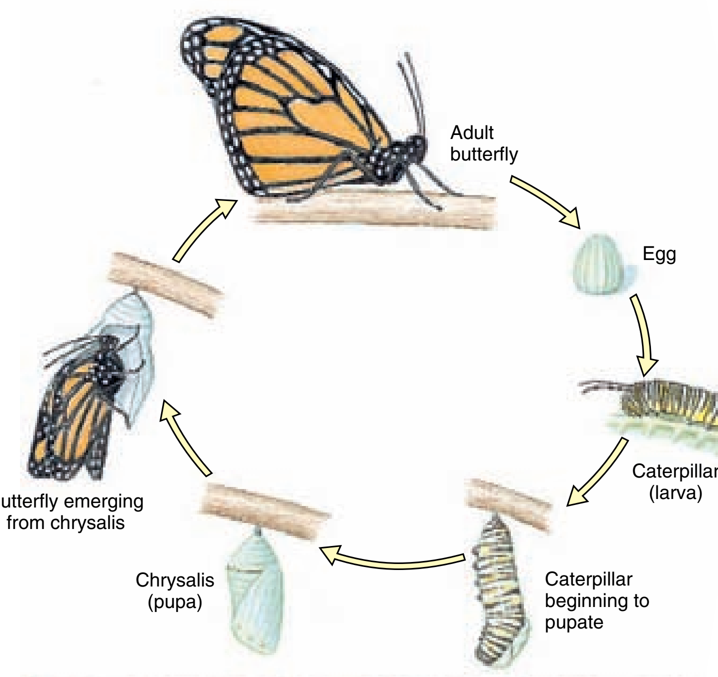


figure 12.46
Holometabolous (complete) metamorphosis in a butterfly, *Danaus plexippus* (order Lepidoptera). Eggs hatch to produce first of several larval instars. Last larval instar molts to become a pupa. Adult emerges at pupal molt.

figure 12.47
An ichneumon wasp with the end of the abdomen raised to thrust her long ovipositor into wood to find a tunnel made by the larva of a wood wasp or wood-boring beetle. She can bore 13 mm or more into wood to lay her eggs in the larva of the wood-boring beetle, which will become host for the ichneumon larvae. Other ichneumon species attack spiders, moths, flies, crickets, caterpillars, and other insects.

different foods from adults. The wormlike larvae, which usually have chewing mouthparts, are known by various common names, such as caterpillars, maggots, bagworms, fuzzy worms, and grubs. After a series of instars a larva forms a case or cocoon about itself and becomes a pupa, or chrysalis, a nonfeeding stage in which many insects pass the winter. When the final molt occurs a full-grown adult emerges (see figure 12.46), pale and with wings wrinkled. In a short time the wings expand and harden, and the insect is on its way. The stages, then, are **egg, larva** (several instars), **pupa,** and **adult.** Adults undergo no further molting.

Some insects undergo **hemimetabolous (gradual,** or **incomplete) metamorphosis** (Gr. *hemi,* half, + *metabolē* change) (figure 12.48). These include insects such as bugs, scale insects, lice, and grasshoppers, which have terrestrial young, and mayflies, stoneflies (figure 12.49A), and dragonflies (figure 12.49B), which lay their eggs in water. The young are called **nymphs** (figure 12.49C), and their wings develop externally as budlike outgrowths in the early instars and increase in size as the animal grows by successive molts and becomes a winged adult. Aquatic nymphs have tracheal gills or other modifications for aquatic life. The stages are **egg, nymph** (several instars), and **adult.**

A few insects, such as silverfish (see figure 12.60) and springtails, undergo direct development. The young, or juveniles, are similar to the adults except in size and sexual maturation. The stages are egg, juvenile, and adult. Such insects include the primitively wingless insects.

> The *biological* meaning of the word "bug" is much more restrictive than in common English usage. People often refer to all insects as "bugs," even extending the word to include such nonanimals as bacteria, viruses, and glitches in computer programs. Strictly speaking, however, a bug is a member of order Hemiptera and nothing else.

Hormones control and regulate metamorphosis in insects. Three major endocrine organs are involved in development through juvenile instars and eventually emergence of adults. These organs and the hormones they produce are the **brain (ecdysiotropin), ecdysial (prothoracic) glands (ecdysone),** and **corpora allata (juvenile hormone).** Hormonal control of molting and metamorphosis is the same in holometabolous and hemimetabolous insects.

Diapause

Many animals can enter a state of dormancy during adverse conditions, and there are periods in the life cycle of many insects when a particular stage can remain dormant for a long time because external climatic conditions are too harsh for normal

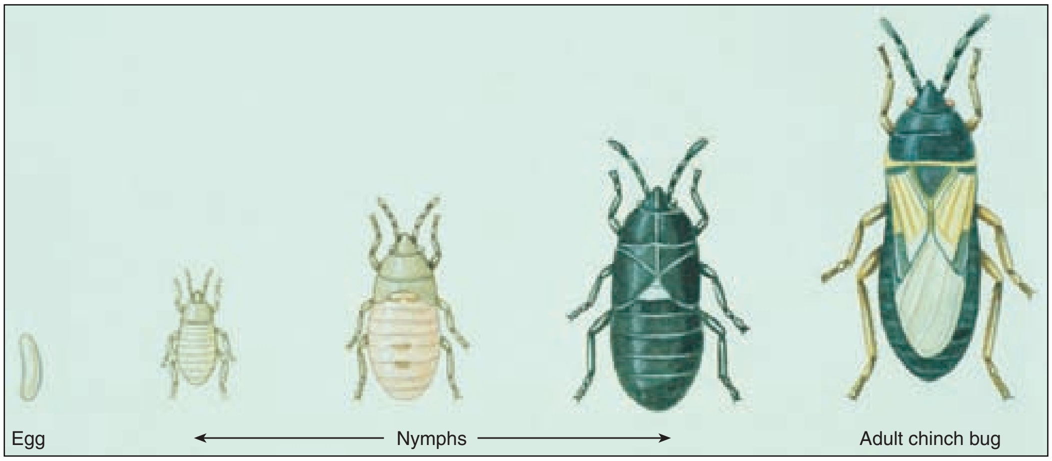


figure 12.48
Life history of a hemimetabolous insect.

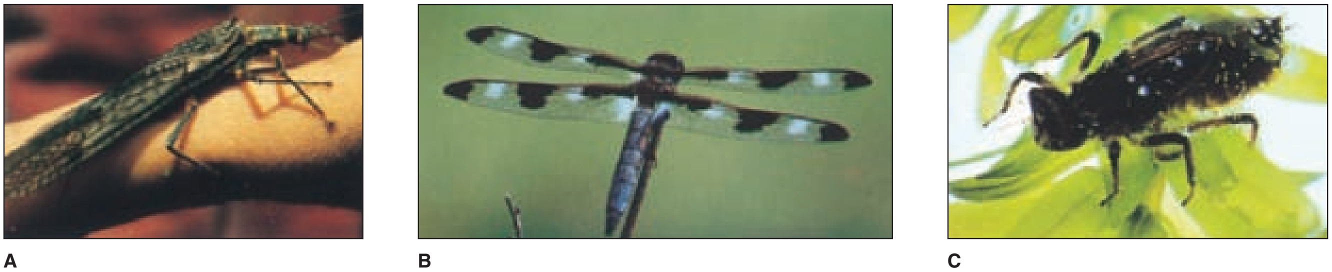


figure 12.49
A, A stonefly, *Perla* sp. (order Plecoptera). **B,** A ten-spot dragonfly, *Libellula pulchella* (order Odonata). **C,** Nymph (larva) of a dragonfly. Both stoneflies and dragonflies have aquatic larvae that undergo gradual metamorphosis.

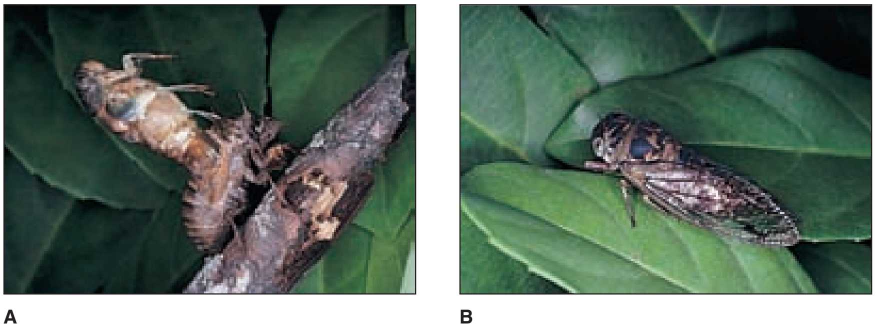


figure 12.50
A, Ecdysis in a cicada, *Tibicen davisi* (order Homoptera). The old cuticle splits along a dorsal midline as a result of increased blood pressure and of air forced into the thorax by muscle contraction. The emerging insect is pale, and its new cuticle is soft. The wings will be expanded by blood pumped into veins, and the insect enlarges by taking in air. **B,** An adult *Tibicen davisi.*

activity. Most insects enter such a stage facultatively when some environmental factor, such as temperature, becomes unfavorable, and the state continues until conditions again become favorable.

However, some species have a prolonged arrest of growth that is internally programmed and is usually seasonal. This type of dormancy is called **diapause** (di´a-poz) (Gr. *dia,* through, dividing into two parts, + *pausis,* a stopping), and it is an important adaptation to survive adverse environmental conditions. Diapause usually is triggered by some external signal, such as shortening day length. Diapause always occurs at the end of an active growth stage of the molting cycle so that, when the diapause period is over, the insect is ready for another molt.

Behavior and Communication

The keen sensory perceptions of insects make them extremely responsive to many stimuli. Stimuli may be internal (physiological) or external (environmental), and responses are governed

figure 12.51

Dung beetles *Canthon pilularis* (order Coleoptera), chew off a bit of dung, roll it into a ball, and then roll it to where they will bury it in soil. One beetle pushes while the other pulls. Eggs are laid in the ball, and larvae feed on dung. Dung beetles are black, an inch or less in length, and common in pastures.

by both the physiological state of the animal and the pattern of nerve pathways involved. Many responses are simple, such as orientation toward or away from a stimulus, for example, attraction of a moth to light, avoidance of light by a cockroach, or attraction of carrion flies to the odor of dead flesh.

Much behavior of insects, however, is not a simple matter of orientation but involves a complex series of responses. A pair of dung beetles chew off a bit of dung, roll it into a ball, and roll the ball laboriously to where they intend to bury it, after laying their eggs in it (figure 12.51). A female cicada slits the bark of a twig and then lays an egg in each of the slits. A female potter wasp *Eumenes* scoops up clay into pellets, carries them one by one to her building site, and fashions them into dainty little narrow-necked clay pots, into each of which she lays an egg. Then she hunts and paralyzes a number of caterpillars, pokes them into the opening of a pot, and closes up the opening with clay. Each egg, in its own protective pot, hatches to find a well-stocked larder of food awaiting it.

Some insects can memorize and perform in sequence tasks involving multiple signals in various sensory areas. Worker honey bees have been trained to walk through mazes that involved five turns in sequence, using such clues as color of a marker, distance between two spots, or angle of a turn. The same is true of ants. Workers of one species of *Formica* learned a six-point maze at a rate only two or three times slower than that of laboratory rats. Foraging trips of ants and bees often wind and loop about in a circuitous route, but once the forager has found food, the return trip is relatively direct. One investigator suggested that the continuous series of calculations necessary to figure the angles, directions, distance, and speed of the trip and to convert it into a direct return could involve a stopwatch, a compass, and integral vector calculus. How an insect does it is unknown.

Much of such behavior is "innate," that is, entire sequences of actions apparently have been programmed. However, a great deal more learning is involved than we once believed. A potter wasp, for example, must learn where she has left her pots if she is to return to fill them with caterpillars one at a time. Social insects, which have been studied extensively, are capable of most of the basic forms of learning used by mammals. An exception is insight learning. Apparently insects, when faced with a new problem, cannot reorganize their memories to construct a new response.

Insects communicate with other members of their species by means of chemical, visual, auditory, and tactile signals. **Chemical signals** take the form of **pheromones,** which are substances secreted by one individual that affect behavior or physiological processes of another individual. Examples of pheromones include sex attractants, releasers of certain behavior patterns, trail markers, alarm signals, and territorial markers. Like hormones, pheromones are effective in minute quantities. Social insects, such as bees, ants, wasps, and termites, can recognize a nestmate—or an alien in the nest—by means of identification pheromones. Pheromones determine caste in termites, and to some extent in ants and bees. In fact, pheromones are probably a primary integrating force in populations of social insects. Many insect pheromones have been extracted and chemically identified.

Sound production and **reception** (phonoproduction and phonoreception) in insects have been studied extensively, and although a sense of hearing is not present in all insects, this means of communication is meaningful to insects that use it. Sounds serve as warning devices, advertisement of territorial claims, or courtship songs. Sounds of crickets and grasshoppers seem to be concerned with courtship and aggression. Male crickets scrape the modified edges of their forewings together to produce their characteristic chirping. The long, drawn-out sound of male cicadas, a call to attract females, is produced by vibrating membranes in a pair of organs located on the ventral side of the basal abdominal segment.

There are many forms of **tactile communication,** such as tapping, stroking, grasping, and antennae touching, which evoke responses varying from recognition to recruitment and alarm. Certain kinds of flies, springtails, and beetles manufacture their own **visual signals** in the form of **bioluminescence.** The best known of luminescent beetles are fireflies, or lightning bugs (which are neither flies nor bugs, but beetles), in which a flash of light helps to locate a prospective mate. Each species has its own characteristic flashing rhythm produced on the ventral side of the last abdominal segments. Females flash an answer to the species-specific pattern to attract males. This interesting "love call" has been adopted by species of *Photuris,* which prey on male fireflies of other species they attract (figure 12.52).

Social Behavior Insects rank very high in the animal kingdom in their organization of social groups, and cooperation within more complex groups depends heavily on chemical and tactile communication. Social communities are not all

figure 12.52
Firefly femme fatale, *Photuris versicolor,* eating a male *Photinus tanytoxus,* which she has attracted with false mating signals.

figure 12.53
An ant (order Hymenoptera) tending a group of aphids (order Homoptera). The aphids feed copiously on plant juices and excrete the excess as a clear liquid rich in carbohydrates (“honey-dew”), which is cherished as a food by ants.

complex, however. Some community groups are temporary and uncoordinated, as are hibernating associations of carpenter bees or feeding gatherings of aphids (figure 12.53). Some are coordinated for only brief periods, such as the tent caterpillars *Malacosoma,* that join in building a home web and a feeding net. However, all these are still open communities with social behavior.

figure 12.54
Queen bee surrounded by her court. The queen is the only egg layer in the colony. The attendants, attracted by her pheromones, constantly lick her body. As food is transferred from these bees to others, the queen’s presence is communicated throughout the colony.

In true societies of some orders, such as Hymenoptera (honey bees and ants) and Isoptera (termites), a complex social life is necessary for perpetuation of the species. Such societies are closed. In them all stages of the life cycle are involved, communities are usually permanent, all activities are collective, and there is reciprocal communication. There is a high degree of efficiency in division of labor. Such a society is essentially a family group in which the mother or perhaps both parents remain with young, sharing duties of the group in a cooperative manner. The society usually demonstrates polymorphism, or **caste** differentiation.

Honey bees have one of the most complex social organizations in the insect world. Instead of lasting one season, their organization continues for a more or less indefinite period. As many as 60,000 to 70,000 honey bees may live in a single hive. Of these, there are three castes—a single sexually mature female, or **queen,** a few hundred **drones,** which are sexually mature males, and thousands of **workers,** which are sexually inactive genetic females (figure 12.54).

Workers take care of young, secrete wax with which they build the six-sided cells of the honeycomb, gather nectar from flowers, manufacture honey, collect pollen, and ventilate and guard the hive. One drone, sometimes more, fertilizes the queen during the mating flight, at which time enough sperm are stored in her seminal receptacle to last her lifetime.

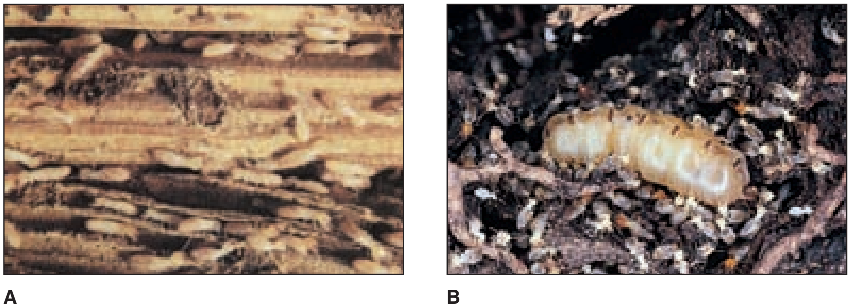


figure 12.55
A, Termite workers, *Reticulitermes flavipes* (order Isoptera), eating yellow pine. Workers are wingless sterile adults that tend the nest and care for the young. **B,** Termite queen becomes a distended egg-laying machine. The queen and several workers and soldiers are shown here.

Castes are determined partly by fertilization and partly by what is fed to the larvae. Drones develop parthenogenetically from unfertilized eggs (and consequently are haploid); queens and workers develop from fertilized eggs (and thus are diploid; see haplodiploidy, p. 164). Female larvae that will become queens are fed **royal jelly,** a secretion from the salivary glands of nurse workers. Royal jelly differs from the "worker jelly" fed to ordinary larvae, but components in it that are essential for queen determination have not yet been identified. Honey and pollen are added to worker diet about the third day of larval life. Pheromones in "queen substance," which is produced by the queen's mandibular glands, prevent female workers from maturing sexually. Workers produce royal jelly only when the level of "queen substance" pheromone in the colony drops. This change occurs when the queen becomes too old, dies, or is removed. Then workers start enlarging a larval cell and feeding a larva royal jelly that produces a new queen.

Honey bees have evolved an efficient system of communication by which, through certain body movements, their scouts inform workers of the location and quantity of food sources.

Termite colonies contain several castes, consisting of fertile individuals, both males and females, and sterile individuals (figure 12.55). Some fertile individuals may have wings and may leave the colony, mate, lose their wings, and as **king** and **queen** start a new colony. Wingless fertile individuals may under certain conditions substitute for the king or queen. Sterile members are wingless and become **workers** and **soldiers.** Soldiers have large heads and mandibles and serve for defense of the colony. As in bees and ants, extrinsic factors cause caste differentiation. Reproductive individuals and soldiers secrete inhibiting pheromones that pass throughout the colony to nymphs through a mutual feeding process, called **trophallaxis,** so that they become sterile workers. Workers also produce pheromones, and if the level of "worker substance" or "soldier substance" falls, as might happen after an attack by marauding predators, for example, the next generation produces compensating proportions of the appropriate caste.

Ants also have highly organized societies. Superficially, they resemble termites, but they are quite different (belong to a different order) and can be distinguished easily. In contrast to termites, ants are usually dark in color, are hard bodied, and have a constriction posterior to their first abdominal somite.

> Entomologists have chosen to describe insect societies by borrowing terms commonly used to describe human societies: queen, king, royal, soldier, worker, and caste. This usage can be misleading by implying a correspondence between human and insect societies that does not exist. For example, "queen" suggests a position of political power in human societies, which has no correspondence to the reproductive female designated a "queen" of a bee colony. Confusion of these terms led a famous population geneticist, Ronald Fisher, to argue that human societies could achieve greater stability by emulating insect societies, specifically by concentrating reproduction among members of upper classes. This argument is now considered an embarrassment of his otherwise highly regarded and influential book, *The Genetical Theory of Natural Selection* (1930).

In ant colonies males die soon after mating and the queen either starts her own new colony or joins some established colony and does the egg laying. Sterile females are wingless workers and soldiers that do the work of the colony—gather food, care for young, and protect the colony. In many larger colonies there may be two or three types of individuals within each caste.

Ants have evolved some striking patterns of "economic" behavior, such as making slaves, farming fungi, herding "ant cows" (aphids or other homopterans, see figure 12.53), sewing their nests together with silk (figure 12.56), and using tools.

Insects and Human Welfare

Beneficial Insects Although most of us think of insects primarily as pests, humanity would have great difficulty in surviving if all insects were suddenly to disappear. Insects are necessary for cross-fertilization of many crops. Bees pollinate over $10 billion worth of food crops per year in the United States alone, and this value does not include pollination of forage crops for livestock or pollination by other insects. In addition, some insects produce useful materials: honey and beeswax from bees, silk from silkworms, and shellac from a wax secreted by lac insects.

figure 12.56
A weaver ant nest in Australia.

Very early in their evolution insects and flowering plants formed a relationship of mutual adaptations that have been to each other's advantage. Insects exploit flowers for food, and flowers exploit insects for pollination. Each floral development of petal and sepal arrangement is correlated with the sensory adjustment of certain pollinating insects. Among these mutual adaptations are amazing devices of allurements, traps, specialized structure, and precise timing.

Many predaceous insects, such as tiger beetles, aphid lions, ant lions, praying mantids, and ladybird beetles, destroy harmful insects (figure 12.57A, B). Some insects control harmful ones by parasitizing them or by laying their eggs where their young, when hatched, may devour the host (figure 12.57C). Dead animals are quickly consumed by maggots hatched from eggs laid on carcasses.

Insects and their larvae serve as an important source of food for many birds, fish, and other animals.

Harmful Insects Harmful insects include those which eat and destroy plants and fruits, such as grasshoppers, chinch bugs, corn borers, boll weevils, grain weevils, San Jose scale, and scores of others (figure 12.58). Practically every cultivated crop has several insect pests. Humans expend enormous resources in all agricultural activities, in forestry, and in the food industry to counter insects and the damage they engender. Outbreaks of bark beetles or defoliators such as spruce budworms and gypsy moths have generated tremendous economic losses and have become a major element in determining the composition of forests in the United States. Gypsy moths, introduced into the United States in 1869 in an ill-advised attempt to breed a better silkworm, have spread throughout the Northeast as far south as Virginia. They defoliate oak forests in years when there are oubreaks. In 1981, they defoliated 13 million acres in 17 northeastern states.

Lice, blood-sucking flies, warble flies, bot flies, and many others attack humans or domestic animals or both. Malaria, carried by the *Anopheles* mosquito (figure 12.59), is still one of the world's major diseases; mosquitos also transmit yellow fever and lymphatic filariasis. Fleas carry plague, which at times in history has wiped out significant portions of human populations. House flies are vectors of typhoid, as are lice for typhus fever; tsetse flies carry African sleeping sickness; and certain blood-sucking bugs, *Rhodnius* and related genera, transmit Chagas' disease.

There is tremendous destruction of food, clothing, and property by weevils, cockroaches, ants, clothes moths, termites, and carpet beetles. Not the least of the insect pests are bed bugs, *Cimex,* blood-sucking hemipterous insects that humans contracted from bats that shared their caves early in human evolution.

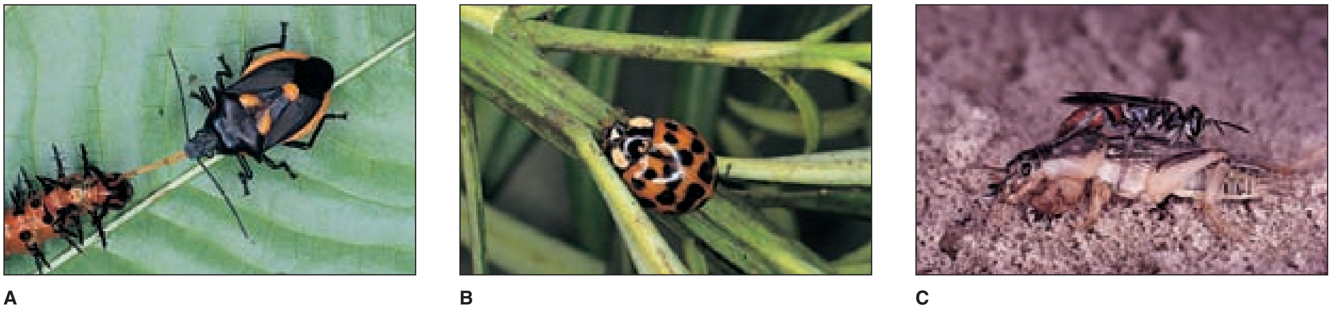


figure 12.57
Some beneficial insects. **A,** A predaceous stink bug (order Hemiptera) feeds on a caterpillar. Note the sucking proboscis of the bug. **B,** A ladybird beetle ("ladybug," order Coleoptera). Adults (and larvae of most species) feed voraciously on plant pests such as mites, aphids, scale insects, and thrips. **C,** A parasitic wasp (*Larra bicolor*) attacking a mole cricket. The wasp drives the cricket from its burrow, then stings and paralyzes it. After the wasp deposits her eggs, the mole cricket recovers and resumes an active life—until it is killed by developing wasp larvae.

figure 12.58

Insect pests. **A,** Japanese beetles, *Popillia japonica* (order Coleoptera) are serious pests of fruit trees and ornamental shrubs. They were introduced into the United States from Japan in 1917. **B,** Longtailed mealybug, *Pseudococcus longispinus* (order Homoptera). Many mealybugs are pests of commercially valuable plants. **C,** Corn ear worms, *Heliothis zea* (order Lepidoptera). An even more serious pest of corn is the infamous corn borer, an import from Europe in 1908 or 1909.

figure 12.59

A mosquito, *Anopheles quadrimaculatus* (order Diptera). *Anopheles* spp. are vectors of malaria.

Control of Insects Because all insects are an integral part of the ecological communities to which they belong, their total destruction would probably do more harm than good. Food chains would be disturbed, some of our favorite birds would disappear, the biological cycles by which dead animal and plant matter disintegrates and returns to enrich the soil would be seriously impeded. The beneficial roles of insects in our environment is often overlooked, and in our zeal to control the pests we spray the landscape indiscriminately with extremely effective "broad-spectrum" insecticides that eradicate good, as well as harmful, insects. We have also found, to our dismay, that many chemical insecticides persist in the environment and accumulate as residues in the bodies of animals higher in the food chain. Furthermore, many insects have developed a resistance to insecticides in common use.

In recent years, methods of control other than chemical insecticides have been under intense investigation, experimentation, and development. Economics, concern for the environment, and consumer demand are causing thousands of farmers across the United States to use alternatives to strict dependence on chemicals.

Several types of biological controls have been developed and are under investigation. All of these areas present problems but also show great possibilities. One is the use of bacterial, viral, and fungal pathogens. A bacterium, ***Bacillus thuringiensis,*** is quite effective in control of lepidopteran pests (cabbage looper, imported cabbage worm, tomato worm, gypsy moth). Other strains of ***B. thuringiensis*** attack insects in other orders, and the species diversity of target insects is being widened by techniques of genetic engineering. Genes coding for the toxin produced by ***B. thuringiensis*** (Bt) also have been introduced into DNA of the plants themselves, which makes the plants resistant to insect attack, and Bt is harmless to humans. Genes for Bt and for herbicide resistance have been incorporated into much of soybeans, corn, cotton, and canola produced in the United States, thus reducing need for hazardous chemical sprays. Concerns about genetically modified crops have arisen, especially in Europe, but such fears are supported by little or no scientific evidence.

Introduction of natural predators or parasites of the insect pests has had some success. In the United States, vedalia beetles from Australia help control the cottony-cushion scale on citrus plants, and numerous instances of control by use of insect parasites have been recorded. Introduction of exotic species for control of insect pests may have unexpected negative consequences, however, and should be done with caution.

Another approach to biological control is to interfere with reproduction or behavior of insect pests with sterile males or with naturally occurring organic compounds that act as hormones or pheromones. Such research, although very promising, is slow because of our limited understanding of insect behavior and the problems of isolating and identifying complex compounds that are produced in such minute amounts. Nevertheless, pheromones may play an important role in biological pest control in the future.

A systems approach referred to as **integrated pest management** is practiced with many crops. This approach involves integrated utilization of all possible, practical techniques

classification of class insecta

Insects are divided into orders chiefly on the basis of morphology and developmental features. Entomologists do not all agree on the names of orders or on the limits of each order. Some tend to combine and others to divide groups. However, the following synopsis of major orders is one that is rather widely accepted.

Order Protura (pro-tu´ra) (Gr. *protos,* first, + *oura,* tail*).* Minute (1 to 1.5 mm); no eyes or antennae; appendages on abdomen as well as thorax; live in soil and dark, humid places; slight, gradual metamorphosis.

Order Diplura (dip-lu´ra) (Gr. *diploos,* double, + *oura,* tail): **japygids.** Usually less than 10 mm; pale, eyeless; a pair of long terminal filaments or pair of caudal forceps; live in damp humus or rotting logs; development direct.

Order Collembola (col-lem´bo-la) (Gr. *kolla,* glue, + *embolon,* peg, wedge): **springtails** and **snowfleas.** Small (5 mm or less); no eyes; respiration by trachea or body surface; a springing organ folded under the abdomen for leaping; abundant in soil; sometimes swarm on pond surface film or on snowbanks in spring; development direct.

Order Thysanura (thy-sa-nu´ra) (Gr. *thysanos,* tassel, + *oura,* tail): **silverfish** (figure 12.60) and **bristletails.** Small to medium size; large eyes; long antennae; three long terminal cerci; live under stones and leaves and around human habitations; development direct.

Order Ephemeroptera (e-fem-er-op´ter-a) (Gr. *ephēmeros,* lasting but a day, + *pteron,* wing): **mayflies** (figure 12.61). Wings membranous; forewings larger than hindwings; adult mouthparts vestigial; nymphs aquatic, with lateral tracheal gills, hemimetabolous development.

Order Odonata (o-do-na´ta) (Gr. *odontos,* tooth, + *ata,* characterized by): **dragonflies** (see figure 12.49B), **damselflies.** Large; membranous wings are long, narrow, net veined, and similar in size; long and slender body; aquatic nymphs with aquatic gills and prehensile labium for capture of prey; hemimetabolous development.

Order Orthoptera (or-thop´ter-a) (Gr. *orthos,* straight, + *pteron,* wing): **grasshoppers, locusts, crickets, cockroaches, walkingsticks, praying mantids** (see figures 12.35 and 12.36). Wings when present, with forewings thickened and hindwings folded like a fan under forewings; chewing mouthparts; hemimetabolous development.

Order Isoptera (i-sop´ter-a) (Gr. *isos,* equal, + *pteron,* wing): **termites** (see figure 12.55). Small; membranous, narrow wings similar in size with few veins; wings shed at maturity; erroneously called "white ants"; distinguishable from true ants by broad union of thorax and abdomen; complex social organization; hemimetabolous development.

Order Mallophaga (mal-lof´a-ga) (Gr. *mallos,* wool, + *phagein,* to eat): **biting lice** (see figure 12.41). As large as 6 mm; wingless; chewing mouthparts; legs adapted for clinging to host; live on birds and mammals; hemimetabolous development.

Order Anoplura (an-o-plu´ra) (Gr. *anoplos,* unarmed, + *oura,* tail): **sucking lice** (see figure 12.42). Depressed body; as large as 6 mm; wingless; mouthparts for piercing and sucking; adapted for clinging to warm-blooded host; includes the head louse, body louse, crab louse, others; hemimetabolous development.

Order Hemiptera (he-mip´ter-a) (Gr. *hemi,* half + *pteron,* wing) **(Heteroptera): true bugs** (see figure 12.57A). Size 2 to 100 mm; wings present or absent; forewings with basal portion leathery, apical portion membranous; hindwings membranous; at rest, wings held flat over abdomen; piercing-sucking mouthparts; many with odorous scent glands; include water scorpions, water striders, bed bugs, squash bugs, assassin bugs, chinch bugs, stink bugs, plant bugs, lace bugs, others; hemimetabolous.

(continued on next page)

figure 12.60
Silverfish *Lepisma* (order Thysanura) is often found in homes.

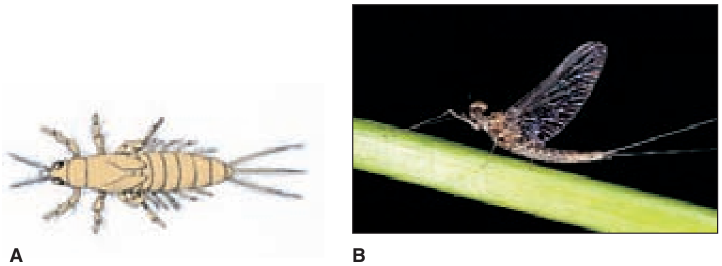


figure 12.61
Mayfly (order Ephemeroptera). **A,** Nymph. **B,** Adult.

Order Homoptera (ho-mop´ter-a) (Gr. *homos,* same, + *pteron,* wing): **cicadas** (figure 12.50), **aphids** (see figure 12.53), **scale insects, mealybugs** (see figure 12.58B), **leafhoppers, treehoppers** (figure 12.62). (Often included as suborder under Hemiptera.) If winged, either membranous or thickened forewings and membranous hindwings; wings held rooflike over body; piercing-sucking mouthparts; all plant eaters; some destructive; a few serving as source of shellac, dyes, etc.; some with complex life histories; hemimetabolous.

Order Neuroptera (neu-rop´ter-a) (Gr. *neuron,* nerve, + *pteron,* wing): **dobsonflies, ant lions** (figure 12.63), **lacewings.** Medium to large size; similar, membranous wings with many cross veins; chewing mouthparts; dobsonflies with greatly enlarged mandibles in males, and with aquatic larvae; ant lion larvae (doodlebugs) make craters in sand to trap ants; holometabolous development.

Order Coleoptera (ko-le-op´ter-a) (Gr. *koleos,* sheath, + *pteron,* wing): **beetles** (see figures 12.57B; 12.58A), **fireflies** (see figure 12.52), **weevils.** The largest order of animals; forewings (elytra) thick, hard, opaque; membranous hindwings folded under forewings at rest; mouthparts for biting and chewing; includes ground beetles, carrion beetles, whirligig beetles, darkling beetles, stag beetles, dung beetles (see figure 12.51), diving beetles, boll weevils, fireflies, ladybird beetles (ladybugs), others; holometabolous.

Order Lepidoptera (lep-i-dop´ter-a) (Gr. *lepidos,* scale, + *pteron,* wing): **butterflies** and **moths** (see figures 12.46 and 12.58C). Membranous wings covered with overlapping scales, wings coupled at base; mouthparts a sucking tube, coiled when not in use; larvae (caterpillars) with chewing mandibles for plant eating, stubby prolegs on the abdomen, and silk glands for spinning cocoons; antennae knobbed in butterflies and usually plumed in moths; holometabolous.

Order Diptera (dip´ter-a) (Gr. *dis,* two, + *pteron,* wing): **true flies.** Single pair of wings, membranous and narrow; hindwings reduced to inconspicuous balancers (halteres); sucking mouthparts or adapted for sponging or lapping or piercing; legless larvae called maggots or, when aquatic, wigglers; include crane flies, mosquitos (see figure 12.59), moth flies, midges, fruit flies, flesh flies, house flies, horse flies (see figure 12.37), bot flies, blow flies, gnats, and many others; holometabolous.

Order Trichoptera (tri-kop´ter-a) (Gr. *trichos,* hair, + *pteron,* wing): **caddisflies.** Small, soft bodied; wings well-veined and hairy, folded rooflike over hairy body; chewing mouthparts; aquatic larvae construct cases of leaves, sand, gravel, bits of shell, or plant matter, bound together with secreted silk or cement; some make silk feeding nets attached to rocks in streams; holometabolous.

Order Siphonaptera (si-fon-ap´ter-a) (Gr. *siphon,* a siphon, + *apteros,* wingless): **fleas** (see figure 12.40). Small; wingless; bodies laterally compressed; legs adapted for leaping; no eyes; ectoparasitic on birds and mammals; larvae legless and scavengers; holometabolous.

Order Hymenoptera (hi-men-op´ter-a) (Gr. *hymen,* membrane, + *pteron,* wing): **ants, bees** (figure 12.54), **wasps.** Very small to large; membranous, narrow wings coupled distally; subordinate hindwings; mouthparts for biting and lapping up liquids; ovipositor sometimes modified into stinger, piercer, or saw; both social and solitary species; most larvae legless, blind, and maggotlike; holometabolous.

figure 12.62
Oak treehoppers *Platycotis vittata* (order Homoptera).

figure 12.63
Adult ant lion (order Neuroptera).

classification of phylum arthropoda

Subphylum Trilobita (tri´lo-bi´ta) (Gr. *tri-,* three, + *lobos,* lobe): **trilobites.** All extinct forms; Cambrian to Carboniferous; body divided by two longitudinal furrows into three lobes; distinct head, thorax, and abdomen; biramous appendages.

Subphylum Chelicerata (ke-lis´e-ra´ta) (Gr. *chēle,* claw, + *keratos,* a horn): **eurypterids, horseshoe crabs, spiders, ticks.** First pair of appendages modified to form chelicerae; pair of pedipalps and four pairs of legs; no antennae, no mandibles; cephalothorax and abdomen often with segments fused.

Class Merostomata (mer´o-sto´ma-ta) (Gr. *meros,* thigh, + *stomatos,* mouth): **aquatic chelicerates.** Cephalothorax and abdomen; compound lateral eyes; appendages with gills; sharp telson; **subclasses Eurypterida** (all extinct) and **Xiphosurida,** the horseshoe crabs.

Class Pycnogonida (pik´no-gon´i-da) (Gr. *pyknos,* compact, + *gonia,* knee, angle): **sea spiders.** Small (3 to 4 mm), but some reach 500 mm; body chiefly cephalothorax; tiny abdomen; usually four pairs of long walking legs (some with five or six pairs); one pair of subsidiary legs (ovigers) for egg bearing; mouth on long proboscis; four simple eyes; no respiratory or excretory system. Example: *Pycnogonum.*

Class Arachnida (ar-ack´ni-da) (Gr. *arachnē,* spider): **scorpions, spiders, mites, ticks, harvestmen.** Four pairs of legs; segmented or unsegmented abdomen with or without appendages and generally distinct from cephalothorax; respiration by gills, tracheae, or book lungs; excretion by Malpighian tubules or coxal glands; dorsal bilobed brain connected to ventral ganglionic mass with nerves; simple eyes; sexes separate; chiefly oviparous; no true metamorphosis. Examples: *Argiope, Centruroides.*

Subphylum Crustacea (crus-ta´she-a) (L. *crusta,* shell, + *acea,* group suffix): **crustaceans.** Mostly aquatic, with gills; cephalothorax usually with dorsal carapace; biramous appendages, modified for various functions; head appendages consisting of two pairs of antennae, one pair of mandibles, and two pairs of maxillae; sexes usually separate; development primitively with nauplius stage.

Class Branchiopoda (bran´kee-op´o-da) (Gr. *branchia,* gills, + *pous, podos,* foot): **branchiopods.** Flattened, leaflike swimming appendages (phyllopodia) with respiratory function. Examples: *Triops, Lynceus, Daphnia.*

Class Maxillopoda (maks´i-lop´o-da) (L. *maxilla,* jawbone, + Gr. *pous, podos,* foot): **ostracods, copepods, branchiurans, barnacles.** Five cephalic, six thoracic, and usually four abdominal somites; no typical appendages on abdomen; unique maxillopodan eye. Examples: *Cypris, Cyclops, Ergasilus, Argulus, Balanus.*

Class Malacostraca (mal´a-kos´tra-ka) (Gr. *malakos,* soft, + *ostrakon,* shell): **shrimps, crayfishes, lobsters, crabs.** Usually with eight thoracic and six abdominal somites, each with a pair of appendages. Examples: *Armadillidium, Gammarus, Megacytiphanes, Grapsus, Homarus, Panulirus.*

Subphylum Uniramia (yu-ni-ra´me-a) (L. *unus,* one, + *ramus,* a branch): **insects** and **myriapods.** All appendages uniramous; head appendages consisting of one pair of antennae, one pair of mandibles, and one or two pairs of maxillae.

Class Diplopoda (di-plop´o-da) (Gr. *diploos,* double, + *pous, podos,* foot): **millipedes.** Subcylindrical body; head with short antennae and simple eyes; body with variable number of somites; short legs, usually two pairs of legs to a somite; separate sexes. Examples: *Julus, Spirobolus.*

Class Chilopoda (ki-lop´o-da) (Gr. *cheilos,* lip, + *pous, podos,* foot): **centipedes.** Dorsoventrally flattened body; variable number of somites, each with one pair of legs; one pair of long antennae; separate sexes. Examples: *Cermatia, Lithobius, Geophilus.*

Class Pauropoda (pau-rop´o-da) (Gr. *pauros,* small, + **pous, podos,** foot): **pauropods.** Minute (1 to 1.5 mm), cylindrical body consisting of double segments and bearing nine or ten pairs of legs; no eyes. Example: *Pauropus.*

Class Symphyla (sim´fi-la) (Gr. *syn,* together, + *phylon,* tribe): **garden centipedes.** Slender (1 to 8 mm) with long, threadlike antennae; body consisting of 15 to 23 segments with 10 to 12 pairs of legs; no eyes. Example: *Scutigerella.*

Class Insecta (in-sek´ta) (L. *insectus,* cut into): **insects.** Body with distinct head, thorax, and abdomen; pair of antennae; mouthparts modified for different food habits; head of six fused somites; thorax of three somites; abdomen with variable number, usually 11 somites; thorax with two pairs of wings (sometimes one pair or none) and three pairs of jointed legs; separate sexes; usually oviparous; gradual or abrupt metamorphosis. (Insect orders on pp. 245–246).

to contain pest infestations at a tolerable level—for example, cultural techniques (resistant plant varieties, crop rotation, tillage techniques, timing of sowing, planting, or harvesting, and others), use of biological controls, and sparing use of insecticides.

Phylogeny and Adaptive Radiation

Phylogeny

Shared derived characters between annelids and arthropods give strong support to a long-held hypothesis that both phyla originated from a common line of coelomate segmented protostomes from which two or more lines then diverged; a protoannelid line with laterally located parapodia and one or more protoarthropod lines with more ventrally located appendages. Molecular evidence now supports a dramatically contrasting hypothesis: placement of annelids in superphylum Lophotrochozoa and arthropods in superphylum Ecdysozoa. Alignment in separate superphyla not only requires that we abandon our view that annelids and arthropods are closely related, it implies that metamerism arose independently in the two groups and is a convergent character. However, analyses supporting an Ecdysozoa-Lophotrochozoa hypothesis (p. 81) suffer an important defect: failure to support monophyly of Annelida and Mollusca.

Whether phylum Arthropoda itself is monophyletic has also been controversial. Some scientists have contended that Arthropoda is polyphyletic and that some or all current subphyla are derived from different annelid-like ancestors that have undergone "arthropodization." A crucial development is the hardening of the cuticle to form an arthropod exoskeleton, and most of the features that distinguish arthropods from annelids result from the stiffened exoskeleton (see Prologue for this chapter). However, other zoologists argue strongly that derived similarities of the arthropod subphyla strongly support monophyly of the phylum. Phylum Tardigrada may be the sister taxon to arthropods, with phylum Onychophora being the sister taxon to the combined Arthropoda and Tardigrada (see Chapter 13). A cladogram depicting possible relationships is presented in Chapter 13 (p. 262). Some evidence based on ribosomal RNA sequences supports monophyly of Arthropoda and inclusion of Onychophora in the phylum.

Crustaceans have traditionally been allied with insects and myriapods in a group known as Mandibulata because they all have mandibles, as contrasted with chelicerae. Critics of this traditional grouping have argued that the mandibles in each group were so different that they could not have been inherited from a common ancestor. However, advocates of the "mandibulate hypothesis" maintain that these differences are not so fundamental that they could not have arisen during the 550-million-year history of mandibulate taxa. They also emphasize numerous other similarities between crustaceans and uniramians, such as basic structure of ommatidia, tripartite brain, and head primitively of five somites, each with a pair of appendages. However, some molecular data suggest that myriapods (millipedes and centipedes) are a sister group to all other arthropods and that crustaceans and insects form a monophyletic group! If these conclusions are supported by further investigations, our concepts of arthropod phylogeny and classification are subject to major revision.

Evolution of insects involved specialization of the first three postcephalic somites to become locomotor segments (thorax) and a loss or reduction of appendages on the rest of the body (abdomen). The wingless orders traditionally have been regarded as having the most primitive characteristics, but placing them in a single subclass (Apterygota) creates a paraphyletic taxon (figure 12.64). Three apterygote orders (Diplura, Collembola, Protura) have their mandibles and first maxillae located deeply in pouches in the head, a condition known as **endognathy.** They share other primitive and derived characters, and there are many similarities between endognathous insects and myriapods. All other insects are **ectognathous,** including the wingless order Thysanura. Ectognathous insects do not have their mandibles and maxillae in pouches, and they share other synapomorphies. Endognathous and ectognathous insects form sister groups, and Thysanura diverged from a common ancestor of ectognathous insects before the advent of flight, which unites the remaining ectognathous orders.

An ancestral winged insect gave rise to three lines, which differed in their ability to flex their wings (figure 12.64). Two of these (Odonata and Ephemeroptera) have outspread wings. The other line has wings that can fold back over the abdomen. It branched into three groups: one with hemimetabolous metamorphosis and chewing mouthparts (Orthoptera, Dermaptera, Isoptera, Embioptera); one group with hemimetabolous metamorphosis and a tendency to have sucking mouthparts (Thysanoptera, Hemiptera, Homoptera, Mallophaga, Anoplura); and a group with holometabolous metamorphosis. Insects in the last group have the most elaborate life history and apparently form a clade.

Adaptive Radiation

Annelids show little specialization or fusion of somites and relatively little differentiation of appendages. However, in arthropods the adaptive trend has been toward tagmatization of the body by differentiation or fusion of somites, giving rise in more derived groups to such tagmata as head and trunk; head, thorax, and abdomen; or cephalothorax (fused head and thorax) and abdomen. A series of similar appendages, one pair on each trunk somite, is the primitive character state, still retained by some crustaceans and by myriapods. More derived forms have appendages specialized for specific functions, and some appendages are lost entirely.

Much of the amazing diversity in arthropods seems to have developed because of modification and specialization of their cuticular exoskeleton and their jointed appendages, thus resulting in a wide variety of locomotor and feeding adaptations. Whether it be in the area of habitat, feeding adaptations, means of locomotion, reproduction, or general mode of living, adaptive achievements of arthropods are truly remarkable.

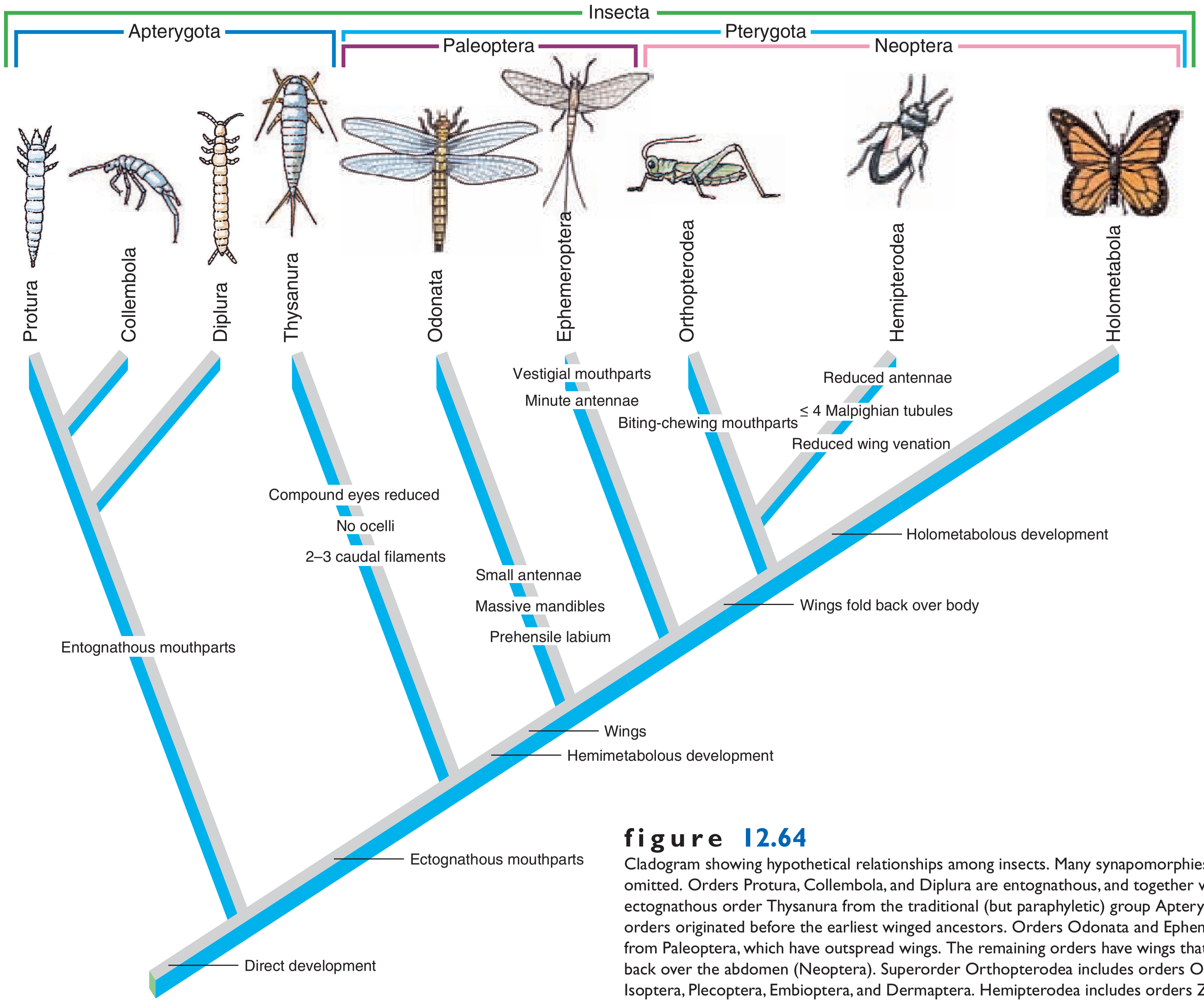


figure 12.64

Cladogram showing hypothetical relationships among insects. Many synapomorphies have been omitted. Orders Protura, Collembola, and Diplura are entognathous, and together with the ectognathous order Thysanura from the traditional (but paraphyletic) group Apterygota. These orders originated before the earliest winged ancestors. Orders Odonata and Ephemeroptera from Paleoptera, which have outspread wings. The remaining orders have wings that can fold back over the abdomen (Neoptera). Superorder Orthopterodea includes orders Orthoptera, Isoptera, Plecoptera, Embioptera, and Dermaptera. Hemipterodea includes orders Zoraptera, Psocoptera, Hemiptera, Homoptera, Thysanoptera, Anoplura, and Mallophaga; and superorder Holometabola encompasses all holometabolous orders. Outgroups for this cladogram would be myriapods.

summary

Arthropoda is the largest, most abundant and diverse phylum in the world. Arthropods are metameric, coelomate protostomes with well-developed organ systems. Most show marked tagmatization. They are extremely diverse and occur in all habitats capable of supporting life. Perhaps more than any other single factor, success of arthropods is explained by adaptations made possible by their cuticular exoskeleton. Other important elements in their success are jointed appendages, tracheal respiration, efficient sensory organs, complex behavior, metamorphosis, and the ability to fly.

Members of subphylum Chelicerata have no antennae, and their main feeding appendages are chelicerae. In addition, they have a pair of pedipalps (which may be similar to walking legs) and four pairs of walking legs. The great majority of living chelicerates are in class Arachnida: spiders (order Araneae), scorpions (order Scorpionida), harvestmen (order Opiliones), and ticks and mites (order Acarina).

Tagmata of spiders (cephalothorax and abdomen) show no external segmentation and join by a waistlike pedicel. Chelicerae of spiders have poison glands for paralyzing or killing their prey. Spiders can spin silk, which they use for a variety of purposes.

The cephalothorax and abdomen of ticks and mites are completely fused, and the anterior capitulum bears the mouthparts. Ticks and mites are the most numerous of any arachnids; some are important disease carriers, and others are serious plant pests.

Crustacea is a large, primarily aquatic subphylum of arthropods. Crustaceans bear two pairs of antennae, mandibles, and two pairs of maxillae on the head. Their appendages are primitively biramous, and major tagmata are head, thorax, and abdomen. Many have a carapace and respire by means of gills.

All arthropods must periodically cast off their cuticle (ecdysis) and grow larger before the newly secreted cuticle hardens. Premolt and postmolt periods are hormonally controlled, as are several other structures and functions.

There are many predators, scavengers, filter feeders, and parasites among Crustacea. Respiration is through the body surface or by gills, and excretory organs take the form of maxillary or antennal glands. Circulation, as in other arthropods, is through an open system of sinuses (hemocoel), and a dorsal, tubular heart is the chief pumping organ. Most crustaceans have compound eyes composed of units called ommatidia.

Members of class Maxillopoda, subclass Copepoda, lack a carapace and abdominal appendages. They are abundant and are among the most important of primary consumers in many freshwater and marine ecosystems. Malacostraca are the largest crustacean class, and the most important orders are Isopoda, Amphipoda, Euphausiacea, and Decapoda. All have both abdominal and thoracic appendages. Decapods include crabs, shrimp, lobster, crayfish, and others; they have five pairs of walking legs (including chelipeds) on their thorax.

Members of subphylum Uniramia have uniramous appendages and bear one pair of antennae, a pair of mandibles, and two pairs of maxillae (one pair of maxillae in millipedes) on the head. Tagmata are head and trunk in myriapods and head, thorax, and abdomen in insects.

Insecta is the largest class of the world's largest phylum. Insects are easily recognized by the combination of their tagmata and possession of three pairs of thoracic legs.

Radiation and abundance of insects are largely explained by several features allowing them to exploit terrestrial habitats, such as waterproof cuticle and other mechanisms to minimize water loss and the ability to become dormant during adverse conditions.

Feeding habits vary greatly among insects, and there is an enormous variety of specialization of mouthparts reflecting the particular feeding habits of a given insect. Insects breathe by means of a tracheal system, which is a system of tubes that opens by spiracles on the thorax and abdomen. Excretory organs are Malpighian tubules.

Sexes are separate in insects, and fertilization is usually internal. Almost all insects undergo metamorphosis during development. In hemimetabolous (gradual) metamorphosis, larval instars are called nymphs, and adults emerge at the last nymphal molt. In holometabolous (complete) metamorphosis, the last larval molt gives rise to a nonfeeding stage (pupa). A winged adult emerges at the final, pupal, molt. Both types of metamorphosis are hormonally controlled.

Insects are important to human welfare, particularly because they pollinate food crop plants, control populations of other, harmful insects by predation and parasitism, and serve as food for other animals. Many insects are harmful to human interests because they feed on crop plants, and many are carriers of important diseases affecting humans and domestic animals.

Until recently zoologists believed that Annelida and Arthropoda were closely related and were derived from a near common ancestor. Molecular evidence suggests that they were derived independently from a protostome ancestor and belong to separate superphyla (Lophotrochozoa and Ecdysozoa). If this hypothesis is supported by further studies, metamerism must have evolved independently in each superphylum.

Preponderance of morphological and molecular evidence supports monophyly of phylum Arthropoda. Traditional alliance of Crustacea and Uniramia (insects and myriapods) in a group called Mandibulata is supported by morphological evidence, but some molecular data suggest that myriapods are the sister group to a clade composed of crustaceans and insects. Endognathous insects have a number of primitive characters and show morphological similarities with myriapods. Wings, hemimetabolous metamorphosis, and holometabolous metamorphosis evolved among ectognathous insects.

Adaptive radiation of the arthropods has been enormous, and they are extremely abundant.

review questions

1. Give some characteristics of arthropods that clearly distinguish them from Annelida.
2. Name the subphyla of arthropods, and give a few examples of each.
3. Much of the success of arthropods has been attributed to their cuticle. Why do you think this is so? Describe some other factors that probably contributed to their success.
4. What is a trilobite?
5. What appendages are characteristic of chelicerates?
6. Briefly describe the appearance of each of the following: eurypterids, horseshoe crabs, pycnogonids.
7. Tell the mechanism of each of the following with respect to spiders: feeding, excretion, sensory reception, webspinning, reproduction.
8. Distinguish each of the following orders from each other: Araneae, Scorpionida, Opiliones, Acarina.
9. People fear spiders and scorpions, but ticks and mites are far more important medically and economically. Why? Give examples.
10. What are tagmata and appendages on the head of crustaceans? What are some other important characteristics of Crustacea?
11. Among classes of Crustacea, Branchiopoda, Maxillopoda, and Malacostraca are the most important. Distinguish them from each other.
12. Distinguish among subclasses Ostracoda, Copepoda, Branchiura, and Cirripedia of class Maxillopoda.
13. Copepods sometimes have been called "insects of the sea" because marine planktonic copepods probably are the most abundant animals in the world. What is their ecological importance?
14. Define each of the following: swimmeret, endopod, exopod, maxilliped, cheliped, uropod, nauplius.
15. Describe molting in Crustacea, including action of hormones.
16. Explain the mechanism of each of the following with respect to crustaceans: feeding, respiration, excretion, circulation, sensory reception, reproduction.
17. Distinguish the following from each other: Diplopoda, Chilopoda, Insecta.
18. Define each of the following with respect to insects: sclerite, notum, tergum, sternum, pleura, labrum, labium, hypopharynx, haltere, instar, diapause.
19. Explain why wings powered by indirect flight muscles can beat much more rapidly than those powered by direct flight muscles.
20. What different modes of feeding are found in insects, and how are these reflected in their mouthparts?
21. Describe each of the following with respect to insects: respiration, excretion and water balance, sensory reception, reproduction.
22. Explain the difference between holometabolous and hemimetabolous metamorphosis in insects, including stages in each.
23. Describe and give an example of each of four ways insects communicate with each other.
24. What are castes found in honey bees and in termites, and what is the function of each? What is trophallaxis?
25. Name several ways in which insects are beneficial to humans and several ways they are detrimental.
26. For the past 50 or more years, people have relied on toxic insecticides for control of harmful insects. What problems have arisen resulting from such reliance on insecticides? What are the alternatives? What is integrated pest management?
27. What is evidence that metamerism evolved independently in Annelida and Arthropoda?
28. We believe that the earliest insects were wingless, that is, lack of wings is the primitive condition, and this was observed in the traditional subclass Apterygota. We now consider the Apterygota paraphyletic. Why?

selected references

See also general references on page 406.

Berenbaum, M. R. 1995. Bugs in the system. Reading, Massachusetts, Addison-Wesley Publishing Company. *How insects impact human affairs. Well written for a wide audience, highly recommended.*

Brown, K. 2001. Seeds of concern. Sci. Am. **284:**52–57 (Apr.). *The first of four articles that examine the pros and cons of genetically modified crops, including those with genes for insecticidal toxin.*

Downs, A. M. R., K. A. Stafford, and G. C. Coles. 1999. Head lice: prevalence in schoolchildren and insecticide resistance. Parasitol. Today **15:**1–4. *This report is mainly concerned with England, but head lice are one of the most common parasites of American schoolchildren.*

Hubbell, S. 1997. Trouble with honeybees. Nat. Hist. **106:**32–43. *Parasitic mites (*Varroa jacobsoni *on bee larvae and* Acarapis woodi *in the trachea of adults) cause serious losses among honey bees.*

Lane, R. P., and R. W. Crosskey (eds). 1993. Medical insects and arachnids. London, Chapman & Hall. *This is the best book currently available on medical entomology.*

Luoma, J. R. 2001. The removable feast. Audubon **103(3):**48–54. *During May and June large numbers of horseshoe crabs ascend the shores of U.S. Atlantic states to breed and lay eggs. Since the 1980s they have been heavily harvested to be chopped up and used for bait. This practice has led to serious declines in* Limulus *populations, with accompanying declines in populations of migrating shore birds that feed on* Limulus *eggs.*

O'Brochta, D. A., and P. W. Atkinson. 1998. Building the better bug. Sci. Am. **279:**90–95 (Dec.). *Inserting new genes* *into certain insect species could render them incapable of being vectors for disease, help agriculture, and have other applications.*

O'Neill, S. L., A. A. Hoffmann, and J. H. Werren. 1997. Influential passengers. Oxford, Oxford University Press. *Symbiotic bacteria* Wolbachia *can determine reproduction and evolution of their insect, crustacean, or nematode hosts.*

Ostfeld, R. S. 1997. The ecology of Lyme-disease risk. Amer. Sci **85:**338–346. *Lyme disease, caused by a bacterium transmitted by ticks, has been reported in 48 of the 50 United States and seems to be increasing in frequency and geographic range.*

Romoser, W. S., and J. G. Stoffolano, Jr. 1997. The science of entomology. Dubuque, Iowa, McGraw-Hill. *A comprehensive general entomology text with keys to insects.*

Suter, R. B. 1999. Walking on water. Amer. Sci. **87:**154–159. *Fishing spiders* (Dolomedes) *depend on surface tension to walk on water.*

Versluis, M., B. Schmitz, A. von der Heydt, and D. Lohse. 2000. How snapping shrimp snap: through cavitating bubbles. Science **289:**2114–2117. *When* Alpheus *snaps the claw on its chela shut, it generates a jet of water with a velocity so high that the pressure decreases below the vapor pressure of water, producing a cavitation bubble. As the water pressure rises again, the bubble collapses with a force sufficient to stun or kill prey.*

custom website

Visit this textbook's Custom Website at www.mhhe.com/zoology (click on this book's cover) to access these interactive study tools, and more:

Key Terms Flashcards

All of the key terms in this chapter are available as study flashcards, for your review of important terms.

Links to the Internet

Explore live links for these topics:

Classification and Phylogeny of Animals
Phylum Arthropoda
Subphylum Chelicerata
Subphylum Crustacea
Subphylum Uniramia
Minor Classes of Uniramids
Class Insecta

Self-Test

Take the online quiz for this chapter to test your knowledge.