CHAPTER 15

THE HEXAPODS AND MYRIAPODS:

TERRESTRIAL TRIUMPHS

Outline

Concepts

1. Flight, along with other arthropod characteristics, has resulted in insects becoming the most abundant and diverse group of terrestrial animals.
2. The members of the subphylum Myriapoda are in the classes Diplopoda, Chilopoda, Pauropoda, and Symphyla.
3. Members of the subphylum Hexapoda are characterized by three pairs of legs and three tagmata. They are divided into two classes, Entognatha and Insecta.
4. Adaptations for living on land are reflected in many aspects of insect structure and function.
5. Insects have important effects on human health and welfare.
6. Arthropoda is a monophyletic grouping; arthropods are among the oldest of all animals; and ancient crustaceans provided the ancestral stock for all modern arthropods.

EVOLUTIONARY PERSPECTIVE

By almost any criterion, the insects have been enormously successful. Zoologists have described approximately 750,000 species, and some estimate that the number of insect species may be as high as 30 million! Most of the undescribed species are in tropical rain forests. Since just the described insect species comprise 75% of all living species, the total number of described and undescribed insect species dwarfs all other kinds of living organisms. Although freshwater and parasitic insect species are numerous, the success of insects has largely been due to their ability to exploit terrestrial habitats (figure 15.1).

During the late Silurian and early Devonian periods (about 400 million years ago), terrestrial environments were largely uninhabited by animals. Low-growing herbaceous plants and the first forests were beginning to flourish, and enough ozone had accumulated in the upper atmosphere to filter ultraviolet radiation from the sun. Animals with adaptations that permitted life on land had a wealth of photosynthetic production available, and unlike in marine habitats, faced little competition from other animals for resources. However, the problems associated with terrestrial life were substantial. Support and movement outside of a watery environment were difficult on land, as were water, ion (electrolyte), and temperature regulation.

A number of factors contributed to insect dominance of terrestrial habitats. *The exoskeleton preadapted the insects for life on land. Not only is the exoskeleton supportive, but the evolution of a waxy epicuticle enhanced the exoskeleton's water-conserving properties. The evolution of flight also played a big role in insect success.*

This chapter contains evolutionary concepts, which are set off in this font.

FIGURE 15.1

Class Insecta. Insects were early inhabitants of terrestrial environments. The exoskeleton and the evolution of flight have contributed to the enormous success of this group of arthropods.

The ability to fly allowed insects to use widely scattered food resources, to invade new habitats, and to escape unfavorable environments. These factors—along with desiccation-resistant eggs, metamorphosis, high reproductive potential, and diversification of mouthparts and feeding habits—permitted insects to become the dominant class of organisms on the earth.

This chapter covers two arthropod subphyla: Myriapoda and Hexapoda (table 15.1). The Myriapoda include the familiar millipedes and centipedes as well as two other less-familiar groups. The Hexapoda include the insects and their relatives. The myriapods and hexapods have been traditionally considered to be closely related based on similar excretory and respiratory structures and uniramous legs. Recent research is causing zoologists to rethink their perceptions of arthropod phylogeny, and this is affecting our view of the relationships between the two subphyla covered in this chapter. Phylogenetic implications of this research are discussed at the end of this chapter.

SUBPHYLUM MYRIAPODA

The subphylum Myriapoda (mir″e-a-pod′ah) (Gr. *myriad,* ten thousand + *podus,* foot) is divided into four classes: Diplopoda (millipedes), Chilopoda (centipedes), Symphyla (symphylans), and Pauropoda (pauropodans) (*see table 15.1*). They are characterized by a body consisting of two tagmata (head and trunk) and uniramous appendages. All modern myriapods are terrestrial.

CLASS DIPLOPODA

The class Diplopoda (dip′lah-pod′ah) (Gr. *diploos,* twofold + *podus,* foot) contains the millipedes. Ancestors of this group appeared on land during the Devonian period and were among the first terrestrial animals. Millipedes have 11 to 100 trunk segments derived from an embryological and evolutionary fusion of primitive metameres. An obvious result of this fusion is the occurrence of two pairs of appendages on each apparent trunk segment. Each segment is actually the fusion of two segments. Fusion is also reflected internally by two ganglia, two pairs of ostia, and two pairs of tracheal trunks per apparent segment. Most millipedes are round in cross section, although some are more flattened (figure 15.2*a*).

Millipedes are worldwide in distribution and are nearly always found in or under leaf litter, humus, or decaying logs. Their epicuticle does not contain much wax; therefore, their choice of habitat is important to prevent desiccation. Their many legs, simultaneously pushing against the substrate, help millipedes bulldoze through the habitat. Millipedes feed on decaying plant matter using their mandibles in a chewing or scraping fashion. A few millipedes have mouthparts modified for sucking plant juices.

(a)

(b)

FIGURE 15.2

Myriapods. (*a*) A woodland millipede (*Ophyiulus pilosus*). (*b*) A centipede (*Scolopendra heros*).

TABLE 15.1
CLASSIFICATION OF THE SUBPHYLA MYRIAPODA AND HEXAPODA*

Phylum Arthropoda (ar″thra-po′dah)
Animals with metamerism and tagmatization, a jointed exoskeleton, and a ventral nervous system.

Subphylum Myriapoda (mir″e-a-pod′ah) (Gr. *myriad*, ten thousand + *podus*, foot)
Body divided into head and trunk; four pairs of head appendages; uniramous appendages. Millipedes and centipedes.

Class Diplopoda (dip″lah-pod′ah)
Two pairs of legs per apparent segment; body usually round in cross section. Millipedes.

Class Chilopoda (ki″lah-pod′ah)
One pair of legs per segment; body oval in cross section; poison claws. Centipedes.

Class Pauropoda (por″o-pod′ah)
Small (0.5 to 2 mm), soft-bodied animals; 11 segments; nine pairs of legs; live in leaf mold. Pauropods.

Class Symphyla (sim-fi′lah)
Small (2 to 10 mm); long antennae; centipede-like; 10 to 12 pairs of legs; live in soil and leaf mold. Symphylans.

Subphylum Hexapoda (hex″sah-pod′ah) (Gr. *hexa*, six + *podus*, foot)
Body divided into head, thorax, and abdomen; five pairs of head appendages; three pairs of uniramous appendages on the thorax. Insects and their relatives.

Class Entognatha (en″to-na′tha) (Gr. *entos*, within + *gnathos*, jaw)
Mouth appendages hidden within the head; mandibles with single articulation; legs with one undivided tarsus.

Order Collembola (col-lem′bo-lah)
Antennae with four to six segments; compound eyes absent; abdomen with six segments, most with springing appendage on fourth segment; inhabit soil and leaf litter. Springtails.

Order Protura (pro-tu′rah)
Minute, with cone-shaped head; antennae, compound eyes, and ocelli absent; abdominal appendages on first three segments; inhabit soil and leaf litter. Proturans.

Order Diplura (dip-lu′rah)
Head with many segmented antennae; compound eyes and ocelli absent; cerci multisegmented or forcepslike; inhabit soil and leaf litter. Diplurans.

Class Insecta (in-sekt′ah) (L. *insectum*, to cut up)
Mouth appendages exposed and projecting from head; mandibles usually with two points of articulation; well developed Malpighian tubules.

Subclass Archaeognatha (ar″ke-ona′tha)

Order Archaeognatha
Small, wingless, cylindrical and scaly body; mandibles with single articulation; abdomen 11 segmented with 3 to 8 pairs of styli and 3 caudal filaments; ametabolous metamorphosis. Jumping bristletails.

Subclass Zygentoma (xi-gen″to-mah)

Order Thysanura (thi-sa-nu′rah)
Tapering abdomen; flattened; scales on body; terminal cerci; long antennae; ametabolous metamorphosis. Silverfish.

Subclass Pterogota (ter-i-go′tah)
Wings on second and third thoracic segments; wings may be modified or lost; no pregenital abdominal appendages; direct sperm transfer.

Infraclass Palaeoptera (pa′le-op″ter-ah)
Wings incapable of being folded at rest, held vertically above the body or horizontally out from the body; wings with many veins and cross-veins; antennae reduced or vestigial in adults.

Order Ephemeroptera (e-fem-er-op′ter-ah)
Elongate abdomen with two or three tail filaments; two pairs of membranous wings with many veins; forewings triangular; short, bristlelike antennae; hemimetabolous metamorphosis. Mayflies.

Order Odonata (o-do-nat′ah)
Elongate, membranous wings with netlike venation; abdomen long and slender; compound eyes occupy most of head; hemimetabolous metamorphosis. Dragonflies, damselflies.

*Selected orders of insects are described.

Infraclass Neoptera (ne-op′ter-ah)
Wings folded at rest; venation reduced.

Order Plecoptera (ple-kop′ter-ah)
Adults with reduced mouthparts; elongate antennae; long cerci; nymphs aquatic with gills; hemimetabolous metamorphosis. Stoneflies.

Order Mantodea (man-to′deah)
Prothorax long; prothoracic legs long and armed with strong spines for grasping prey; predators; hemimetabolous metamorphosis. Mantids.

Order Blattaria (blat-tar′eah)
Body oval and flattened; head concealed from above by a shieldlike extension of the prothorax; hemimetabolous metamorphosis. Cockroaches.

Order Isoptera (i-sop′ter-ah)
Workers white and wingless; front and hindwings of reproductives of equal size; reproductives and some soldiers may be sclerotized; abdomen broadly joins thorax; social; hemimetabolous metamorphosis. Termites.

Order Dermaptera (der-map′ter-ah)
Elongate; chewing mouthparts; threadlike antennae; abdomen with unsegmented forcepslike cerci; hemimetabolous metamorphosis. Earwigs.

Order Orthoptera (or-thop′ter-ah)
Forewing long, narrow, and leathery; hindwing broad and membranous; chewing mouthparts; hemimetabolous metamorphosis. Grasshoppers, crickets, katydids.

Order Phasmida (fas′mi-dah)
Body elongate and sticklike; wings reduced or absent; some tropical forms are flattened and leaflike; hemimetabolous metamorphosis. Walking sticks, leaf insects.

Order Phthiraptera (fthi-rap′ter-ah)
Small, wingless ectoparasites of birds and mammals; body dorsoventrally flattened; white; hemimetabolous metamorphosis. Sucking and chewing lice.

Order Hemiptera (hem-ip′ter-ah)
Piercing-sucking mouthparts; mandibles and first maxillae styletlike and lying in grooved labium; wings membranous; hemimetabolous metamorphosis. Bugs, cicadas, leafhoppers, aphids.

Order Thysanoptera (thi-sa-nop′ter-ah)
Small bodied; sucking mouthparts; wings narrow and fringed with long setae; plant pests; hemimetabolous metamorphosis. Thrips.

Order Neuroptera (neu-rop′ter-ah)
Wings membranous; hindwings held rooflike over body at rest; holometabolous metamorphosis. Lacewings, snakeflies, antlions, dobsonflies.

Order Coleoptera (ko-le-op′ter-ah)
Forewings sclerotized, forming covers (elytra) over the abdomen; hindwings membranous; chewing mouthparts; the largest insect order; holometabolous metamorphosis. Beetles.

Order Trichoptera (tri-kop′ter-ah)
Mothlike with setae-covered antennae; chewing mouthparts; wings covered with setae and held rooflike over abdomen at rest; larvae aquatic and often dwell in cases that they construct; holometabolous metamorphosis. Caddis flies.

Order Lepidoptera (lep-i-dop′ter-ah)
Wings broad and covered with scales; mouthparts formed into a sucking tube; holometabolous metamorphosis. Moths, butterflies.

Order Diptera (dip′ter-ah)
Mesothoracic wings well developed; metathoracic wings reduced to knoblike halteres; variously modified but never chewing mouthparts; holometabolous metamorphosis. Flies.

Order Siphonaptera (si-fon-ap′ter-ah)
Laterally flattened, sucking mouthparts; jumping legs; parasites of birds and mammals; holometabolous metamorphosis. Fleas.

Order Hymenoptera (hi-men-op′ter-ah)
Wings membranous with few veins; well-developed ovipositor, sometimes modified into a sting; mouthparts modified for biting and lapping; social and solitary species; holometabolous metamorphosis. Ants, bees, wasps.

Millipedes roll into a ball when faced with desiccation or when disturbed. Many also possess repugnatorial glands that produce hydrogen cyanide, which repels other animals. Hydrogen cyanide is not synthesized and stored as hydrogen cyanide because it is caustic and would destroy millipede tissues. Instead, a precursor compound and an enzyme mix as they are released from separate glandular compartments. Repellants increase the likelihood that the millipede will be dropped unharmed and decrease the chances that the same predator will try to feed on another millipede.

Male millipedes transfer sperm to female millipedes with modified trunk appendages, called gonopods, or in spermatophores. Eggs are fertilized as they are laid and hatch in several weeks. Immatures acquire more legs and segments with each molt until they reach adulthood.

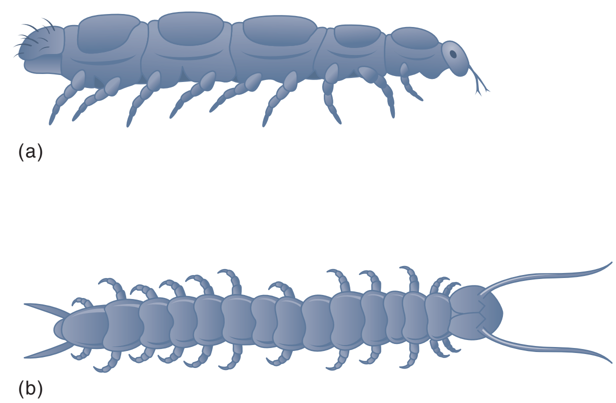


FIGURE 15.3

Subphylum Myriapoda. (*a*) A member of the class Pauropoda (*Pauropus*). (*b*) A member of the class Symphyla (*Scutigerella*).

CLASS CHILOPODA

Members of the class Chilopoda (ki″lah-pod′ah) (Gr. *cheilos*, lip + *podus*, foot) are the centipedes. Most centipedes are nocturnal and scurry about the surfaces of logs, rocks, or other forest-floor debris. Like millipedes, most centipedes lack a waxy epicuticle and therefore require moist habitats. Their bodies are flattened in cross section, and they have a single pair of long legs on each of their 15 or more trunk segments. The last pair of legs is usually modified into long sensory appendages.

Centipedes are fast-moving predators (figure 15.2*b*). Food usually consists of small arthropods, earthworms, and snails; however, some centipedes feed on frogs and rodents. Poison claws (modified first-trunk appendages called maxillipeds) kill or immobilize prey. Maxillipeds, along with mouth appendages, hold the prey as mandibles chew and ingest the food. Most centipede venom is essentially harmless to humans, although many centipedes have bites that are comparable to wasp stings; a few human deaths have been reported from large, tropical species.

Centipede reproduction may involve courtship displays in which the male lays down a silk web using glands at the posterior tip of the body. He places a spermatophore in the web, which the female picks up and introduces into her genital opening. Eggs are fertilized as they are laid. A female may brood and guard eggs by wrapping her body around the eggs, or they may be deposited in the soil. Young are similar to adults except that they have fewer legs and segments. Legs and segments are added with each molt.

CLASSES PAUROPODA AND SYMPHYLA

Members of the class Pauropoda (por″o-pod′ah) (Gr. *pauros*, small + *podus*, foot) are soft-bodied animals with 11 segments (figure 15.3*a*). These animals live in forest-floor litter, where they feed on fungi, humus, and other decaying organic matter. Their very small size and thin, moist exoskeleton allow gas exchange across the body surface and diffusion of nutrients and wastes in the body cavity.

Members of the class Symphyla (sim-fi′lah) (Gr. *sym*, same + *phyllos*, leaf) are small arthropods (2 to 10 mm in length) that occupy soil and leaf mold, superficially resemble centipedes, and are often called garden centipedes (figure 15.3*b*). They lack eyes and have 12 leg-bearing trunk segments. The posterior segment may have one pair of spinnerets or long, sensory bristles. Symphylans normally feed on decaying vegetation; however, some species are pests of vegetables and flowers.

SUBPHYLUM HEXAPODA

The subphylum Hexapoda (hex″sah-pod′ah) (Gr. *hexa*, six + *podus*, foot) includes animals whose bodies are divided into three tagmata, have five pairs of head appendages, and three pairs of legs on the thorax. The subphylum is divided into two classes. Entognatha (en″to-na′tha) (Gr. *entos*, within + *gnathos*, jaw) includes the collembolans, proturans, and diplurans (*see table 15.1*). Members of this class have mouthparts that are hidden inside the head capsule, thus the class name. It is probably not a monophyletic grouping because the entognathous mouthparts of the diplurans are apparently not homologous to the mouthparts of the other two orders. Insecta (L. *insectum*, to cut up) includes the 30 orders of insects. Table 15.1 provides a partial listing of these orders. They are all characterized by mouthparts that project from the head capsule. A new insect order, Mantophasmatodea, is the first new insect order to be described since 1914.

CLASS INSECTA

Members of the class Insecta are, in terms of numbers of species and individuals, the most successful land animals. In spite of obvious diversity, common features make insects easy to recognize. Many insects have wings and one pair of antennae, and virtually all adults have three pairs of legs.

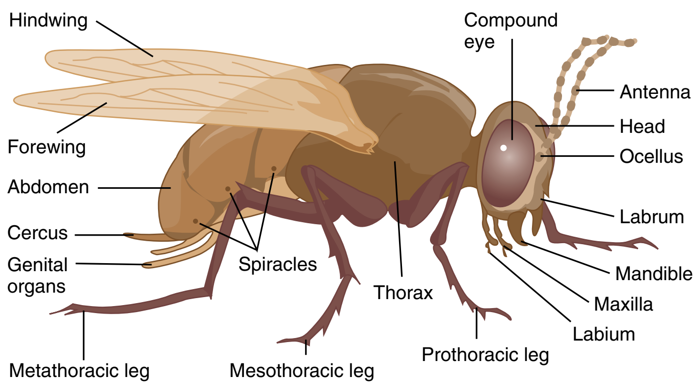


FIGURE 15.4

External Structure of a Generalized Insect. Insects are characterized by a body divided into head, thorax, and abdomen; three pairs of legs; and two pairs of wings.

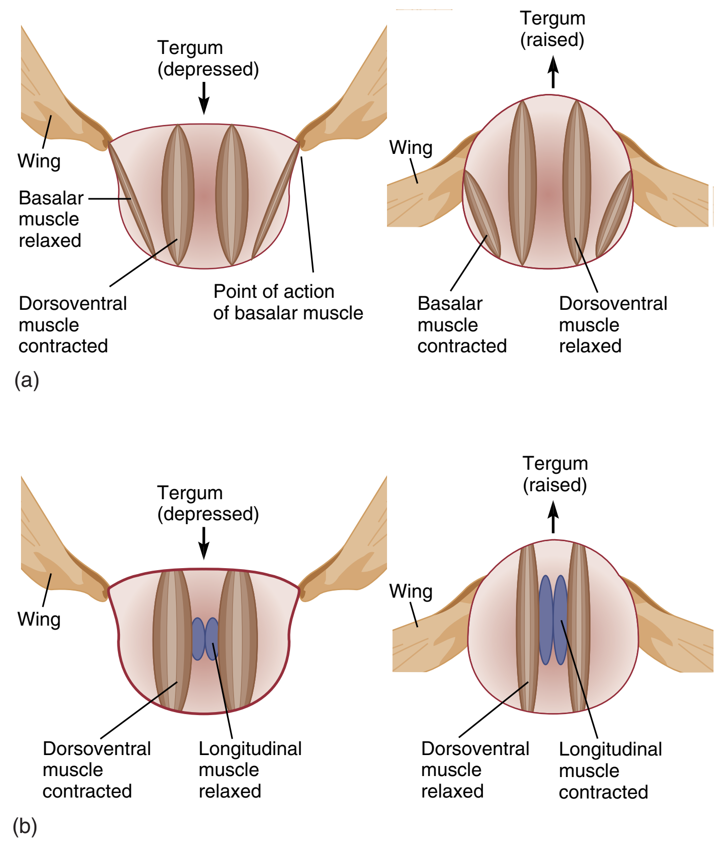


FIGURE 15.5

Insect Flight. (*a*) Muscle arrangements for the direct or synchronous flight mechanism. Note that muscles responsible for the downstroke attach at the base of the wings. (*b*) Muscle arrangements for the indirect or asynchronous flight mechanism. Muscles changing the shape of the thorax cause wings to move up and down.

External Structure and Locomotion

The body of an insect is divided into three tagmata: head, thorax, and **abdomen** (figure 15.4). The head bears a single pair of antennae, mouthparts, compound eyes, and zero, two, or three ocelli. The thorax consists of three segments. They are, from anterior to posterior, the **prothorax,** the **mesothorax,** and the **metathorax.** One pair of legs attaches along the ventral margin of each thoracic segment, and a pair of wings, when present, attaches at the dorsolateral margin of the mesothorax and metathorax. Wings have thickened, hollow veins for increased strength. The thorax also contains two pairs of spiracles, which are openings to the tracheal system. Most insects have 10 or 11 abdominal segments, each of which has a lateral fold in the exoskeleton that allows the abdomen to expand when the insect has gorged itself or when it is full of mature eggs. Each abdominal segment has a pair of spiracles. Also present are genital structures used during copulation and egg deposition, and sensory structures called cerci. Gills are present on abdominal segments of certain immature aquatic insects.

Insect Flight Insects move in diverse ways. *From an evolutionary perspective, however, flight is the most important form of insect locomotion. Insects were the first animals to fly.* One of the most popular hypotheses on the origin of flight states that wings may have evolved from rigid, lateral outgrowths of the thorax that probably protected the legs or spiracles. Later, these fixed lobes could have been used in gliding from the tops of tall plants to the forest floor. The ability of the wing to flap, tilt, and fold back over the body probably came later.

Another requirement for flight was the evolution of limited thermoregulatory abilities. Thermoregulation is the ability to maintain body temperatures at a level different from environmental temperatures. Relatively high body temperatures, perhaps 25° C or greater, are needed for flight muscles to contract rapidly enough for flight.

Some insects use a **direct** or **synchronous flight** mechanism, in which muscles acting on the bases of the wings contract to produce a downward thrust, and muscles attaching dorsally and ventrally on the exoskeleton contract to produce an upward thrust (figure 15.5*a*). The synchrony of direct flight mechanisms depends on the nerve impulse to the flight muscles that must precede each wingbeat. Butterflies, dragonflies, and grasshoppers are examples of insects with a synchronous flight mechanism.

Other insects use an **indirect** or **asynchronous flight** mechanism. Muscles act to change the shape of the exoskeleton for both upward and downward wing strokes. Dorsoventral muscles pulling the dorsal exoskeleton (tergum) downward produce the upward wing thrust. The downward thrust occurs when longitudinal muscles contract and cause the exoskeleton to arch upward (figure 15.5*b*). The resilient properties of the exoskeleton enhance the power and velocity of these strokes. During a wingbeat, the thorax is deformed, storing energy in the exoskeleton. At a critical point midway into the downstroke, stored energy reaches a maximum, and at the same time, resistance to wing movement suddenly decreases. The wing then "clicks" through the rest of the cycle, using energy stored in the exoskeleton. Asynchrony of this flight mechanism arises from the lack of one-to-one correspondence between nerve impulses and wingbeats. A single nerve impulse can result in approximately 50 cycles of the wing, and frequencies of 1,000 cycles per second (cps) have been recorded in some midges! The asynchrony between wingbeat and nerve impulses is dependent on flight muscles being stretched during the "click" of the thorax. The stretching of longitudinal flight muscles during the upward beat of the wing initiates the subsequent contraction of these muscles. Similarly, stretching during the downward beat of the wing initiates subsequent contraction of dorsoventral flight muscles. Indirect flight muscles are frequently called **fibrillar flight muscles.** Flies and wasps are examples of insects with an asynchronous flight mechanism.

Simple flapping of wings is not enough for flight. The tilt of the wing must be controlled to provide lift and horizontal propulsion. In most insects, muscles that control wing tilting attach to sclerotized plates at the base of the wing.

Other Forms of Locomotion Insects walk, run, jump, or swim across the ground or other substrates. When they walk, insects have three or more legs on the ground at all times, creating a very stable stance. When they run, fewer than three legs may be in contact with the ground. A fleeing cockroach (order Blattaria) reaches speeds of about 5 km/hour, although it seems much faster when trying to catch one. The apparent speed is the result of their small size and ability to quickly change directions. Jumping insects, such as grasshoppers (order Orthoptera), usually have long, metathoracic legs in which leg musculature is enlarged to generate large, propulsive forces. Energy for a flea's (order Siphonaptera) jump is stored as elastic energy of the exoskeleton. Muscles that flex the legs distort the exoskeleton. A catch mechanism holds the legs in this "cocked" position until special muscles release the catches and allow the stored energy to quickly extend the legs. This action hurls the flea for distances that exceed 100 times its body length. A comparable distance for a human long jumper would be the length of two football fields!

Nutrition and the Digestive System

The diversity of insect feeding habits parallels the diversity of insects themselves. There are many variations on mouthparts of insects, but the mouthparts are based on a common arrangement of structures shown in figure 15.6, which shows the biting-chewing mouthparts of a grasshopper. An upper liplike structure is called the labrum. It is sensory, and unlike the remaining mouthparts, is not derived from segmental, paired appendages. Mandibles are sclerotized chewing mouthparts. They usually bear teeth for grinding and cutting and have a side-to-side movement. The maxillae have cutting surfaces and palps that are sensory and food-holding structures. The **labium** is a sensory lower lip and its palps are also used in food holding. A hypopharynx is a tonguelike sensory structure. The efficiency of these biting-chewing mouthparts is obvious in watching a caterpillar feeding on a leaf or considering a termite feeding on wooden structures.

The structure of mouthparts is modified in insects that suck liquid food, although the basic arrangement of mouthparts is

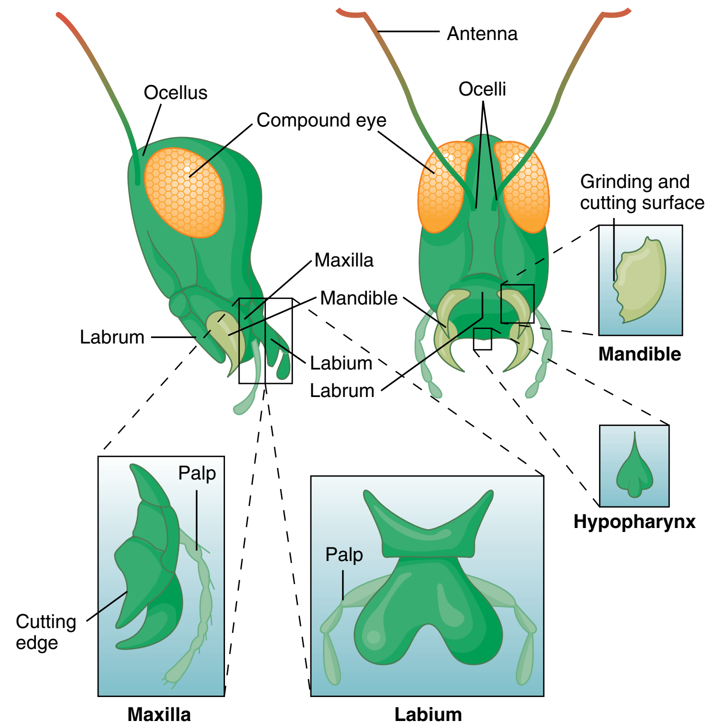


FIGURE 15.6

Head and Mouthparts of a Grasshopper. All mouthparts except the labrum are derived from segmental appendages. The labrum is a sensory upper lip. The mandibles are heavily sclerotized and used for tearing and chewing. The maxillae have cutting edges and a sensory palp. The labium forms a sensory lower lip. The hypopharynx is a sensory, tonguelike structure.

retained. There are many variations in sucking mouthparts. In mosquitoes, six stylets are formed from the labrum, hypopharynx, mandibles, and maxillae and are used to pierce flesh and suck blood. In the butterflies and moths, the maxillae form a long, coiled tube that is used to suck nectar from flowers (figure 15.7).

The housefly has sponging mouthparts. The labium is expanded into a labellum. Saliva is secreted from the mouth, and minute channels on the labellum provide pathways for liquefied food to move the mouth through capillary action.

The digestive tract, as in all arthropods, is long and straight and consists of three regions: a foregut, a midgut, and a hindgut (figure 15.8). The foregut is often modified into a muscular pharynx. In sucking insects, the pharynx (or in some, the oral cavity) is used for sucking fluids into the digestive tract. Behind the pharynx is a crop that is used in storage. A proventriculus or gizzard regulates movement to the midgut and may function in grinding food. The midgut provides the surfaces for digestion and absorption, and gastric cecae increase the surface area for these functions. The hindgut or intestine is primarily involved with the reabsorption of water.

Gas Exchange

Gas exchange with air requires a large surface area for the diffusion of gases. In terrestrial environments, these surfaces are also

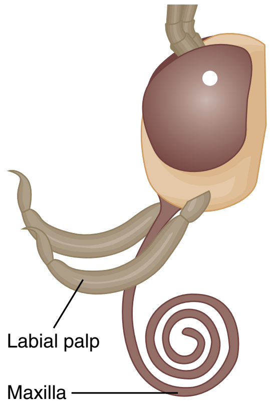


FIGURE 15.7

Specialization of Insect Mouthparts. The mouthparts of insects are often highly specialized for specific feeding habits. For example, the sucking mouthparts of a butterfly consist of modified maxillae that coil when not in use. Mandibles, labia, and the labrum are reduced in size. A portion of the anterior digestive tract is modified as a muscular pump for drawing liquids through the mouthparts.

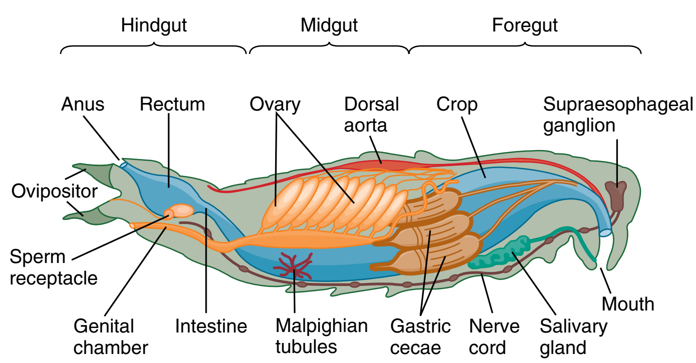


FIGURE 15.8

Internal Structure of a Generalized Insect. Salivary glands produce enzymes but may be modified for the secretion of silk, anticoagulants, or pheromones. The crop is an enlargement of the foregut and stores food. The proventriculus is a grinding and/or straining structure at the junction of the midgut and hindgut. Gastric cecae secrete digestive enzymes. The intestine and the rectum are modifications of the hindgut that absorb water and the products of digestion.

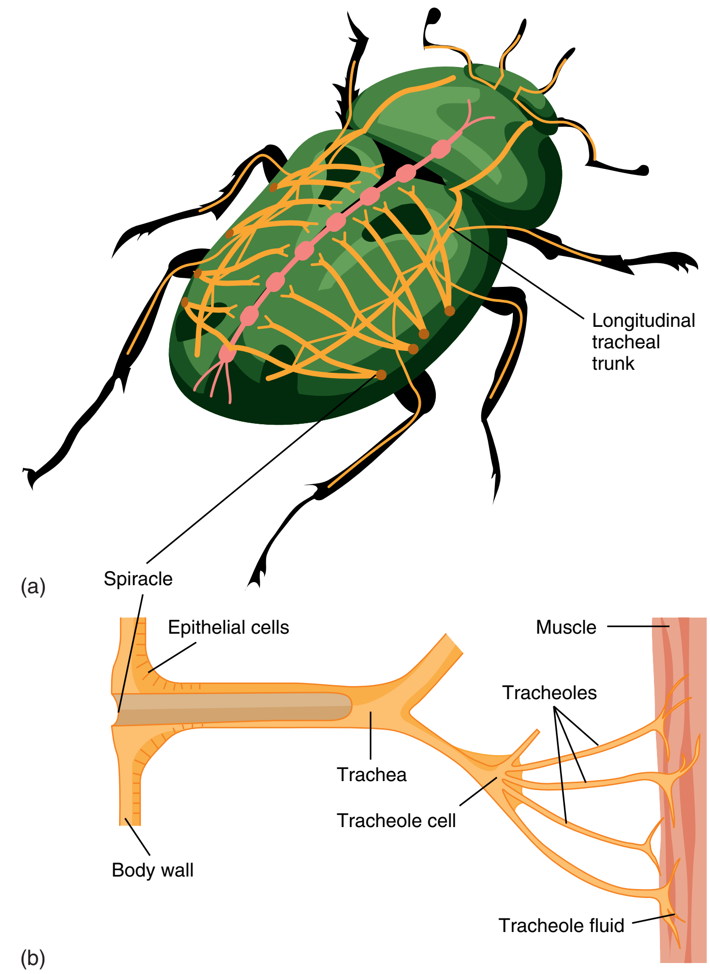


FIGURE 15.9

Tracheal System of an Insect. (*a*) Major tracheal trunks. (*b*) Tracheoles end in cells, and the terminal portions of tracheoles are fluid filled.

avenues for water loss. Respiratory water loss in insects, as in some arachnids, is reduced through the invagination of respiratory surfaces to form highly branched systems of chitin-lined tubes, called tracheae.

Tracheae open to the outside of the body through spiracles, which usually have some kind of closure device to prevent excessive water loss. Spiracles lead to tracheal trunks that branch, eventually giving rise to smaller branches, the tracheoles. Taenidia are rings or spiral thickenings of tracheal trunks that keep tracheae from collapsing and allow lengthwise expansion with body movements. Tracheoles end intracellularly and are especially abundant in metabolically active tissues, such as flight muscles. No cells are more than 2 or 3 μm from a tracheole (figure 15.9).

Most insects have ventilating mechanisms that move air into and out of the tracheal system. For example, contracting flight muscles alternately compress and expand the larger tracheal trunks and thereby ventilate the tracheae. In some insects, carbon dioxide that metabolically active cells produce is sequestered in the hemocoel as bicarbonate ions (HCO_3^-). As oxygen diffuses from the tracheae to the body tissues, and is not replaced by carbon dioxide, a vacuum is created that draws more air into the spiracles. This process is called passive suction. Periodically, the sequestered bicarbonate ions are converted back into carbon dioxide, which escapes through the tracheal system. Other insects contract abdominal muscles in a pumplike fashion to move air into and out of their tracheal systems.

In many aquatic insects, spiracles are nonfunctional and gases diffuse across the body wall. In others (some aquatic beetles and hemipterans), a bubble of air covers the spiracles and is carried underwater with the insect, which may periodically surface to refresh the air. Alternatively, gases may diffuse into and out of the bubble directly from the water. Some aquatic insects (immature mayflies and some immature stoneflies) have tracheal gills. Gases diffuse across the gill surface into branches of the tracheal system that extend into the gills.

Circulation and Temperature Regulation

The circulatory system of insects is similar to that described for other arthropods, although the blood vessels are less well developed. Blood distributes nutrients, hormones, and wastes, and amoeboid blood cells participate in body defense and repair mechanisms. Blood is not important in gas transport.

As described earlier, thermoregulation is a requirement for flying insects. Virtually all insects warm themselves by basking in the sun or resting on warm surfaces. Because they use external heat sources in temperature regulation, insects are generally considered ectotherms. Other insects (e.g., some moths, alpine bumblebees, and beetles) can generate heat by rapid contraction of flight muscles, a process called shivering thermogenesis. Metabolic heat generated in this way can raise the temperature of thoracic muscles from near 0 to 30° C. Because some insects rely to a limited extent on metabolic heat sources, they have a variable body temperature and are sometimes called heterotherms. Insects can also cool themselves by seeking cool, moist habitats. Honeybees can cool a hive by beating their wings at the entrance of the hive, thus circulating cooler outside air through the hive.

Nervous and Sensory Functions

The nervous system of insects is similar to the pattern described for annelids and other arthropods (*see figure 15.8*). The supraesophageal ganglion is associated with sensory structures of the head. Connectives join the supraesophageal ganglion to the subesophageal ganglion, which innervates the mouthparts and salivary glands and has a general excitatory influence on other body parts. Segmental ganglia of the thorax and abdomen fuse to various degrees in different taxa. Insects also possess a well-developed visceral nervous system that innervates the gut, reproductive organs, and heart.

Research has demonstrated that insects are capable of some learning and have a memory. For example, bees (order Hymenoptera) instinctively recognize flowerlike objects by their shape and ability to absorb ultraviolet light, which makes the center of the flower appear dark. If a bee is rewarded with nectar and pollen, it learns the odor of the flower. Bees that feed once at artificially scented feeders choose that odor in 90% of subsequent feeding trials. Odor is a very reliable cue for bees because it is more constant than color and shape. Wind, rain, and herbivores may damage the latter.

Sense organs of insects are similar to those found in other arthropods, although they are usually specialized for functioning on land. Mechanoreceptors perceive physical displacement of the body or of body parts. Setae are distributed over the mouthparts, antennae, and legs (*see figure 14.10*a). Touch, air movements, and vibrations of the substrate can displace setae. Stretch receptors at the joints, on other parts of the cuticle, and on muscles monitor posture and position.

Hearing is a mechanoreceptive sense in which airborne pressure waves displace certain receptors. All insects can respond to pressure waves with generally distributed setae; others have specialized receptors. For example, **Johnston's organs** are in the base of the antennae of most insects, including mosquitoes and midges (order Diptera). Long setae that vibrate when certain frequencies of sound strike them cover the antennae of these insects. Vibrating setae move the antenna in its socket, stimulating sensory cells. Sound waves in the frequency range of 500 to 550 cycles per second (cps) attract and elicit mating behavior in the male mosquito *Aedes aegypti*. These waves are in the range of sounds that the wings of females produce. **Tympanal (tympanic) organs** are in the legs of crickets and katydids (order Orthoptera), in the abdomen of grasshoppers (order Orthoptera) and some moths (order Lepidoptera), and in the thorax of other moths. Tympanal organs consist of a thin, cuticular membrane covering a large air sac. The air sac acts as a resonating chamber. Just under the membrane are sensory cells that detect pressure waves. Grasshopper tympanal organs can detect sounds in the range of 1,000 to 50,000 cps. (The human ear can detect sounds between 20 and 20,000 cps.) Bilateral placement of tympanal organs allows insects to discriminate the direction and origin of a sound.

Insects use chemoreception in feeding, selection of egg-laying sites, mate location, and sometimes, social organization. Chemoreceptors are usually abundant on the mouthparts, antennae, legs, and ovipositors, and take the form of hairs, pegs, pits, and plates that have one or more pores leading to internal nerve endings. Chemicals diffuse through these pores and bind to and excite nerve endings.

All insects are capable of detecting light and may use light in orientation, navigation, feeding, or other functions. **Compound eyes** are well developed in most adult insects. They are similar in structure and function to those of other arthropods, and recent evidence points to their homology (common ancestry) with those of crustaceans. Compound eyes consist of a few to 28,000 receptors, called **ommatidia,** that fuse into a multifaceted eye. The outer surface of each ommatidium is a lens and is one facet of the eye. Below the lens is a crystalline cone. The lens and the crystalline cone are light-gathering structures. Certain cells of an ommatidium, called retinula cells, have a special light-collecting area, called the rhabdom. The rhabdom converts light energy into nerve impulses. Pigment cells surround the crystalline cone, and sometimes the rhabdom, and prevent the light that strikes one rhabdom from reflecting into an adjacent ommatidium (figure 15.10).

Although many insects form an image of sorts, the concept of an image has no real significance for most species. The compound eye is better suited for detecting movement. Movement of a point of light less than 0.1° can be detected as light successively strikes adjacent ommatidia. For this reason, bees are attracted to flowers blowing in the wind, and predatory insects select moving prey. Compound eyes detect wavelengths of light that the human

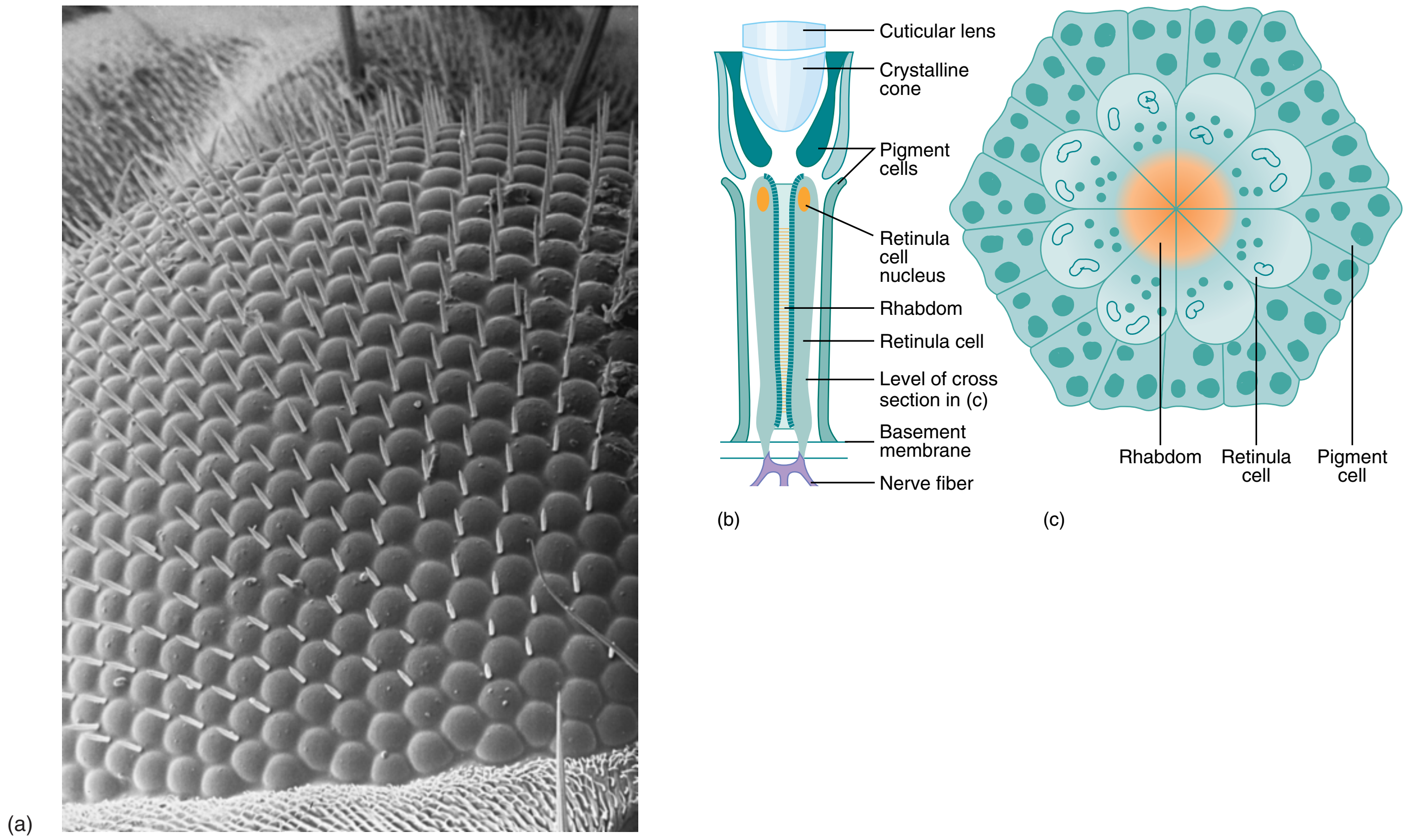


FIGURE 15.10

Compound Eye of an Insect. (*a*) Compound eye of *Drosophila* (SEM ×300). Each facet of the eye is the lens of a single sensory unit called an ommatidium. (*b*) Structure of an ommatidium. The lens and the crystalline cone are light-gathering structures. Retinula cells have light-gathering areas, called rhabdoms. Pigment cells prevent light in one ommatidium from reflecting into adjacent ommatidia. In insects that are active at night, the pigment cells are often migratory, and pigment can be concentrated around the crystalline cone. In these insects, low levels of light from widely scattered points can excite an ommatidium. (*c*) Cross section through the rhabdom region of an ommatidium.

eye cannot detect, especially in the ultraviolet end of the spectrum. In some insects, compound eyes also detect polarized light, which may be used for navigation and orientation.

Ocelli consist of 500 to 1,000 receptor cells beneath a single cuticular lens (*see figure 14.10*b). Ocelli are sensitive to changes in light intensity and may be important in the regulation of daily rhythms.

Excretion

The primary insect excretory structures are the Malpighian tubules and the rectum. Malpighian tubules end blindly in the hemocoel and open to the gut tract at the junction of the midgut and the hindgut. Microvilli cover the inner surfaces of their cells. Various ions are actively transported into the tubules, and water passively follows. Uric acid is secreted into the tubules and then into the gut, as are amino acids and ions (figure 15.11). In the rectum, water, certain ions, and other materials are reabsorbed, and the uric acid is eliminated.

As described in chapter 14, the excretion of uric acid is advantageous for terrestrial animals because it minimizes water loss. There is, however, an evolutionary trade-off. The conversion of primary nitrogenous wastes (ammonia) to uric acid is energetically costly. Nearly half of the food energy a terrestrial insect consumes may be used to process metabolic wastes! In aquatic insects, ammonia simply diffuses out of the body into the surrounding water.

Chemical Regulation

The endocrine system controls many physiological functions of insects, such as cuticular sclerotization (*see chapter 14*), osmoregulation, egg maturation, cellular metabolism, gut peristalsis, and heart rate. As in all arthropods, ecdysis is under neuroendocrine control. In insects, the subesophageal ganglion and two endocrine glands—the corpora allata and the prothoracic glands—control these activities.

Neurosecretory cells of the subesophageal ganglion manufacture ecdysiotropin. This hormone travels in neurosecretory cells to a structure called the corpora cardiaca. The corpora cardiaca then releases thoracotropic hormone, which stimulates the prothoracic gland to secrete ecdysone. Ecdysone initiates the

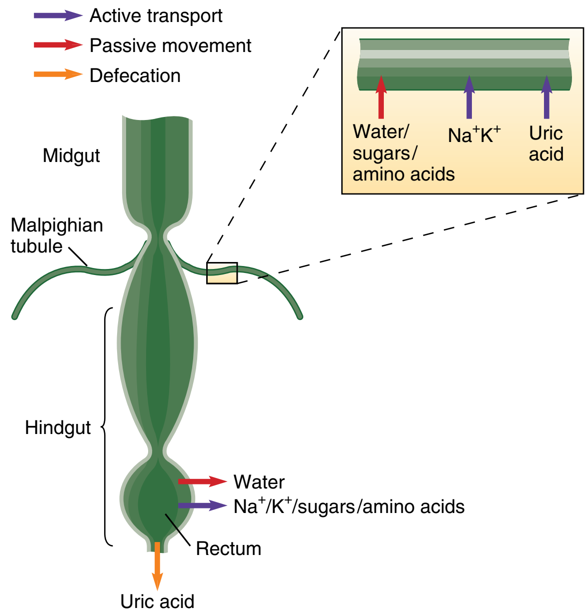


FIGURE 15.11

Insect Excretion. Malpighian tubules remove nitrogenous wastes from the hemocoel. Various ions are actively transported across the outer membranes of the tubules. Water follows these ions into the tubules and carries amino acids, sugars, and some nitrogenous wastes along passively. Some water, ions, and organic compounds are reabsorbed in the basal portion of the Malpighian tubules and the hindgut; the rest are reabsorbed in the rectum. Uric acid moves into the hindgut and is excreted.

TABLE 15.2
FUNCTIONS OF INSECT PHEROMONES

Sex pheromones—Excite or attract members of the opposite sex; accelerate or retard sexual maturation. Example: Female moths produce and release pheromones that attract males.

Caste-regulating pheromones—Used by social insects to control the development of individuals in a colony. Example: The amount of "royal jelly" fed a female bee larva determines whether the larva will become a worker or a queen.

Aggregation pheromones—Produced to attract individuals to feeding or mating sites. Example: Certain bark beetles aggregate on pine trees during an attack on a tree.

Alarm pheromones—Released to warn other individuals of danger; may cause orientation toward the pheromone source and elicit a subsequent attack or flight from the source. Example: A sting from one bee alarms other bees in the area, who are are likely to attack.

Trailing pheromones—Laid down by foraging insects to help other members of a colony identify the location and quantity of food found by one member of the colony. Example: Ants often trail on a pheromone path to and from a food source. The pheromone trail is reinforced each time an ant travels over it.

reabsorption of the inner portions of the procuticle and the formation of the new exoskeleton. Chapter 25 discusses these events further. Other hormones are also involved in ecdysis. The recycling of materials absorbed from the procuticle, changes in metabolic rates, and pigment deposition are a few of probably many functions that hormones control.

In immature stages, the corpora allata produces and releases small amounts of juvenile hormone. The amount of juvenile hormone circulating in the hemocoel determines the nature of the next molt. Large concentrations of juvenile hormone result in a molt to a second immature stage, intermediate concentrations result in a molt to a third immature stage, and low concentrations result in a molt to the adult stage. Decreases in the level of circulating juvenile hormone also lead to the degeneration of the prothoracic gland so that, in most insects, molts cease once adulthood is reached. Interestingly, after the final molt, the level of juvenile hormone increases again, but now it promotes the development of accessory sexual organs, yolk synthesis, and the egg maturation.

Pheromones are chemicals an animal releases that cause behavioral or physiological changes in another member of the same species. Zoologists have described many different insect uses of pheromones (table 15.2). Pheromones are often so specific that the stereoisomer (chemical mirror image) of the pheromone may be ineffective in initiating a response. Wind or water may carry pheromones several kilometers, and a few pheromone molecules falling on a chemoreceptor of another individual may be enough to elicit a response.

Reproduction and Development

One of the reasons for insects' success is their high reproductive potential. Reproduction in terrestrial environments, however, has its risks. Temperature, moisture, and food supplies vary with the season. Internal fertilization requires highly evolved copulatory structures because gametes dry quickly on exposure to air. In addition, mechanisms are required to bring males and females together at appropriate times.

Complex interactions between internal and external environmental factors regulate sexual maturity. Internal regulation includes interactions between endocrine glands (primarily the corpora allata) and reproductive organs. External regulating factors may include the quantity and quality of food. For example, the eggs of mosquitoes (order Diptera) do not mature until after the female takes a meal of blood, and the number of eggs produced is proportional to the quantity of blood ingested. Many insects use the photoperiod (the relative length of daylight and darkness in a 24-hour period) for timing reproductive activities because it indicates seasonal changes. Population density, temperature, and humidity also influence reproductive activities.

A few insects, including silverfish (order Thysanura) and springtails (order Collembola) have indirect fertilization. The male deposits a spermatophore that the female picks up later. Most insects have complex mating behaviors for locating and recognizing a potential mate, for positioning a mate for copulation, or for pacifying an aggressive mate. Mating behavior may involve pheromones (moths, order Lepidoptera), visual signals (fireflies, order Coleoptera), and auditory signals (cicadas, order Hemiptera; and grasshoppers, crickets, and katydids, order Orthoptera). Once other stimuli have brought the male and female together, tactile stimuli from the antennae and other appendages help position the insects for mating.

Abdominal copulatory appendages of the male usually transfer the sperm to an outpocketing of the female reproductive tract, the sperm receptacle (*see figure 15.8*). Eggs are fertilized as they leave the female and are usually laid near the larval food supply. Females may use an **ovipositor** to deposit eggs in or on some substrate.

Insect Development and Metamorphosis Insect evolution has resulted in the divergence of immature and adult body forms and habits. For insects in the superorder Endopterygota (*see table 15.1*), immature stages, called **larval instars,** are a time of growth and accumulation of reserves for the transition to adulthood. The adult stage is associated with reproduction and dispersal. In these orders, insects tend to spend a greater part of their lives in juvenile stages. The developmental patterns of insects reflect degrees of divergence between immatures and adults and are classified into three (or sometimes four) categories.

In insects that display **ametabolous** (Gr. *a,* without + *metabolos,* change) **metamorphosis,** the primary differences between adults and larvae are body size and sexual maturity. Both adults and larvae are wingless. The number of molts in the ametabolous development of a species varies, and unlike most other insects, molting continues after sexual maturity. Silverfish (order Thysanura) have ametabolous metamorphosis.

Hemimetabolous (Gr. *hemi,* half) **metamorphosis** involves a species-specific number of molts between egg and adult stages, during which immatures gradually take on the adult form. The external wings develop (except in those insects, such as lice, that have secondarily lost wings), adult body size and proportions are attained, and the genitalia develop during this time. Immatures are called **nymphs.** Grasshoppers (order Orthoptera) and chinch bugs (order Hemiptera) show hemimetabolous metamorphosis (figure 15.12). When immature stages are aquatic, they often have gills (e.g., mayflies, order Ephemeroptera; dragonflies, order Odonata). These immatures are called **naiads** (L. *naiad,* water nymph).

In **holometabolous** (Gr. *holos,* whole) **metamorphosis,** immatures are called larvae because they are very different from the adult in body form, behavior, and habitat (figure 15.13). The number of larval instars is species specific, and the last larval molt forms the **pupa.** The pupa is a time of apparent inactivity but is actually a time of radical cellular change, during which all characteristics of the adult insect develop. A protective case may enclose the pupal stage. The last larval instar (e.g., moths, order Lepidoptera) constructs a **cocoon** partially or entirely from silk. The **chrysalis** (e.g., butterflies, order Lepidoptera) and **puparium** (e.g., flies, order Diptera) are the last larval exoskeletons and are retained through the pupal stage. Other insects (e.g., mosquitoes, order Diptera) have pupae that are unenclosed by a larval exoskeleton, and the pupa may be active. The final molt to the adult stage usually occurs within the cocoon, chrysalis, or puparium, and the adult then exits, frequently using its mandibles to open the cocoon or other enclosure. This final process is called emergence or eclosion.

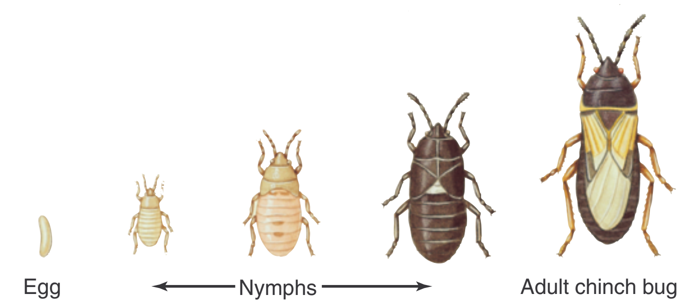


FIGURE 15.12
Hemimetabolous Development of the Chinch Bug, *Blissus leucopterus* (Order Hemiptera). Eggs hatch into nymphs. Note the gradual increase in nymph size and the development of external wing pads. In the adult stage, the wings are fully developed, and the insect is sexually mature.

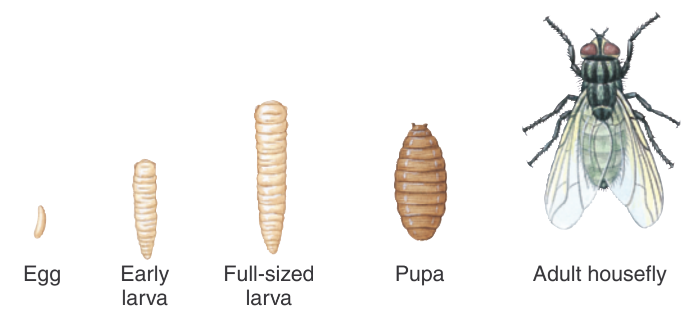


FIGURE 15.13
Holometabolous Development of the Housefly, *Musca domestica* (Order Diptera). The egg hatches into a larva that is different in form and habitat from the adult. After a certain number of larval instars, the insect pupates. During the pupal stage, all adult characteristics form.

Insect Behavior

Insects have many complex behavior patterns. Most of these are innate (genetically programmed). For example, a newly emerged queen in a honeybee hive will search out and try to destroy other queen larvae and pupae in the hive. This behavior is innate because no experiences taught the potential queen that her survival in the hive required the death or dispersal of all other potential queens. Similarly, no experience taught her how queen-rearing cells differ from the cells containing worker larvae and pupae. Some insects are capable of learning and remembering, and these abilities play important roles in insect behavior.

Social Insects Social behavior has evolved in many insects and is particularly evident in those insects that live in colonies. Usually, different members of the colony are specialized, often structurally as well as behaviorally, for performing different tasks.

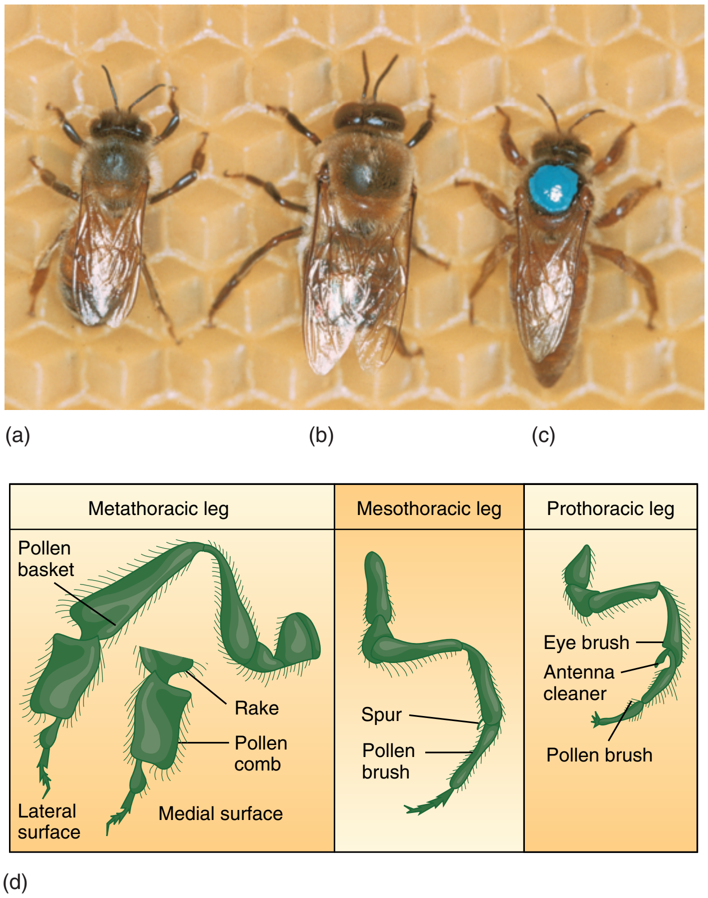


FIGURE 15.14

Honeybees (Order Hymenoptera). Honeybees have a social organization consisting of three castes. Eye size and overall body size distinguish the castes. (*a*) A worker bee. (*b*) A drone bee. (*c*) A queen bee marked with blue to identify her. (*d*) The inner surface of metathoracic legs have setae, called the pollen comb, that remove pollen from the mesothoracic legs and the abdomen. Pollen is then compressed into a solid mass by being squeezed in a pollen press and moved to a pollen basket on the outer surface of the leg, where the pollen is carried. The mesothoracic legs gather pollen from body parts. The prothoracic legs of a worker bee clean pollen from the antennae and body.

Social behavior is most highly evolved in the bees, wasps, and ants (order Hymenoptera) and in termites (order Isoptera). Each kind of individual in an insect colony is called a **caste.** Often, three or four castes are present in a colony. Reproductive females are referred to as queens. Workers may be sterile males and females (termites) or sterile females (order Hymenoptera), and they support and protect the colony. Their reproductive organs are often degenerate. Reproductive males inseminate the queen(s) and are called kings or drones. Soldiers are usually sterile and may possess large mandibles to defend the colony.

Honeybees (order Hymenoptera) have three of these castes in their colonies (figure 15.14). A single queen lays all the eggs. Workers are female, and they construct the comb out of wax that they produce. They also gather nectar and pollen, feed the queen and drones, care for the larvae, and guard and clean the hive. These tasks are divided among workers according to age. Younger workers take care of jobs around the hive, and older workers forage for nectar and pollen. Except for those that overwinter, workers live for about one month. Drones develop from unfertilized eggs, do not work, and are fed by workers until they leave the hive to attempt mating with a queen.

A pheromone that the queen releases controls the honeybee caste system. Workers lick and groom the queen and other workers. In so doing, they pick up and pass to other workers a caste-regulating pheromone. This pheromone inhibits the workers from rearing new queens. As the queen ages, or if she dies, the amount of caste-regulating pheromone in the hive decreases. As the pheromone decreases, workers begin to feed the food for queens ("royal jelly") to several female larvae developing in the hive. This food contains chemicals that promote the development of queen characteristics. The larvae that receive royal jelly develop into queens, and as they emerge, the new queens begin to eliminate each other until only one remains. The queen that remains goes on a mating flight and returns to the colony, where she lives for several years.

The evolution of social behavior involving many individuals leaving no offspring and sacrificing individuals for the perpetuation of the colony has puzzled evolutionists for many years. It may be explained by the concepts of kin selection and altruism.

Insects and Humans

Only about 0.5% of insect species adversely affect human health and welfare. Many others have provided valuable services and commercially valuable products, such as wax, honey, and silk, for thousands of years. Insects are responsible for the pollination of approximately 65% of all plant species. Insects and flowering plants have coevolutionary relationships that directly benefit humans. The annual value of insect-pollinated crops is estimated at $19 billion per year in the United States.

Insects are also agents of biological control. The classic example of one insect regulating another is the vedalia (lady bird) beetles' control of cottony-cushion scale. The scale insect, *Icerya purchasi*, was introduced into California in the 1860s. Within 20 years, the citrus industry in California was virtually destroyed. The vedalia beetle (*Vedalia cardinalis*) was brought to the United States in 1888 and 1889 and cultured on trees infested with scale. In just a few years, the scale was under control, and the citrus industry began to recover.

Many other insects are also beneficial. Soil-dwelling insects play important roles in aeration, drainage, and turnover of soil, and they promote decay processes. Other insects serve important roles in food webs. Insects are used in teaching and research, and have contributed to advances in genetics, population ecology, and physiology. Insects have also given endless hours of pleasure to those who collect them and enjoy their beauty.

Some insects, however, are parasites and vectors of disease. Parasitic insects include head, body, and pubic lice (order Anoplura); bedbugs (order Hemiptera); and fleas (order Siphonaptera). Other insects transmit disease-causing microorganisms, nematodes, and flatworms. Insect-transmitted diseases, such as

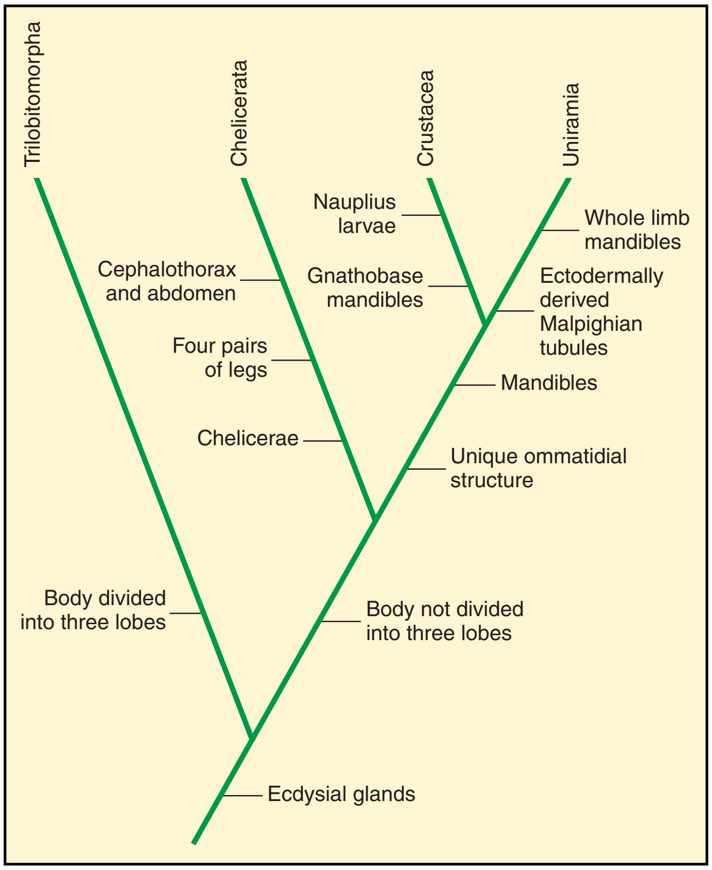


FIGURE 15.15

A Traditional Interpretation of Arthropod Phylogeny. Systematists have considered the trilobites to be the ancestors all arthropods. The Myriapoda and Hexapoda have been considered closely related and grouped here into a single subphylum, Uniramia. Crustaceans are represented as having close ties to the Myriapoda and Hexapoda (Uniramia). Alternate traditional phylogenies have been proposed, but virtually all represented the trilobites as ancestral and the crustaceans as a true monophyletic group.

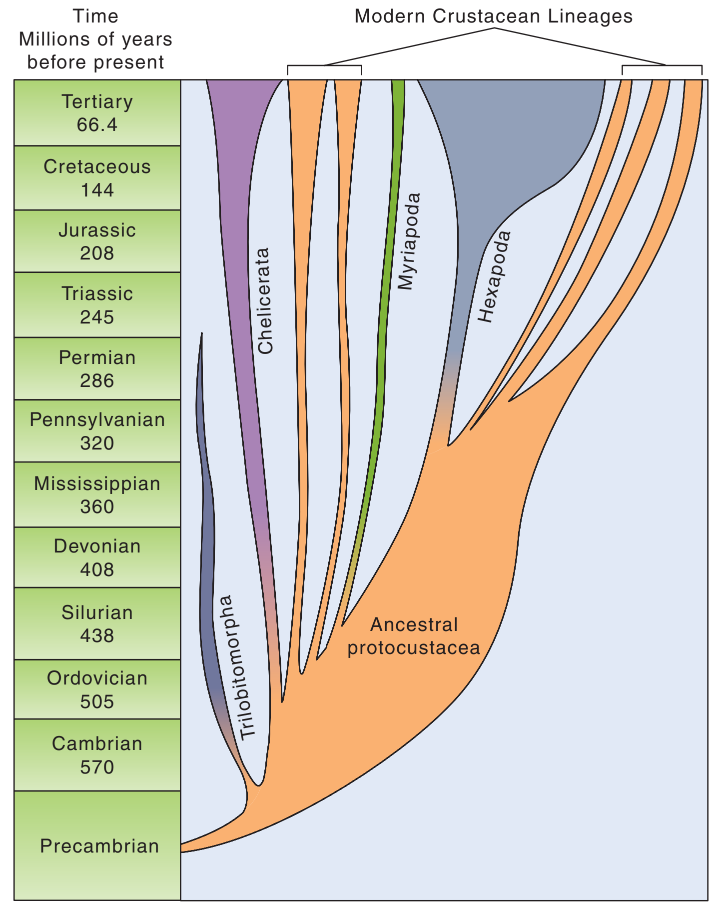


FIGURE 15.16

A Highly Speculative Interpretation of Arthropod Phylogeny. Recent research is interpreted to suggest that ancient crustaceans are the ancestors of all arthropods. Crustacea is a paraphyletic grouping with modern crustaceans diverging from the ancestral stock at various points. Trilobites were the first noncrustacean lineage to diverge from ancient crustaceans. The uniramous appendages, Malpighian tubules, and tracheal systems of myriapods and hexapods are probably convergent, and these groups are represented as having separate ancestry.

malaria, yellow fever, bubonic plague, encephalitis, leishmaniasis, and typhus, have changed the course of history.

Other insects are pests of domestic animals and plants. Some reduce the health of domestic animals and the quality of animal products. Insects feed on crops and transmit plant diseases, such as Dutch elm disease, potato virus, and asters yellow. Annual lost revenue from insect damage to crops or insect-transmitted diseases in the United States is approximately $5 billion.

FURTHER PHYLOGENETIC CONSIDERATIONS

A fundamental question regarding arthropod evolution has been whether or not the Arthropoda is a monophyletic taxon, that is, whether or not the arthropods originated from a single ancestral species. That question seems to be settled in the minds of virtually all arthropod systematists. *Arthropoda is a monophyletic grouping.*

Until recently, zoologists thought they had a good idea of the relationships of taxa within the phylum—at least there were only two major competing views regarding relationships among the arthropod subphyla. These ideas were based primarily on paleontological and morphological data. One example is shown in figure 15.15. Recently, data from developmental biology, molecular biology, and new paleontological studies are causing a major rethinking of these relationships. This revision is in its infancy, and so any representation of arthropod relationships, such as that shown in figure 15.16, is highly speculative. A few of the major points that are emerging are described in the following paragraphs.

Arthropods were some of the earliest animals to evolve. They are represented in the fossils of the Ediacaran fauna (*see chapter 7*) and, therefore, date to Precambrian times about 600 million years ago (*see table 4.1*). Interestingly, these earliest fossils are not of trilobites but are similar to crustaceans. This evidence,

WILDLIFE ALERT

The Karner Blue Butterfly (*Lycaeides melissa samuelis*)

VITAL STATISTICS

Classification: Phylum Arthropoda, class Hexapoda, order Lepidoptera

Range: New England to the Great Lakes Region (historical), Western Great Lakes Region (current)

Habitat: Sand plains, oak savannas, or pine barrens in association with wild lupine

Number remaining: Less than 1% of its population in 1900

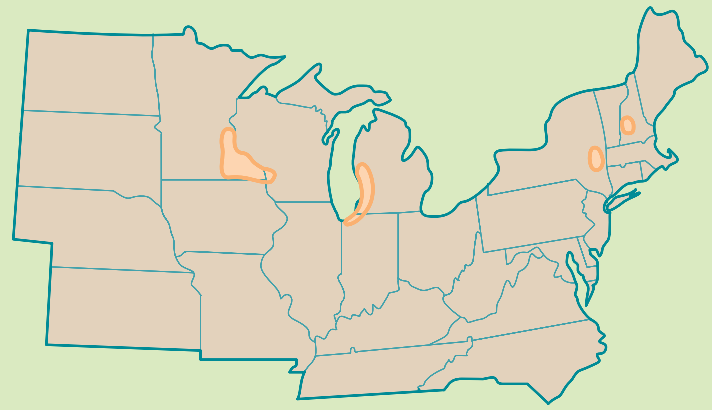
Status: Endangered

NATURAL HISTORY AND ECOLOGICAL STATUS

The male Karner blue butterfly is silvery or dark blue with a narrow black margin on the upper surface of the wing (box figure 15.1). The female has grayish brown wings with a dark border and orange bands.

The Karner blue butterfly lives in sand plains, oak savannas, or pine barrens. These habitats are patchily distributed across the northeastern and midwestern parts of the United States (box figure 15.2). They consist of grassland areas with scattered trees and are maintained in their natural state by periodic disturbances from fire. Without fire disturbance, shrub and tree vegetation soon overruns these habitats. These grassy islands are the home of a plant called wild lupine (*Lupinus perennis*), which is the sole food source for caterpillars of the Karner blue butterfly.

BOX FIGURE 15.1 Male Karner Blue Butterfly (*Lycaeides melissa samuelis*).



BOX FIGURE 15.2 Approximate Distribution of Karner Blue Butterfly (*Lycaeides melissa samuelis*).

In the spring, Karner blue eggs, which have overwintered, hatch, and the larvae feed on wild lupine. By the end of May, the larvae have grown and pupated. Adults emerge and mate, and the females lay eggs on or near wild lupine. Eggs quickly hatch, and the larvae feed, grow, and pupate. By the end of July, the second generation of adults emerges and mates. This generation of females lays eggs among the plant litter near wild lupine. These eggs remain dormant until the following April. After August, no adults or larvae of the Karner blue butterfly are found.

The endangered status of the Karner blue butterfly is a result of habitat loss. As humans develop land, they quickly bring fires under control. Fire control allows a wild lupine habitat to overgrow with shrubs and trees, making it no longer suitable for wild lupine or the Karner blue butterfly. Habitat loss is devastating for a species, especially if habitat distribution is patchy. Patchy distribution does not provide corridors for movement and dispersal to new areas. When a patch of habitat is lost, the species present in that patch usually have no place to go. Even when patches of habitat are not entirely lost, but simply broken up by human development, dispersal within the habitat may be nearly impossible. The construction of roads, buildings, and off-road vehicle trails presents formidable obstacles for a species as fragile and specialized as the Karner blue butterfly.

This example vividly illustrates an organism's dependence on habitat preservation. The struggle of the Karner blue butterfly is a subtle reminder that something is wrong in our treatment of the land. Protecting pine barrens and oak savannas will improve the chances for the survival of wild lupine, the Karner blue butterfly, and other species specialized for life in these fragile habitats.

along with data from molecular biology, is causing zoologists to reject the prior assumption that the first arthropods were trilobites. *We now view ancestral crustaceans, or protocrustaceans, as the stem group from which other arthropods evolved.*

The trilobites appeared in the early Cambrian and were probably the first major lineage to diverge from ancestral crustaceans. They were the most abundant arthropods until their extinction at the Permian-Triassic boundary 240 million years ago.

The Chelicerata were common in the Ordovician period about 500 million years ago, and by the Silurian period (450 million years ago) chelicerates had become the first, or some of the first, land animals.

The Myriapoda is the next lineage to appear in the fossil record. Even though all modern myriapods are terrestrial, the first myriapods were marine animals. *Terrestrial myriapods—millipedes and centipedes—quickly joined the chelicerates on land during the Silurian period.*

The Hexapoda is the last arthropod lineage to appear. Collembolans and archaeognathans are found in the Devonian fossil record and date to about 400 million years ago. The rise of flowering plants about 130 million years ago, along with the evolution of flight, probably promoted the rapid diversification of insects during the Cretaceous period.

Recent research is challenging former ideas regarding the relationships of the Myriapoda and Hexapoda. Shared characteristics like their tracheal systems, uniramous legs, and Malpighian tubules have been interpreted as supporting a close relationship of these taxa. In figure 15.15, these two groups are united under the subphylum Uniramia. *New evidence from molecular, developmental, and morphological investigations suggests that the Hexapoda are more closely related to the Crustacea than to the Myriapoda.* This means that the shared myriapod/hexapod characters are convergent, not homologous. On the other hand, shared crustacean/hexapod characters like the compound eye may be homologous.

Modern crustacean lineages probably arose at various times from the ancestral crustaceans. In figure 15.16, these lineages are not labeled because of the highly speculative nature of the tree. What is emerging from all of these studies is that Arthropoda is a monophyletic grouping; arthropods are among the oldest of all animals; and that ancient crustaceans provided the ancestral stock for all modern arthropods. The subphylum Crustacea is thus paraphyletic

SUMMARY

1. During the Devonian period, insects began to exploit terrestrial environments. Flight, the exoskeleton, and metamorphosis are probably keys to insect success.
2. The subphylum Myriapoda includes four classes of arthropods. Members of the class Diplopoda (the millipedes) are characterized by apparent segments bearing two pairs of legs. Members of the class Chilopoda (the centipedes) are characterized by a single pair of legs on each of their 15 segments and a body that is flattened in cross section. The class Pauropoda contains soft-bodied animals that feed on fungi and decaying organic matter in forest-floor litter. Members of the class Symphyla are centipede-like arthropods that live in soil and leaf mold, where they feed on decaying vegetation.
3. Animals in the subphylum Hexapoda are characterized by bodies divided into three tagmata, five pairs of head appendages, and three pairs of legs. It includes two classes, Entognatha and Insecta.
4. Insect flight involves either a direct (synchronous) flight mechanism or an indirect (asynchronous) flight mechanism.
5. Mouthparts of insects are adapted for chewing, piercing, and/or sucking, and the gut tract may be modified for pumping, storage, digestion, and water conservation.
6. In insects, gas exchange occurs through a tracheal system.
7. The insect nervous system is similar to that of other arthropods. Sensory structures include tympanal organs, compound eyes, and ocelli.
8. Malpighian tubules transport uric acid to the digestive tract. Conversion of nitrogenous wastes to uric acid conserves water but is energetically expensive.
9. Hormones regulate many insect functions, including ecdysis and metamorphosis. Pheromones are chemicals emitted by one individual that alter the behavior of another member of the same species.
10. Insect adaptations for reproduction on land include resistant eggs, external genitalia, and behavioral mechanisms that bring males and females together at appropriate times.
11. Metamorphosis of an insect may be ametabolous, hemimetabolous, or holometabolous. Neuroendocrine and endocrine secretions control metamorphosis.
12. Insects show both innate and learned behavior.
13. Many insects are beneficial to humans, and a few are parasites and/or transmit diseases to humans or agricultural products. Others attack cultivated plants and stored products.
14. New research is causing zoologists to rethink arthropod phylogeny. Arthropods are considered monophyletic, and ancestral crustaceans are probably the stock from which other arthropods evolved. Crustacea is a paraphyletic grouping.

SELECTED KEY TERMS

ametabolous metamorphosis (p. 245)
caste (p. 246)
direct or synchronous flight (p. 239)
hemimetabolous metamorphosis (p. 245)
holometabolous metamorphosis (p. 245)
indirect or asynchronous flight (p. 239)
larval instars (p. 245)
nymphs (p. 245)
pupa (p. 245)

CRITICAL THINKING QUESTIONS

1. What problems are associated with living and reproducing in terrestrial environments? Explain how insects overcome these problems.
2. List as many examples as you can of how insects communicate with each other. In each case, what is the form and purpose of the communication?
3. In what way does holometabolous metamorphosis reduce competition between immature and adult stages? Give specific examples.
4. What role does each stage play in the life history of holometabolous insects?
5. Discuss the phylogenetic implications of recent research that has been interpreted to suggest that Crustacea is a paraphyletic group. How might future analyses deal with this group?

ONLINE LEARNING CENTER

Visit our Online Learning Center www.mhhe.com/zoology (click on this book's title) to find the following chapter-related materials:

- CHAPTER QUIZZING
- RELATED WEB LINKS
  - Subphylum Hexapoda
  - Minor Classes of Myriapods
  - Class Insecta
- BOXED READINGS ON
  - A Fearsome Twosome
  - *Sacculina:* A Highly Modified Parasite
  - How Insects Fly—Secrets Revealed
  - Communication in Honeybees
  - "Killer Bees?"
- READINGS ON LESSER-KNOWN INVERTEBRATES
  - Possible Arthropod Relatives
- SUGGESTED READINGS
- LAB CORRELATIONS

Check out the OLC to find specific information on these related lab exercises in the *General Zoology Laboratory Manual*, 5th edition, by Stephen A. Miller:

Exercise 15 *Arthropoda*