



Phylum Arthropoda

The Hexapoda: Insects and Their Kin

Hexapods stand out among all other invertebrates for being far and away the most diverse group of animals on Earth, the only invertebrates to fly, and the only terrestrial invertebrates to undergo indirect development or complete metamorphosis.

The arthropod subphylum Hexapoda comprises the class Insecta and three other small, closely related, wingless, insect-like groups: Collembola, Protura, and Diplura. The Hexapoda are united on the basis of a distinct body plan of a head, 3-segmented thorax, and 11-segmented abdomen, 3 pairs of thoracic legs, a single pair of antennae, 3 sets of “jaws” (mandibles, maxillae, and labium), an aerial gas exchange system composed of tracheae and spiracles, Malpighian tubules formed as proctodeal (ectodermal) evaginations, and, among the

Pterygota, wings (Box 22A). The presence of a thorax fixed at 3 segments, each with a pair of walking legs, is a unique synapomorphy for the Hexapoda. Other synapomorphies include the presence of a large fat body (mainly concentrated in the abdomen), and fusion of the second maxillae to form a lower lip (the labium).

Hexapods evolved on land; groups inhabiting aquatic environments today have secondarily invaded those habitats through behavioral adaptations and modifications of their aerial gas exchange systems. The earliest undisputed fossils of hexapods are early Devonian (412 Ma). However, there are Silurian trace fossils that are very hexapod-like, and molecular clock data suggest an Early Ordovician origin for Hexapods at about 479 million years ago and an early Silurian origin about 441 million years ago for Insecta.

The most spectacular evolutionary radiation among the Hexapoda (in fact among all eukaryotic life) has, of course, been within the insects, which inhabit nearly every conceivable terrestrial and freshwater habitat and, less commonly, even the sea surface and the marine littoral region. Insects are also found in such unlikely places as oil swamps and seeps, sulfur springs, glacial streams, and brine ponds. They often live where few other

Classification of The Animal Kingdom (Metazoa)

Non-Bilateria*

(a.k.a. the diploblasts)

- PHYLUM PORIFERA
- PHYLUM PLACOZOA
- PHYLUM CNIDARIA
- PHYLUM CTENOPHORA

Bilateria

(a.k.a. the triploblasts)

- PHYLUM XENACOELOMORPHA

Protostomia

- PHYLUM CHAETOGNATHA

SPIRALIA

- PHYLUM PLATYHELMINTHES
- PHYLUM GASTROTRICHA
- PHYLUM RHOMBOZOA
- PHYLUM ORTHONECTIDA
- PHYLUM NEMERTEA
- PHYLUM MOLLUSCA
- PHYLUM ANNELIDA
- PHYLUM ENTOPROCTA
- PHYLUM CYCLOPHORA

Gnathifera

- PHYLUM GNATHOSTOMULIDA
- PHYLUM MICROGNATHOZOA
- PHYLUM ROTIFERA

Lophophorata

- PHYLUM PHORONIDA
- PHYLUM BRYOZOA
- PHYLUM BRACHIOPODA

ECDYSOZOA

Nematoida

- PHYLUM NEMATODA
- PHYLUM NEMATOMORPHA

Scalidophora

- PHYLUM KINORHYNCHA
- PHYLUM PRIAPULA
- PHYLUM LORICIFERA

Panarthropoda

- PHYLUM TARDIGRADA
- PHYLUM ONYCHOPHORA

PHYLUM ARTHROPODA

- SUBPHYLUM CRUSTACEA*
- SUBPHYLUM HEXAPODA
- SUBPHYLUM MYRIAPODA
- SUBPHYLUM CHELICERATA

Deuterostomia

- PHYLUM ECHINODERMATA
- PHYLUM HEMICHORDATA
- PHYLUM CHORDATA

*Paraphyletic group

BOX 22A Characteristics of the Subphylum Hexapoda

1. Body composed of 20 true somites (plus acron) organized as a head (6 somites), thorax (3 somites) and abdomen (11 somites). Due to fusion of somites, these body segments are not always externally obvious.
2. Head segments bear the following structures (from anterior to posterior): compound eyes and ocelli; antennae; clypeolabrum; mandibles; maxillae, labium (fused second maxillae). Ocelli (and compound eyes) are secondarily lost in some groups.
3. Legs uniramous; present on the three thoracic segments of adults; legs composed of 6 articles: coxa, trochanter, femur, tibia, tarsus, pretarsus; tarsus often subdivided; pretarsus typically clawed
4. Gas exchange by spiracles and tracheae
5. Gut with gastric (digestive) ceca
6. With large fat body (mainly concentrated in abdomen)
7. Fused exoskeleton of head forms unique internal tentorium
8. With ectodermally derived Malpighian tubules (proctodeal evaginations)
9. Gonopores open on the last abdominal segment, or on abdominal segment 7, 8, or 9
10. Gonochoristic; direct or indirect development

animals or plants can exist. It is no exaggeration to say that insects rule the land. Their diversity and abundance defy imagination (Figures 22.1–22.7).

We do not know how many species of insects there are, or even how many have been described. Published estimates of the number of described species range from 890,000 to well over a million (we calculate about 926,990). An average of about 3,500 new species have been described annually since the publication of Linnaeus's *Systema Naturae* in 1758, although in recent years the average has climbed to 7,000 new species annually. Estimates of the number of insect species remaining to be described range from 3 million to 100 million. The Coleoptera (beetles), with an estimated 380,000 described species, is far and away the largest insect order (more than a quarter of all animal species are beetles). The beetle family Curculionidae (the weevils) contains about 65,000 described species (nearly 5% of all described animal species). The rich diversity of insects seems to have come about through a combination of advantageous features, including the evolutionary exploitation of developmental genes working on segmented and compartmentalized bodies, coevolution with plants (particularly the flowering plants), miniaturization, and the invention of flight.

Insects are not only diverse, but also incredibly abundant. For every human alive, there are an estimated 200 million insects. Howard Ensign Evans estimated that an acre of ordinary English pasture supports an astonishing 248,375,000 springtails and 17,825,000 beetles. In tropical rain forests, insects can constitute 40% of the total animal biomass (dry weight), and the biomass of the ants can be far greater than that of the combined mammal fauna (up to 15% of the total animal biomass). A single colony of the African driver ant *Anomma wilverthi* may contain as many as 22 million workers. Based on his research in the tropics, biodiversity sleuth Terry Erwin has calculated that there are about 3.2×10^8 individual arthropods per hectare, representing more than 60,000 species, in the western Amazon. In Maryland, a single population of the mound-building ant *Formica exsectoides* comprised 73 nests covering an area of 10 acres and containing approximately 12 million workers. Termites have colonies of similar magnitudes. E. O. Wilson has calculated that, at any given time, 10^{15} (a million billion) ants are alive on Earth!

In most parts of the world, insects are among the principal predators of other invertebrates. Insects are also key items in the diets of many terrestrial vertebrates, and they play a major role as reducer-level organisms (detritivores and decomposers) in food webs. Due to their sheer numbers, they constitute much of the matrix of terrestrial food webs. Their biomass and energy consumption exceed those of vertebrates in most terrestrial habitats. In deserts and in the tropics, ants replace earthworms as the most abundant earth movers (ants are nearly as important as earthworms even in temperate regions). Termites are among the chief decomposers of dead wood and leaf litter around the world, and without dung beetles African savannahs would be buried under the excrement of the tens of thousands of large grazing mammals.

Without insects, life as we know it would cease to exist. In fact, E. O. Wilson has stated, "so important are insects and other land-dwelling arthropods that if all were to disappear, humanity probably could not last more than a few months." Eighty percent of the world's crop species, including food, medicine, and fiber crops, rely on animal pollinators, nearly all of which are insects. Insects also play key roles in pollinating wild, native plants. Beekeeping began long ago, at least by 600 BC in the Nile Valley and probably well before that. The first migratory beekeepers were Egyptians who floated hives up and down the Nile to provide pollination services to floodplain farmers while simultaneously producing a honey crop. Domestic honeybees (*Apis mellifera*), introduced to North America from Europe in the mid-1600s, are now the dominant pollinators of most food crops grown around the world, and they play some role



Figure 22.1 Representatives of the three orders of entognathous (noninsect) hexapods. (A) *Anurida granaria*, a springtail (order Collembola). (B) *Ptenothrix* sp., a springtail showing entognathous mouthparts. (C) A dipluran from New Zealand (order Diplura). (D) A proturan from British Columbia (order Protura).

in pollinating 80% of the crop varieties grown in the United States (they are estimated to be directly responsible for \$10 to \$20 billion in crops annually).¹

Interactions between insects and flowering plants have been going on for a very long time, beginning over 100 million years ago with the origin of the angiosperms and accelerating with the ascendancy of these flowering plants during the early Cenozoic. Millions of years of plant–insect coevolution have

¹The study of bees is called “melittophily.” The study of honeybees (*Apis* spp.) and their management is called “apiculture.” The management of bumblebees (*Bombus* spp.) is “bombiculture.” The ritualized keeping of stingless bees is “meliponiculture.” The Asian honeybee, *Apis dorsata*, not yet introduced to the U.S., is a giant reaching an inch in length. Its droppings are quite noticeable, and the mass defecations of these bees at sunset create a “golden shower” that provides significant nutrient enrichment to tropical soils. Their droppings were once confused with the dreaded “yellow rain,” a deadly form of biochemical warfare that poisoned thousands of villagers during the Vietnam War.

resulted in flowers with anatomy and scents that are finely tuned to their insect partners. In exchange for pollination services, flowers provide insects with food (nectar, pollen), shelter, and chemicals used by the insects to produce such things as pheromones. In general, insect pollination is accomplished coincidentally, as the pollinators visit flowers for other reasons. But in a few cases, such as that of the yucca moths of the American Southwest (*Tegiticula* spp.), the insects actually gather up pollen and force it into the receptive stigma of the flower, initiating pollination. The moth’s goal is to assure a supply of yucca seed for its larvae, which develop within the yucca’s fruits. Some insects also play important roles as seed dispersers, especially ants. More than 3,000 plant species (in 60 families) are known to rely on ants for the dispersal of their seeds.

Like all other animals on Earth, insects are facing enormous threats of extinction. Certainly many thousands of species have become extinct over the past century as a result of rampant land use change and deforestation. With accelerating biodiversity losses worldwide, estimates of the number of insect species that have already gone extinct range into the millions. Further, widespread and often inappropriate use of

pesticides has created a “pollination crisis” in many parts of the world, as pollinating insects are locally extirpated and native plant and domestic crop pollination plummets.

As valuable as insects are to human life, some species seem to conspire to give the whole group a bad name. Some insect species are pests and consume about a third of our potential annual harvest, and some other species transmit many major human diseases. Every year we spend billions of dollars on insect control. Malaria, transmitted by mosquitoes, kills 1 to 3 million people annually (mostly children), and each year nearly 500 million people contract the disease. It is the leading cause of death from infectious disease, and it has plagued humans for at least 3,000 years (Egyptian mummies have been found with malaria antigens in their blood). One of the most widespread and fastest spreading human viral diseases, dengue, is transmitted by mosquitoes of the genus *Aedes*. Dengue is essentially an urban disease, almost entirely associated with anthropogenic environments because its main vectors, *A. albopictus* and *A. aegypti*, breed primarily in artificial containers (e.g., flower vases, discarded tires, water tanks). In recent years, these species have spread throughout the tropics, often following the international trade in used tires. Although these mosquitoes have not penetrated very far into the temperate zones, they have become established in the southern United States. A variety of mosquitoes transmits the filarial nematode *Wuchereria bancrofti*, the causative agent of lymphatic filariasis (“elephantiasis”) throughout the world’s tropics. Chagas’ disease (American trypanosomiasis) is transmitted by certain hemipteran bugs in the subfamily Triatominae (family Reduviidae), and causes chronic degenerative disease of the heart and intestine. The species of triatomine bugs that occur in the southwestern United States tend not to defecate when they feed, greatly reducing the possibility of humans contracting Chagas’ disease in that area. However, global warming is now increasing the spread of *Aedes*, *Culex*, triatomines, and other tropical disease vectors.

The natural history writer David Quammen, speaking of the blood-sucking varieties of mosquitoes, notes that the average blood meal of a female (the only sex that feeds on blood) amounts to 2.5 times the original weight of the insect—the equivalent, Quammen notes, “of Audrey Hepburn sitting down to dinner and getting up from the table weighting 380 pounds, then, for that matter, flying away.” But as Quammen also points out, mosquitoes have made tropical rain forests (the most diverse ecosystems on Earth) largely uninhabitable to humans, thus helping to preserve them!

The enormous diversification of Hexapoda is often attributed to the evolution of three key innovations: the

ability to fly, the ability to fold back their wings, and the evolution of holometabolous development (= indirect development, = complete metamorphosis). The persistence of the main lineages of insects since the Devonian and their ecological and morphological versatility have undoubtedly contributed to making Hexapoda the dominant group in extant terrestrial ecosystems, with respect to species diversity, functional diversity, and overall biomass. Obviously, the subject of insect biology, or entomology, is a discipline in its own right, and a multitude of books and college courses on the subject exists. If we apportioned pages to animal groups on the basis of numbers of species, overall abundance, or economic importance, insect chapters could easily fill 90% of this textbook. The Selected References at the end of this chapter provide entry into some of the current literature on insects.

Because the Hexapoda comprises such a large and diverse assemblage of arthropods, we first present a brief classification of the 31 recognized orders, followed by more detailed synopses, brief diagnoses, and comments, on each order. These two sections serve as a preface to the body plan discussion that follows, and also provide a reference that the reader can turn to as needed.

CLASSIFICATION OF THE SUBPHYLUM HEXAPODA

Our classification scheme recognizes 31 orders of living hexapods. Three entognathous, or non-insect hexapod orders (the Entognatha), are basal to the monophyletic class Insecta. The Insecta comprise two monophyletic sister groups, the order Archaeognatha (with monocondylic mandibles) and all the others (with dicondylic mandibles). The subclass Pterygota, or flying insects, comprise two groups: the Palaeoptera (Ephemeroptera, Odonata), which may be a paraphyletic group, and the monophyletic infraclass Neoptera. We recognize three superorders within the modern winged insects, or Neoptera: the Polyneoptera (Plecoptera, Zoraptera, Blattodea, Mantodea, Dermaptera, Orthoptera, Phasmida, Grylloblattodea, Embioptera, Mantophasmatodea), the Acercaria (Psocodea, Thysanoptera, Hemiptera), and the Holometabola (all the remaining orders). Within the Holometabola we recognize four well supported, but unranked clades: Coleopetrada (Coleoptera, Strepsiptera), Neuropterida (Neuroptera, Megaloptera, Raphidioptera), Antliophora (Mecoptera, Siphonaptera, Diptera), and Amphiesmenoptera (Trichoptera, Lepidoptera). With nearly a million named species of Hexapoda, we have opted to include representative families of only the most diverse and common orders in the taxonomic synopses.

SUBPHYLUM HEXAPODA

(Note: "Entognatha" and "Palaeoptera" are likely paraphyletic groups)

Entognatha

- Order Collembola: Springtails
- Order Protura: Proturans
- Order Diplura: Diplurans

CLASS INSECTA (= ECTOGNATHA)

- Order Archaeognatha: Jumping bristletails

Dicondylia

- Order Thysanura (= Zygentoma): Silverfish

Subclass Pterygota: Winged insects

Palaeoptera: Ancient winged insects

- Order Ephemeroptera: Mayflies
- Order Odonata: Dragonflies and damselflies

Infraclass Neoptera: Modern, wing-folding insects

Superorder Polyneoptera

- Order Plecoptera: Stoneflies
- Order Blattodea: Cockroaches and termites
- Order Mantodea: Mantises
- Order Phasmida (= Phasmatodea): Stick and leaf insects
- Order Grylloblattodea: Rock crawlers
- Order Dermaptera: Earwigs
- Order Orthoptera: Locusts, katydids, crickets, grasshoppers
- Order Mantophasmatodea: Heel-walkers or gladiators
- Order Embioptera (= Embiidina): Web-spinners
- Order Zoraptera: Zorapterans

Superorder Acercaria (= Paraneoptera)

- Order Thysanoptera: Thrips
- Order Hemiptera: True bugs
- Order Psocodea: Book lice, bark lice, true lice

Superorder Holometabola

- Order Hymenoptera: Ants, bees, wasps

Coleopterida

- Order Coleoptera: Beetles
- Order Strepsiptera: Twisted-wing parasites

Neuropterida

- Order Megaloptera: Alderflies, dobsonflies, fishflies
- Order Raphidioptera: Snakeflies
- Order Neuroptera: Lacewings, ant lions, mantisflies, owlflies

Antliophora

- Order Mecoptera: Scorpionflies, hangingflies, snow scorpionflies
- Order Siphonaptera: Fleas
- Order Diptera: True flies, mosquitoes, gnats

Amphiesmenoptera

- Order Trichoptera: Caddisflies
- Order Lepidoptera: Butterflies, moths

Hexapod Classification

Subphylum Hexapoda

Body differentiated into head (acron + 6 segments), thorax (3 segments), and abdomen (11 or fewer segments); cephalon with one pair lateral compound eyes and often with a triad or pair of medial ocelli; with one pair of uniramous multiarticulate antennae, mandibles, and maxillae; second pair of maxillae fused to form a complex labium; each thoracic segment with one pair of uniramous legs; wings often present on second and third thoracic segments (in pterygote insects); abdomen without fully developed legs, but "prolegs" (presumably homologous to the ancestral arthropod abdominal appendages) occur in at least seven orders (in adults of some Diplura, Thysanura, and Archaeognatha; in larvae of some Diptera, Trichoptera, Lepidoptera, and Hymenoptera); abdomen with a large fat body; gonopores open on the last abdominal segment or on the seventh, eighth, or ninth abdominal segment; paired cerci often present; males commonly with intromittent and clasping structures; development direct, involving relatively slight changes in body form (ametabolous or hemimetabolous), or indirect with striking changes (holometabolous).

Entognatha

Mouthparts with bases hidden within the head capsule (ento-gnathous); mandibles with single articulation; most or all antennal articles with intrinsic musculature; wingless; without, or with poorly developed, Malpighian tubules; legs with one (undivided) tarsus. The three orders of entognathous hexapods do not form a monophyletic group. While the entognathous conditions of Collembola and Protura appear to be homologous (these two orders are often placed together in the class Ellipura), entognathy in the Diplura may be a product of convergent evolution. Recent data from paleontology, comparative anatomy, and molecular phylogenetics suggest that the Diplura are the sister group of the Insecta, and are therefore more closely related to the Insecta than they are to the other entognathous orders.

Order Collembola Approximately 6,000 described species (Figure 22.1A,B). Small (most less than 6 mm); biting-chewing mouthparts; with or without small compound eyes; ocelli vestigial; antennae 4-articulate, first 3 articles with intrinsic muscles; tarsus of legs indistinct (perhaps fused with tibia); pretarsus of legs with single claw; abdomen with a reduced number of

segments (six); first abdominal segment with ventral tube (collophore) of unknown function; third abdominal segment with small process (retinaculum); a forked tail-like appendage on fourth or fifth abdominal segment (furcula); without cerci; with gonopores on last abdominal segment; without Malpighian tubules; often without spiracles or tracheae.

The earliest known hexapods in the fossil record are collembolans. *Rhyniella praecursor* and other species from the Lower Devonian closely resemble some modern collembolan families. Unlike other hexapods, which breathe using internal tubes called trachea, springtails breathe air directly through their cuticle and epidermis. Their cuticle repels water, allowing them to live in moist environments without suffocating. They also have a remarkable system for escaping predators. While at rest, the furcula is retracted under the abdomen and held in place by the retinaculum. When the furcula and retinaculum disassociate, the furcula swings downwards with such force that it hits the substrate, and quickly propels the collembolan high into the air. Many workers believe that springtails evolved via neoteny.

Order Protura Approximately 200 described species (Figure 22.1D). Minute (smaller than 2 mm); whitish; without eyes, abdominal spiracles, hypopharynx, or cerci; Malpighian tubules are small papillae; sucking mouthparts; stylet-like mandibles; vestigial antennae; first pair of legs carried in an elevated position and used as surrogate “antennae”; pretarsus of legs with single claw; abdomen 11-segmented, with a telson (perhaps reminiscent of their crustacean ancestors); the segmental nature of this telson or twelfth “segment” has not been confirmed; first 3 abdominal segments with small appendages; without external genitalia, but male gonopores on protrusible phallic complex; gonopores on last abdominal segment; with or without tracheae; simple development.

Proturans are the only hexapods with anamorphic development, a type of development in which a new abdominal segment is added with each instar (or molt). All other insects have epimorphic development, in which segmentation is complete before hatching. Proturans are rare, and live in leaf litter, moist soils, and rotting vegetation.

Order Diplura Approximately 800 described species (Figure 22.1C); fossils date to the Carboniferous. Small (less than 4 mm); whitish; without eyes, ocelli, external genitalia or Malpighian tubules; chewing mouthparts; abdomen 11-segmented, but embryonic segments 10 and 11 fuse before hatching; gonopores on ninth abdominal segment; 7 pairs of lateral abdominal leglets; 2 caudal cerci; with tracheae and up to 7 pairs of abdominal spiracles; antennae multiarticulate, each

article with intrinsic musculature; simple development. Most species live in mesic habitats beneath rocks, rotting logs, leaf litter, humus, and soil.

Class Insecta

Mouth appendages ectognathous (exposed and projecting from the head capsule); mandibles with two points of articulation (except Archaeognatha); intrinsic musculature of antennal articles greatly reduced; antennal pedicel with a mechanoreceptor that perceives the movement of the flagellum, called the Johnston’s organ; head with a tentorial bridge connecting the posterior tentorial arms; tarsi subdivided into tarsomeres; with well-developed Malpighian tubules; ovipositor formed from modifications of the appendages of abdominal segments 8 and 9. The Insecta comprise two clades, the order Archaeognatha (with monocondylic mandibles) and all other insects (the clade Dicondylia, with dicondylic mandibles). Dicondylia also comprise two clades, the order Thysanura and the subclass Pterygota (winged insects).

Order Archaeognatha Approximately 390 described species (Figure 22.2A,B). Small (to 15 mm), wingless (perhaps secondarily), resembling silverfish but body more cylindrical; ocelli present; compound eyes large and contiguous; body usually covered with scales; mandibles biting–chewing; with a single condyle (articulation point); maxillary palp large and leglike; tarsi 3-articulate; middle and hind coxae usually with exites (“styli”); abdomen 11-segmented, with 3 to 8 pairs of lateral leglets (“styli”) and 3 caudal filaments; simple development. Jumping bristletails are usually found in grassy or wooded areas under leaves, bark, or stones.

Dicondylia

Includes Thysanura and the Pterygota. These insects have mandibles with a two condyles (articulation points).

Order Thysanura Approximately 450 described species (Figure 22.2C,D). Small, wingless, resembling Archaeognatha but with flattened body; with or without ocelli; compound eyes reduced, not contiguous; body usually covered with scales; mandibles biting–chewing; antennae multiarticulate, but only basal article with musculature; tarsi 3- to 5-articulate; abdomen 11-segmented, with lateral leglets (often called styli) on segments 2–9, 7–9, or 8–9; 3 caudal cerci; female gonopores on eighth abdominal segment, male gonopores on tenth; without copulatory organs; with tracheae; simple development. Silverfish occur in leaf litter or under bark or stones, or in buildings, where they may feed on wallpaper paste, bookbindings, and the starch sizing of some fabrics.

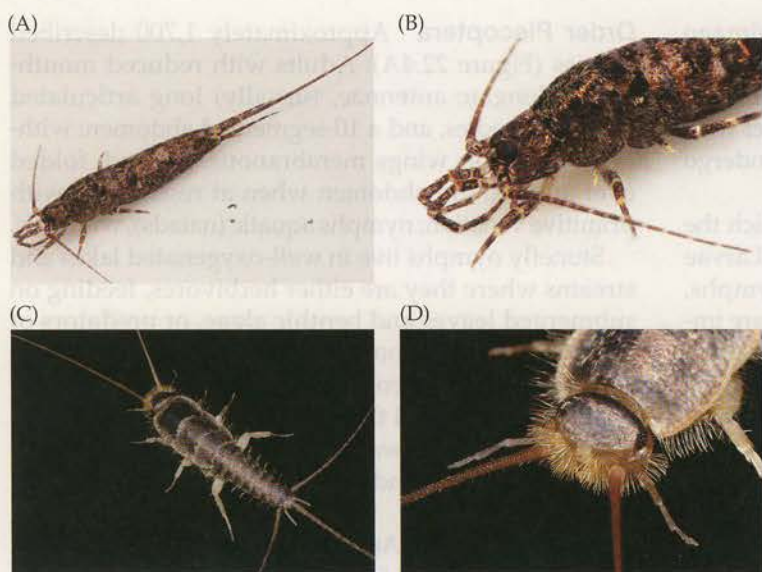


Figure 22.2 Representatives of the two orders of wingless Insecta. (A) Jumping bristletail (order Archaeognatha) and (B) Close-up of jumping bristletail head, note the eyes are contiguous. (C) A silverfish (order Thysanura). (D) Close-up of silverfish head. Note that eyes are not contiguous, but set wide apart, and that the bodies of both of these groups are covered with scales.

Subclass Pterygota

The winged insects (with a pair of wings on the second and third thoracic segments), the forewings (front wings) and hindwings; wings may be secondarily lost in one or both sexes, or modified for functions other than flight; adults without abdominal leglets except on genital segments; female gonopores on eighth abdominal segment, male on tenth; female often with ovipositor; molting ceases at maturity.

Palaeoptera

Wings cannot be folded, and when at rest wings are either held straight out to the side or vertically above the abdomen (with dorsal surfaces pressed together); wings always membranous, with many longitudinal veins and cross veins; wings tend to be fluted, or ac-

cordion-like; antennae highly reduced or vestigial in adults; hemimetabolous development; larvae aquatic. Two extant orders; many extinct groups.

Order Ephemeroptera Approximately 2,500 described species (Figure 22.3A). Adults with vestigial mouthparts, minute antennae, and soft bodies; wings held vertically over body when at rest; forewings present; hindwings absent or present but much smaller than forewings; long, articulated cerci, usually with medial caudal filament; male with first pair of legs elongated for clasping female in flight; second and third legs of male, and all legs of female, may be vestigial or absent (Polymitarcyidae); abdomen 10-segmented; larvae aquatic; young (nymphs) with paired articulated lateral gills, caudal filaments, and well developed

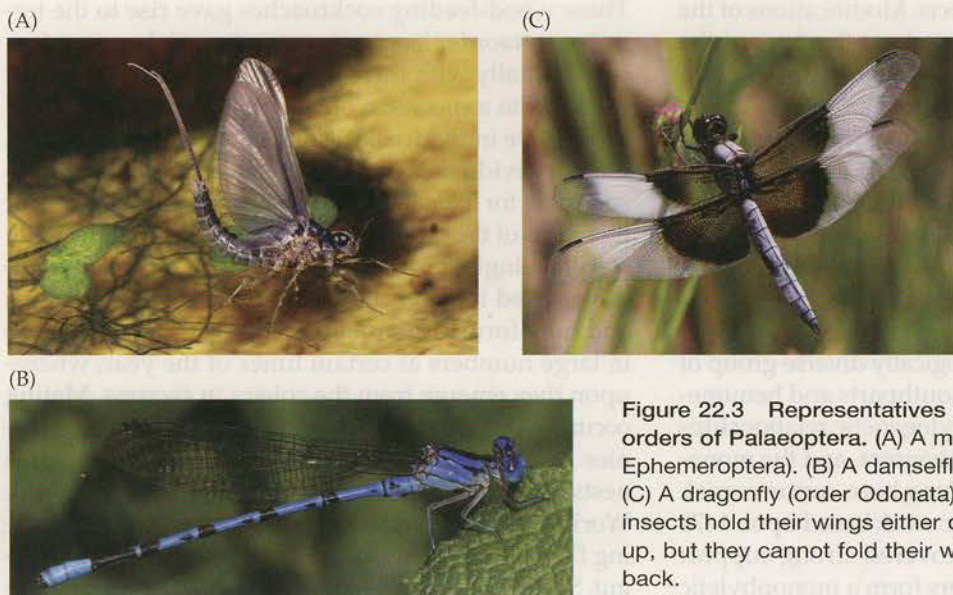


Figure 22.3 Representatives of the two orders of Palaeoptera. (A) A mayfly (order Ephemeroptera). (B) A damselfly (order Odonata). (C) A dragonfly (order Odonata). Note all of these insects hold their wings either out flat or straight up, but they cannot fold their wings over their back.

mouthparts; adults preceded by winged subimago stage. The mayfly subimago (subadult) is the only winged insect known to undergo an additional molt. It is the one exception to the rule, that an insect with wings is a mature adult insect and will never undergo another molt.

Mayflies are primitive winged insects in which the aquatic nymphal stage dominates the life cycle. Larvae hatch in fresh water and become long-lived nymphs, passing through many instars. Mayfly nymphs are important food for many stream and lake fishes. Adults eclose in synchrony and live only a few hours or days (hence the name, “ephemeral winged”), do not feed, and copulate in the air, sometimes in large nuptial swarms.

Order Odonata Approximately 6,000 described species (Figure 22.3B,C). Adults with small filiform antennae, large compound eyes, and chewing mouthparts with massive mandibles; larval labium modified into prehensile organ; two pairs of large wings, held outstretched (dragonflies) or straight up over body (damselflies) when at rest; abdomen slender and elongate, 10-segmented; male with accessory genitalia on second and third abdominal sternites; eggs and larvae aquatic, with caudal or rectal gills.

Dragonflies and damselflies are spectacular insects with broad public appeal, not only for their beauty but because they are fast flyers and consume large numbers of insect pests, including mosquitoes, on the wing. Larvae and adults are both highly active predators, with larvae consuming various invertebrates and adults capturing other flying insects. Many species are 7–8 cm long, while some extinct forms had a wingspan of over 70 cm.

Infraclass Neoptera

The modern, wing-folding insects. Modifications of the sclerites and an associated muscle at the base of the wings, allow neopterans to rotate their wing joint and fold back their wings when they are not flying. This is one of the most important evolutionary innovations in hexapods. Wing folding allows insects to protect their fragile wings, especially from abrasion, thereby allowing them to live in tight spaces such as crevices under bark, under rocks, in burrows, nests, and tunnels.

Superorder Polyneoptera

Polyneopterans are a morphologically diverse group of insects with biting–chewing mouthparts and hemimetabolous development. The phylogenetic relationships among the orders within Polyneoptera, and the monophyly of the group itself have long been controversial. However, recent phylogenomic work based upon 1478 single-copy nuclear genes, recovered strong support that the 10 polyneopteran orders form a monophyletic group (Misof et al. 2014).

Order Plecoptera Approximately 1,700 described species (Figure 22.4A). Adults with reduced mouthparts, elongate antennae, (usually) long articulated cerci, soft bodies, and a 10-segmented abdomen; without ovipositor; wings membranous, pleated, folded over and around abdomen when at rest; wings with primitive venation; nymphs aquatic (naiads), with gills.

Stonefly nymphs live in well-oxygenated lakes and streams where they are either herbivores, feeding on submerged leaves and benthic algae, or predators of other aquatic arthropods. They are an important food resource for fish. Plecopteran nymphs are intolerant of water pollution, and their presence is often used as a bioindicator of high water quality. Adults of most species are short-lived and die soon after mating.

Order Blattodea Approximately 7,000 described species (Figure 22.4B,C). Two major body forms: cockroaches and termites. Cockroaches have a dorsoventrally flattened body; large pronotum, with expanded margins extending over head; forewings (when present) leathery; hindwings expansive and fanlike; ovipositor reduced; cerci multiarticulate; legs adapted for running; eggs laid in cases (ootheca). Termites are small; soft-bodied; wings equal-sized, elongate, membranous, dehiscent (shed by breaking at basal line of weakness); antennae short, filamentous, with 11–33 articles; cerci small to minute; ovipositor reduced or absent; many with rudimentary or no external genitalia; marked polymorphism.

Of the 4,000 described species of cockroaches, fewer than 40 are domestic (household inhabitants). Some species are omnivores, while others are restricted in diet. Most species are tropical, but some live in temperate habitats, caves, deserts, and ant and bird nests. Some live in and feed on wood and have intestinal flora that aid in cellulose digestion (*Cryptocercus*). These wood-feeding cockroaches gave rise to the termites (infraorder Isoptera), a strictly social group of insects, usually with three distinct types of individuals, or castes, in a species: workers, soldiers, and alates (reproductive individuals). Workers are generally sterile, blind individuals with normal mandibles; they are responsible for foraging, nest construction, and caring for members of the other castes. Soldiers are blind, usually sterile, wingless forms with powerful enlarged mandibles used to defend the colony. Alates have wings and fully formed compound eyes. They are produced in large numbers at certain times of the year, whereupon they emerge from the colony in swarms. Mating occurs at this time, and individual pairs start new colonies. Wings are shed after copulation. Colonies form nests (termitaria) in wood that is in or on the ground. Workers harbor a variety of symbiotic cellulose-digesting flagellate protists in special chambers in the hindgut. Some families contain symbiotic bacteria that serve the same purpose. Termites often occur in enormous

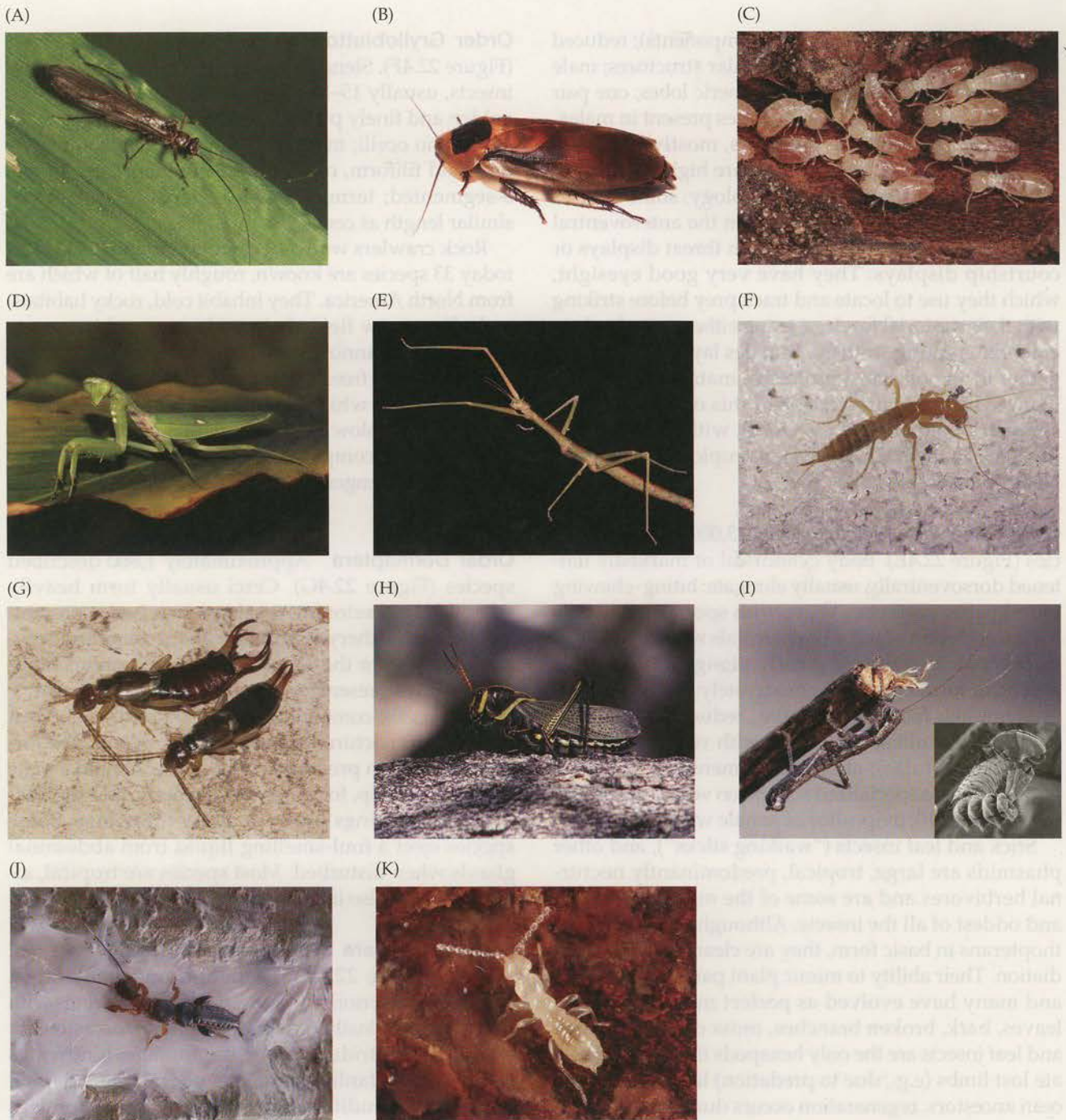


Figure 22.4 Representatives of the ten orders of Polyneoptera. (A) A stonefly (order Plecoptera). (B) A cockroach (order Blattodea). (C) Termites (order Blattodea, infraorder Isoptera). (D) A mantid (order Mantodea). (E) A stick insect (order Phasmida). (F) A rock crawler (order Grylloblattodea). (G) Earwigs (order Dermaptera). (H) A horse lubber grasshopper (order Orthoptera). (I) A heelwalker (order Mantophasmatodea), inset SEM of the tarsus of a heelwalker showing enlarged arolium. (J) A webspinner (order Embioptera). (K) A zorapteran (order Zoraptera).

numbers; one spectacular estimate suggests that there are about three-quarters of a ton of termites for every person on Earth! There is strong morphological and

molecular evidence that order Blattodea is the sister group of the order Mantodea. Together these two groups are referred to as the Dictyoptera.

Order Mantodea Approximately 2,400 described species (Figure 22.4D). First pair of legs large and raptorial; prothorax elongate; head highly mobile due to cervical sclerites that lend structural and musculature support, with very large compound eyes, not covered by the pronotum; forewings thickened, hindwings membranous; abdomen 11-segmented, 10 visible segments and the fragmented epiproct (which is made

up of a median and two lateral components); reduced ovipositor made up of three valvular structures; male genitalia made up of three phallogomeric lobes; one pair multiarticulate cerci; styli sometimes present in males.

Mantises are obligate predators, mostly on insects and spiders. While many species are highly cryptic in both color and structural morphology, some species feature brightly colored patches on the anteroventral surface of their forecoxae to use in threat displays or courtship displays. They have very good eyesight, which they use to locate and track prey before striking with their raptorial forelegs, using either an ambush or cursorial hunting strategy. Females lay many eggs together in an ootheca, a protective matrix of hardened foam, which is characteristic of this order. Mantises are distributed around the world, with their greatest diversity in the Indo-Malaysian, tropical African, and Neotropical regions.

Order Phasmida Approximately 3,000 described species (Figure 22.4E). Body cylindrical or markedly flattened dorsoventrally, usually elongate; biting-chewing mouthparts; prothorax short, with specialized glands for the excretion of noxious chemicals when disturbed; meso- and metathorax greatly elongate; forewings absent, or forming small to moderately elongate, leathery tegmina; hindwings absent, reduced to leathery tegmina, or fanlike; tarsomeres with ventral adhesive pads (euplantulae); short, unsegmented cerci; male with vomer—a specialized sclerite on venter of abdominal segment 10; ovipositor of female weak.

Stick and leaf insects (“walking sticks”), and other phasmids are large, tropical, predominantly nocturnal herbivores and are some of the most spectacular and oddest of all the insects. Although resembling orthopterans in basic form, they are clearly a distinct radiation. Their ability to mimic plant parts is legendary, and many have evolved as perfect mimics of twigs, leaves, bark, broken branches, moss or lichens. Stick and leaf insects are the only hexapods that can regenerate lost limbs (e.g., due to predation) like their crustacean ancestors; regeneration occurs during molts, with the new legs markedly smaller than original limbs but increasing in relative size with each successive molt (as in Crustacea). Phasmids are the only insect order with species-specific egg morphology across the entire order. The eggs of some species even mimic angiosperm seeds and are spread via ant-mediated dispersal. The order includes the longest extant insects on Earth, including the world's longest at just over 56 cm in length, though some are less than 4 cm. Sexual dimorphism is so striking that males and females have often mistakenly been given different species names. Phasmids are facultatively parthenogenetic; in the absence of males, females can produce viable eggs that are genetic clones of their mother.

Order Grylloblattodea Approximately 30 species (Figure 22.4F). Slender, elongate, cylindrical, wingless insects, usually 15–30 mm long. Body usually pale or golden and finely pubescent; compound eyes small or absent; no ocelli; mouthparts mandibulate; antennae long and filiform, of 23–45 antennomeres, cerci long, 8-segmented; terminal sword-shaped ovipositor of similar length as cerci.

Rock crawlers were not discovered until 1914, and today 33 species are known, roughly half of which are from North America. They inhabit cold, rocky habitats, including snow fields below glaciers and ice caves. Most species cannot tolerate warm temperatures, but thrive at below freezing temperatures. Due to the cold temperature at which they live, growth and development are very slow. Rock crawlers may require up to seven years to complete a single generation. They are nocturnal scavengers on dead insects and other organic matter.

Order Dermaptera Approximately 1,800 described species (Figure 22.4G). Cerci usually form heavily sclerotized posterior forceps; forewings (when present) form short, leathery tegmina, without veins and serving as covers for the semicircular, membranous hindwings (when present); ovipositor reduced or absent.

Earwigs are common in urban environments. Most appear to be nocturnal scavenging omnivores. The forceps are used in predation, for defense, to hold a mate during courtship, for grooming the body, and for folding the hindwings under leathery forewings. Some species eject a foul-smelling liquid from abdominal glands when disturbed. Most species are tropical, although many also inhabit temperate regions.

Order Orthoptera Approximately 23,000 described species (Figure 22.4H). Pronotum unusually large, extending posteriorly over mesonotum; forewings with thickened and leathery region (tegmina), occasionally modified for stridulation or camouflage; hindwings membranous, fanlike; hindlegs often large, adapted for jumping; auditory tympana present on forelegs and abdomen; tarsomeres with ventral adhesive pads (euplantulae); ovipositor large; male genitalia complex; cerci distinct, short, and jointed.

Grasshoppers and their kin are common and abundant insects at all but the coldest latitudes. This order includes some of the largest living insects. Most are herbivores, but many are omnivorous, and some are predatory. Stridulation, which is common among males, is usually accomplished by rubbing the specially modified forewings (tegmina) together, or by rubbing a ridge on the inside of the hind femur against a special vein of the tegmen. No orthopterans stridulate by rubbing the hindlegs together, as is often thought. Common families include Acrididae (short-horned

grasshoppers), Gryllotalpidae (mole crickets), Gryllacrididae (Jerusalem crickets), Tetrigidae (pygmy grasshoppers); Tridactylidae (pygmy mole crickets); Gryllacrididae (cave crickets); Gryllidae (crickets); Tetti-goniidae (long-horned grasshoppers, katydids).

Order Mantophasmatodea Approximately 20 species (Figure 22.4I). Head hypognathous, with generalized mouthparts; antennae long, filiform; ocelli absent; wings entirely lacking; coxae elongate; tarsi with 5 tarsomeres, pretarsus of all legs with an unusually large arolium; cerci short, one-segmented.

The Mantophasmatodea is the most recently described order of insects (2002) and the only new insect order described since 1914. The order includes several living species (from Namibia, South Africa, Tanzania, and Malawi) and six fossil species (5 from Baltic amber and one fossil from China). They resemble a mix between praying mantises and phasmids, but molecular evidence indicates that they are most closely related to the Grylloblattodea.

Mantophasmatodeans have several distinct characteristics, including a hypognathous head and, most strikingly, when walking all species keep the fifth tarsomere and pretarsus (a greatly enlarged arolium plus two tarsal claws) of each leg turned upwards and off the substrate, giving them the appearance of “walking on their heels.” Both sexes are wingless. They are highly flexible along their longitudinal body axis enabling them to clean their external genitalia with their mouthparts. During the day they hide in bushes, rock crevices or clumps of grass and prey on spiders and insects at night. Males and females produce percussive signals by tapping their abdomens on the substrate to locate mates.

Order Embioptera (Embiidina) Approximately 400 described species (Figure 22.4J). Males somewhat flattened; females and young cylindrical. Most about 10 mm long, however Southeast Asian species in the genus *Ptilocerembia* are approximately 20 mm long. Antennae filiform; ocelli lacking; chewing mouthparts; head prognathous; legs short and stout; tarsi 3-articulate; hind femora greatly enlarged. The basal article of the front tarsus is enlarged and contains glands that produce silk, which is spun from a dense field of hollow hairlike structures on the ventral surface. Males of most species are winged, but some are wingless; females and nymphs are always wingless. Abdomen 10-segmented, with rudiments of the eleventh segment, and a pair of short cerci.

Webspinners are small, slender, chiefly tropical insects. They live gregariously in silken galleries that they construct in leaf litter, under or on stones, in soil cracks, in bark crevices, and in epiphytic plants. Wings are made rigid for flight and flexible in galleries, by regulating the hemocoelic fluid pressure in the radial

blood sinuses in both pairs of wings. They feed mostly on dead plant material and also graze on the outer bark of trees, and on mosses and lichens.

Order Zoraptera Approximately 40 species (Figure 22.4K). Minute (to 3 mm); termite-like; colonial; wingless or with wings; wings eventually shed; antennae moniliform, 9-articulate; abdomen short, oval, 10-segmented; chewing mouthparts; simple development. These uncommon insects are usually found in gregarious colonies in dead wood, but they do not have a division of labor or polymorphism (as in termites and ants). They feed chiefly on mites and other small arthropods. All extant species are classified in the single genus *Zorotypus*. The sister group relationship of this order remains controversial and elusive.

Superorder Acercaria

The superorder Acercaria is sometimes referred to as the Paraneoptera or the “hemipteroids.” These insects are characterized by (usually) short antennae, enlarged cibarial (feeding) muscles, visible externally as an enlarged portion of the head; lacinia slender and elongate; sucking mouthparts, tarsi with three or fewer tarsomeres, absence of cerci, lack of true male gonopods, wings (when present) with reduced venation, and hemimetabolous development (although life cycles in several groups includes one or two inactive pupa-like stages).

Order Thysanoptera Approximately 5,000 described species (Figure 22.5D). Slender, minute (0.5–1.5 mm) insects with long, narrow wings (when present) bearing long marginal setal fringes; mouthparts form a conical, asymmetrical sucking beak; left mandible a stylet, right mandible vestigial; with compound eyes; antennae with 4–10 flagellomeres; abdomen 10-segmented; without cerci; tarsi 1–2 segmented, with an eversible, pretarsal eversible adhesive sac, or arolium. Thrips are mostly herbivores or predators, and many pollinate flowers. They are known to transmit plant viruses and fungal spores. “Thrips” is both singular and plural.

Order Hemiptera Approximately 85,000 species (Figure 22.5A,B). Piercing–sucking mouthparts form an articulated beak, mandibles and first maxillae stylet-like, lying in dorsally grooved labium; forewings either completely membranous, or hardened basally and membranous only distally; hindwings membranous; pronotum large.

Hemipterans occur worldwide and in virtually all habitats. Hemipterans are liquid feeders. Most feed on the xylem or phloem of plants, although many feed on the hemolymph of arthropods or blood of vertebrates and some are specialized ectoparasites. They are of considerable economic importance because many

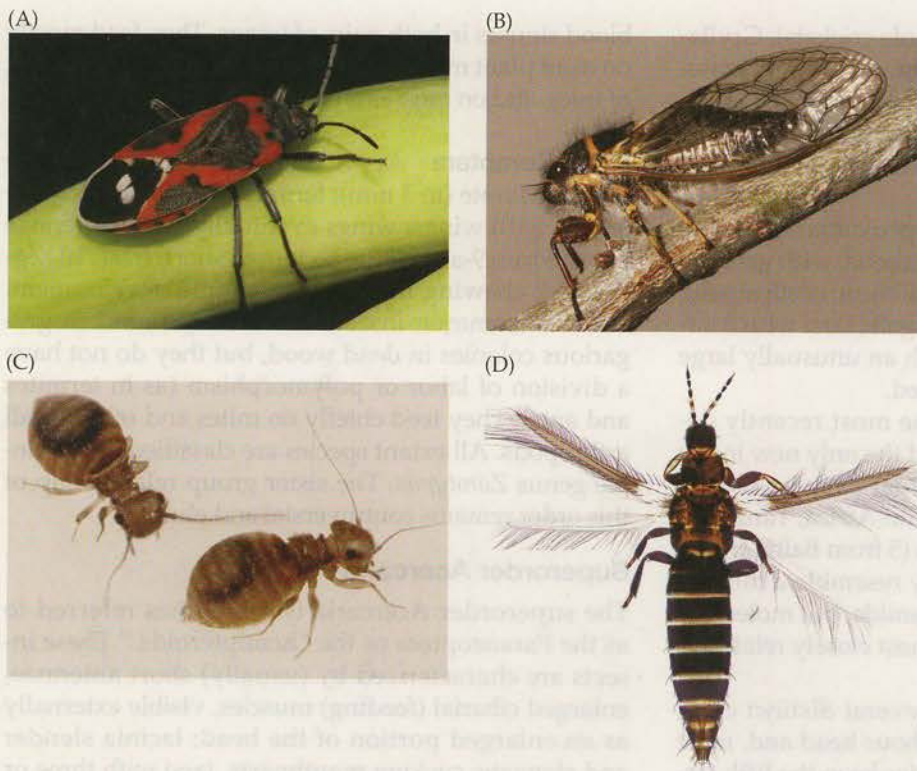


Figure 22.5 Representatives of the three orders of Acercaria. (A) A true bug (order Hemiptera). (B) A cicada (order Hemiptera). (C) Two bark lice (order Psocodea). (D) A thrips (order Thysanoptera). Note that “thrips” is both singular and plural.

are serious crop pests. Members of one subfamily of Reduviidae (Triatominae, the assassin or kissing bugs) transmit Chagas disease. Others have more positive economic importance to humans, such as the cochineal bugs (Dactylopiidae), from which a safe red dye (cochineal) is extracted for use in the food industry. Shellac is made from lac, a chemical produced by members of the family Kerriidae (lac insects). One of the most famous hemipterans are the 17-year cicadas (genus *Magiciada*), which have a very long life cycle and synchronized development and can reach plague-like levels of abundance (to 3.7 million individuals per hectare). Common predacious hemipteran families include Nepidae (water scorpions), Belostomatidae (giant water bugs or “toe biters”), Corixidae (water boatmen), Notonectidae (backswimmers), Gerridae (water striders), Saldidae (shore bugs), Cimicidae (bedbugs), and Reduviidae (assassin bugs).

Many others are plant feeders (hence the common name “plant bugs”). Heavy infestations of these insects on plants may cause wilting, stunting, or even death, and some are vectors of important plant diseases. Common herbivorous families include the Cicadidae (cicadas), Cicadellidae (leafhoppers), Fulgoridae (planthoppers), Membracidae (treehoppers), Cercopidae (spittle bugs and froghoppers), Aleyrodidae (whiteflies), and Aphidae (aphids), as well as members of the large superfamily Coccoidea (coccoids, scale insects, mealybugs, and many others).

Order Psocodea Approximately 8,500 described species (Figure 22.5C). Until recently, species in this order

were classified in two separate orders: the Psocoptera (the book and bark lice) and the Phthiraptera (the true lice). Psocopterans are small (1–10 mm long); with long, filiform, multiarticulate antennae; short prothorax; meso- and metathorax often fused; chewing mouthparts; abdomen 9-segmented; without cerci. Phthirapterans are even smaller (less than 5 mm), wingless, blood-sucking, obligate ectoparasites of birds and mammals; thoracic segments completely fused; cuticle largely membranous and expandable to permit engorgement; compound eyes absent or of 1–2 ommatidia; ocelli absent; piercing-sucking mouthparts retractable into a buccal pouch; antennae short (5 or fewer flagellomeres), exposed or concealed in grooves beneath the head; with 1 pair dorsal thoracic spiracles and 6 or fewer abdominal spiracles; without cerci; females lack ovipositor.

Psocids—the book and bark lice—generally feed on algae and fungi, and occur in suitably moist areas (e.g., under bark, in leaf litter, under stones, in human habitations where humid climates prevail). They are often pests that get into various stored food products or consume insect and plant collections; some species live in books and eat the bindings. Commonly called sucking lice (“Anoplura”) and biting lice (“Mallophaga”), phthirapterans spend their entire life on one host. Eggs (nits) are usually attached to the hair or feathers of the host, although the human body louse (a “sucking louse”) may attach eggs to clothing. No biting lice are known to infest humans. Posthatching development comprises three nymphal instars. Some species that infest domestic birds and mammals are of economic significance.

Superorder Holometabola

Holometabola is a monophyletic group strongly supported by both morphological and molecular data. One of its key synapomorphies is indirect (holometabolous) development, with distinct egg, larval, pupal, and adult states. During the pupal stage, most tissues undergo a complete reorganization (e.g., larval eyes [stemmata] disintegrate and adult compound eyes and ocelli form *de novo*). Another key apomorphy is the presence of internal wing buds (imaginal discs) in the larval stage; these clusters of early embryonic cells arise from localized invaginations of the ectoderm in the early embryo and form adult structures during pupation.

Order Hymenoptera Approximately 115,000 described species (Figure 22.6A). Mouthparts often elongate and modified for ingesting floral nectar, although mandibles usually remain functional; labium often (bees) distally expanded as paired lobe-like structures called glossae and paraglossae; three ocelli; usually with two pairs of membranous wings; hindwings small, coupled to forewings by hooks (hamuli); wing venation highly reduced; antennae well developed, of various forms and with 3–70 flagellomeres, reduced metathorax usually fused to first abdominal segment; males with complex genitalia; females with ovipositor (in most), modified for sawing, piercing, or stinging.

The earliest fossil Hymenoptera date from the Triassic (220–207 Ma). Ants, bees, wasps, sawflies, and their relatives are all active insects with a tendency to form polymorphic social communities. Two suborders are generally recognized. Suborder Symphyta contains the primitive, wasplike, “thick-waisted” hymenopterans (sawflies, horntails, and their kin). They rarely show conspicuous sexual dimorphism and are always fully winged. The first and second abdominal segments are broadly joined. Larvae are mostly caterpillar-like, with a well-developed head capsule, true legs, and often also with abdominal prolegs. Suborder Apocrita contains the “narrow-waisted” hymenopterans (true wasps, bees, and ants), in which the first and second abdominal segments are joined by a distinct and often elongate constriction. Adults tend to be strongly social and display marked polymorphism. Social communities often include distinct castes of queens, haploid males, parthenogenetic females, and individuals with other sex-related specializations, as well as non-reproducing worker and soldier forms. Common families of Hymenoptera include the Apidae (bumblebees and honeybees), Formicidae (ants), Vespidae (yellow jackets, hornets, paper wasps, and potter wasps), Halictidae (sweat bees), Sphecidae (sand wasps, digger wasps, and mud-daubers), and three large groups of parasitic wasps (Ichneumonidae, Braconidae, Chalcidoidea).

Coleoptera

The Coleoptera includes two orders the Coleoptera (beetles) and the Strepsiptera (twisted wing parasites). This clade includes the most diverse order of insects (Coleoptera) and one with the most highly modified and morphologically and developmentally aberrant groups of parasites (Strepsiptera). Largely due to their bizarre combination of morphological characters, and the high rate of molecular evolution in many strepsipteran genes, the sister group relationship of the Strepsiptera eluded researchers until very recently. In the past, Strepsiptera were considered at various times to be close relatives of either Hymenoptera, Diptera, or Coleoptera. Recent genome-wide analyses and new morphological evidence strongly suggests that they are in fact the sister group to the Coleoptera.

Order Coleoptera Approximately 380,000 described species (Figure 22.6B). Body usually heavily sclerotized; forewings sclerotized and modified as rigid covers (elytra) over hindwings and body; membranous hindwings fold both transversely and longitudinally, and are often reduced or absent; biting-chewing mouthparts; antennae usually with 8–11 flagellomeres; prothorax large and mobile; mesothorax reduced; abdomen typically of 5 (or up to 8) segments; without ovipositor; male genitalia retractable.

Coleoptera is the largest order of insects. Many hypotheses have been proposed to explain the extraordinary diversity of beetles, including: (1) their age, the oldest fossils date to the early Permian but they most probably arose in the late Carboniferous (300 Ma); (2) their heavily sclerotized bodies, including their protective elytra, and general lack of exposed membranous surfaces facilitates their adaptation to a wide variety of tight narrow spaces and reduced their risk of predation; and (3) their co-evolution with the great angiosperm radiation in the Cretaceous period. Today, beetles range from minute (0.35 mm, *Nanosella fungi*) to very large (20 cm, *Titanus giganteus*) and occur in all the world’s environments (except the open sea). Some of the world’s strongest animals are beetles: rhinoceros beetles can carry up to 100 times their own weight for short distances, and 30 times their weight indefinitely (equivalent to a 150-pound man walking with a Cadillac on his head—without tiring). Humans have had a long fascination with beetles, and beetle worship can be traced back to at least 2500 BC. (The venerated scarab of early Egyptians was actually a dung beetle.)

Some common coleopteran families include Carabidae (ground beetles), Dytiscidae (predaceous diving beetles), Gyrinidae (whirligig beetles), Hydrophilidae (water scavenger beetles), Staphylinidae (rove beetles), Cantharidae (soldier beetles), Lampyridae (fireflies and lightning bugs), Phengodidae (glowworms), Elateridae (click beetles), Buprestidae (metallic wood-boring beetles), Coccinellidae (ladybird

beetles), Meloidae (blister beetles), Tenebrionidae (darkling beetles), Scarabaeidae (scarab beetles, dung beetles, June "bugs"), Cerambycidae (long-horned beetles), Chrysomelidae (leaf beetles), Curculionidae (weevils), Brentidae (primitive weevils), and Ptiliidae (featherwinged beetles, the smallest of all beetles, some with body lengths of just 0.35 mm).

Order Strepsiptera Approximately 600 described species (Figure 22.6C). Extreme sexual dimorphism; males free-living and winged; females wingless, usually parasitic. Females of free-living species with distinct head, simple antennae, chewing mouthparts, and compound eyes. Females of parasitic species neotenuous, larviform, usually without eyes, antennae, and legs; with indistinct body segmentation. Male antennae often with elongate processes on flagellomeres; forewings reduced to club-like structures resembling halteres of Diptera; hindwings large and membranous, with reduced venation; raspberry-like eyes.

Most of these minute insects are parasitic on other insects. Adult females of parasitic species are larviform and most commonly live between the abdominal sclerites of flying insects that pollinate flowers, such as bees and wasps. Winged males find the females on the bee or wasp abdomen and mate with her. The fertilized eggs hatch into first instar larvae inside their mother's body. These larvae, called triungulins, have well developed eyes and legs and they actively crawl out of their mother to invade the soil and vegetation. The triungulins eventually locate a new host insect and enter it, wherein they molt into a legless wormlike larval stage that feeds in the host's body cavity. Pupation also takes place within the host's body, where the females remain for the rest of their lives and the free-living males emerge as fully formed adults.

Neuropterida

The three orders of Neuropterida have always been considered close relatives. Some workers subsume the Megaloptera and Raphidioptera within the Neuroptera, but all three groups are monophyletic making such a taxonomic decision arbitrary. These three orders have two pairs of membranous wings with many cross veins, 5-segmented tarsi, adults with mandibles, and denticious pupae (with articulated mandibles).

Order Megaloptera Approximately 300 described species (Figure 22.6D). Ocelli present or absent; larvae aquatic, with lateral abdominal gills. Megalopterans (alderflies, dobsonflies, fishflies) strongly resemble neuropterans (and are often regarded as a suborder), but their hindwings are broader at the base than the forewings, and the longitudinal veins do not have branches near the wing margin. Larvae of some megalopterans (hellgrammites) are commonly used as fish bait.

Order Raphidioptera Approximately 260 described species (Figure 22.6E). Snakeflies strongly resemble neuropterans (and are often regarded as a suborder), but are unique in having the prothorax elongate (as in the mantises), but the forelegs similar to the other legs. The head can be raised above the rest of the body, as in a snake preparing to strike. Adults and larvae are predators on small insect prey.

Order Neuroptera Approximately 6,000 described species (Figure 22.6F). Adults soft-bodied; with two pairs of similar, highly veined wings held tent-like over the abdomen when at rest; with biting-chewing mouthparts; abdomen 10-segmented; without cerci; larvae with mandibles and maxillae co-adapted to create a sucking tube; mouth closed off by modified labrum and labium; well developed legs; larval midgut is closed off posteriorly, larval waste accumulates until the adult emerges; Malpighian tubules secrete silk, via the anus, to construct the pupal cocoon.

The lacewings, ant lions, mantisflies, spongillafles, and owlflies form a complex group, the adults of which are often important predators of insect pests (e.g., aphids). The larvae of many species have piercing-sucking mouthparts, and those of other species are predaceous and have biting mouthparts. The pupae are often unusual in possessing free appendages and functional mandibles used for defense; they may actively walk about prior to the adult molt, but do not feed. Common families include Chrysopidae (green lacewings), Myrmeleontidae (ant lions); Ascalaphidae (owlflies); Mantispidae (mantisflies).

Antliophora

The Antliophora include three orders, the Mecoptera, Siphonaptera, and Diptera. There is strong molecular and morphological support for the monophyly of this group. The males of all members of Antliophora have a sperm pump, a structure that aids in sperm transfer during copulation. Many other more characters also define this grouping, most of which have to do with relatively subtle aspects of the adult mouthparts.

Order Mecoptera Approximately 600 described species (Figure 22.6G). Two pairs of similar, narrow, membranous wings, held horizontally from sides of body when at rest; antennae long, slender, and of many flagellomeres (about half the body length); head with ventral rostrum and reduced biting mouthparts; long, slender legs; mesothorax, metathorax, and first abdominal tergum fused; abdomen 11-segmented; female with two cerci; male genitalia prominent and complex, at apex of attenuate abdomen and often resembling a scorpion's stinger. The larvae of some species are remarkable in having compound eyes, a condition unknown among larvae of other insects having complete metamorphosis.

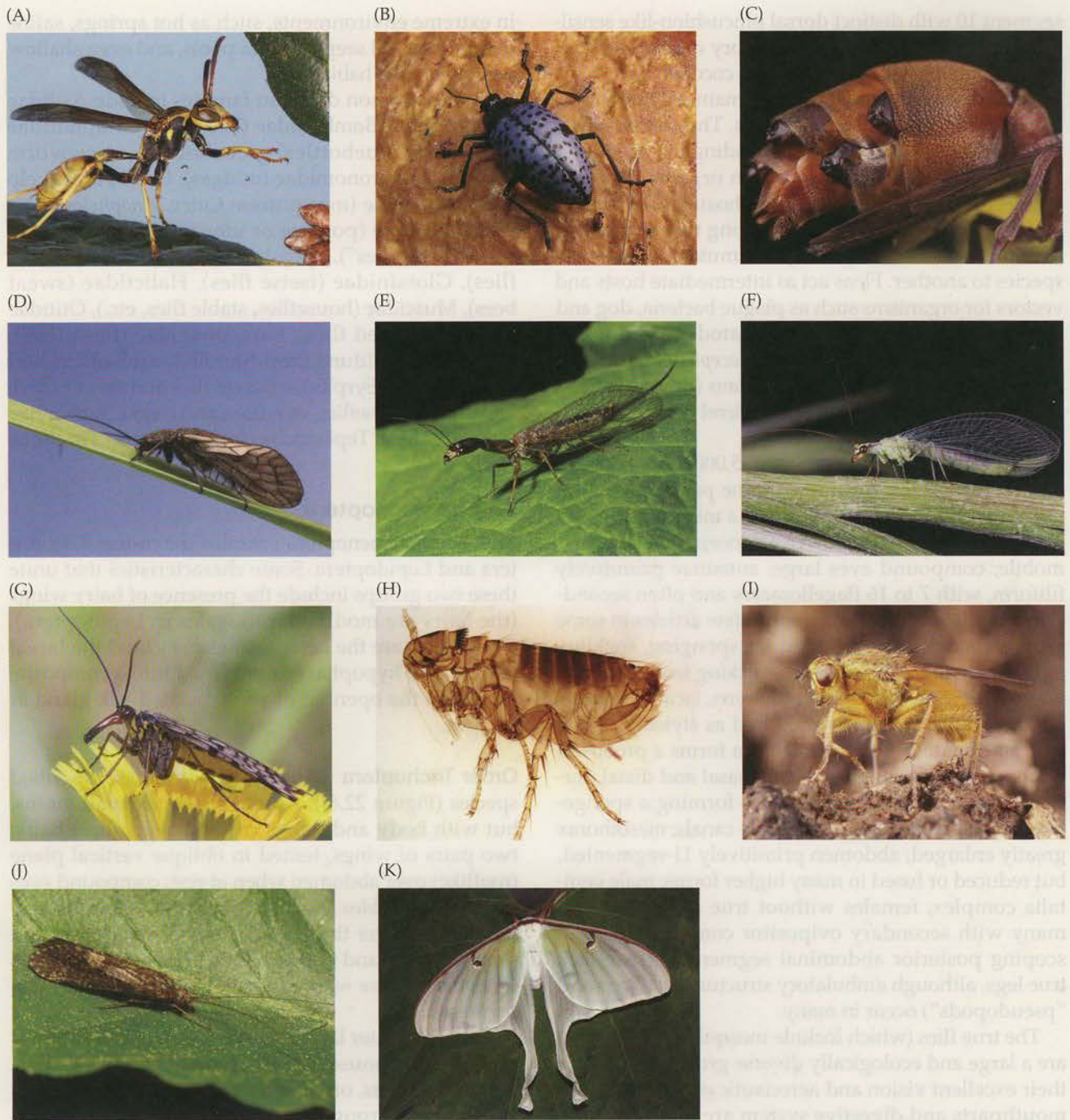


Figure 22.6 Representatives of the eleven orders of Holometabola. (A) A paper wasp (order Hymenoptera). (B) A pleasing fungus beetle, *Gibbifer californicus* (order Coleoptera). (C) Female twisted wing parasites (order Strepsiptera) visible between the abdominal sclerites of a wasp (order Hymenoptera). (D) An alderfly (order

Megaloptera). (E) A snakefly (order Raphidioptera). (F) A green lacewing (order Neuroptera). (G) A scorpionfly (order Mecoptera). (H) A adult male *Oropsylla montana* flea (order Siphonaptera). (I) A golden dung fly (*Scathophaga stercoraria*) (order Diptera). (J) A caddisfly (order Trichoptera). (K) A luna moth (order Lepidoptera).

Mecopterans are usually found in moist places, often in forests, where most are diurnal flyers. They are best represented in the Holarctic region. Some feed on nectar; others prey on insects or are scavengers. There are several families, including Panorpidae (scorpionflies), Bittacidae (hangingflies), and Boreidae (snow scorpionflies).

Order Siphonaptera Approximately 3,000 described species (Figure 22.6H). Small (less than 3 mm long); wingless; body laterally compressed and heavily sclerotized; short antennae lie in deep grooves on sides of head; mouthparts piercing-sucking; compound eyes often absent; legs modified for clinging and (especially hindlegs) jumping; abdomen 11-segmented; abdominal

segment 10 with distinct dorsal pincushion-like sensillum, containing a number of sensory organs; without ovipositor; pupal stage passed in a cocoon.

Adult fleas are ectoparasites on mammals and birds, from which they take blood meals. They occur wherever suitable hosts are found, including the Arctic and Antarctic. Larvae usually feed on organic debris in the nest or dwelling place of the host. Host specificity is often weak, particularly among the parasites of mammals, and fleas regularly commute from one host species to another. Fleas act as intermediate hosts and vectors for organisms such as plague bacteria, dog and cat tapeworms, and various nematodes. Commonly encountered species include *Ctenocephalides felis* (cat flea), *C. canis* (dog flea), *Pulex irritans* (domestic flea), and *Diamus montanus* (western squirrel flea).

Order Diptera Approximately 135,000 described species (Figure 22.6I). Adults with one pair of membranous mesothoracic forewings and a metathoracic pair of club-like halteres (organs of balance); head large and mobile; compound eyes large; antennae primitively filiform, with 7 to 16 flagellomeres and often secondarily annulated (reduced to only a few articles in some groups); mouthparts adapted for sponging, sucking, or lapping; mandibles of blood-sucking females developed as piercing stylets; hypopharynx, laciniae, galeae, and mandibles variously modified as stylets in parasitic and predatory groups; labium forms a proboscis ("tongue"), consisting of distinct basal and distal portions, the latter in higher families forming a sponge-like pad (labellum) with absorptive canals; mesothorax greatly enlarged; abdomen primitively 11-segmented, but reduced or fused in many higher forms; male genitalia complex; females without true ovipositor, but many with secondary ovipositor composed of telescoping posterior abdominal segments; larvae lack true legs, although ambulatory structures (prolegs and "pseudopods") occur in many.

The true flies (which include mosquitoes and gnats) are a large and ecologically diverse group, notable for their excellent vision and aeronautic capabilities. The mouthparts and digestive system are modified for a fluid diet, and several groups feed on blood or plant juice. Dipterans are vastly important carriers of human diseases, such as sleeping sickness, yellow fever, African river blindness, and various enteric diseases. It has been said that mosquitoes (and the diseases they carry) prevented Genghis Khan from conquering Russia, killed Alexander the Great, and played pivotal roles in both world wars. Myiasis—the infestation of living tissue by dipteran larvae—is often a problem for livestock and occasionally for humans. Many dipterans are also beneficial to humans as parasites or predators of other insects and as pollinators of flowering plants. Dipterans occur worldwide and in virtually every major environment (except the open sea). Some breed

in extreme environments, such as hot springs, saline desert lakes, oil seeps, tundra pools, and even shallow benthic marine habitats.

Some common dipteran families include Asilidae (robber flies), Bombyliidae (bee flies), Calliphoridae (blowflies, bluebottles, greenbottles, screwworm flies, etc.), Chironomidae (midges), Coelopidae (kelp flies), Culicidae (mosquitoes: *Culex*, *Anopheles*, etc.), Drosophilidae (pomace or vinegar flies; often also called "fruit flies"), Ephydriidae (shore flies and brine flies), Glossinidae (tsetse flies), Halictidae (sweat bees), Muscidae (houseflies, stable flies, etc.), Otitidae (picture-winged flies), Sarcophagidae (flesh flies), Scatophagidae (dung flies), Simuliidae (blackflies and buffalo gnats), Syrphidae (hover flies and flower flies), Tabanidae (horseflies, deerflies, and clegs), Tachinidae (tachinid flies), Tephritidae (fruit flies), and Tipulidae (crane flies).

Amphiesmenoptera

The Amphiesmenoptera contains the orders Trichoptera and Lepidoptera. Some characteristics that unite these two groups include the presence of hairy wings (the hairs are modified into scales in Lepidoptera), the females are the heterogametic sex, and the larval labium and hypopharynx are fused into a composite lobe with the opening of an associated silk gland at its apex.

Order Trichoptera Approximately 12,000 described species (Figure 22.6J). Adults resemble small moths, but with body and wings covered with short hairs; two pairs of wings, tented in oblique vertical plane (rooflike) over abdomen when at rest; compound eyes present; mandibles minute or absent; antennae usually as long or longer than body, setaceous; legs long and slender; larvae and pupae mainly in fresh water, adults terrestrial; larvae with abdominal prolegs on terminal segment.

The freshwater larvae of caddisflies construct fixed or portable "houses" (cases) made of sand grains, wood fragments, or other material bound together by silk emitted through the labium. Larvae are primarily herbivorous scavengers; some use silk to produce food-filtering devices. Most larvae inhabit benthic habitats in temperate streams, ponds, and lakes. Adults are strictly terrestrial and have liquid diets.

Order Lepidoptera Approximately 120,000 described species (Figure 22.6K). Minute to large; sucking mouthparts; mandibles usually vestigial; maxillae coupled, forming a tubular sucking proboscis, coiled between labial palps when not in use; head, body, wings, and legs usually densely scaled; compound eyes well developed; usually with two pairs of large and colorfully scaled wings, coupled to one another by various mechanisms; protibia with epiphysis used

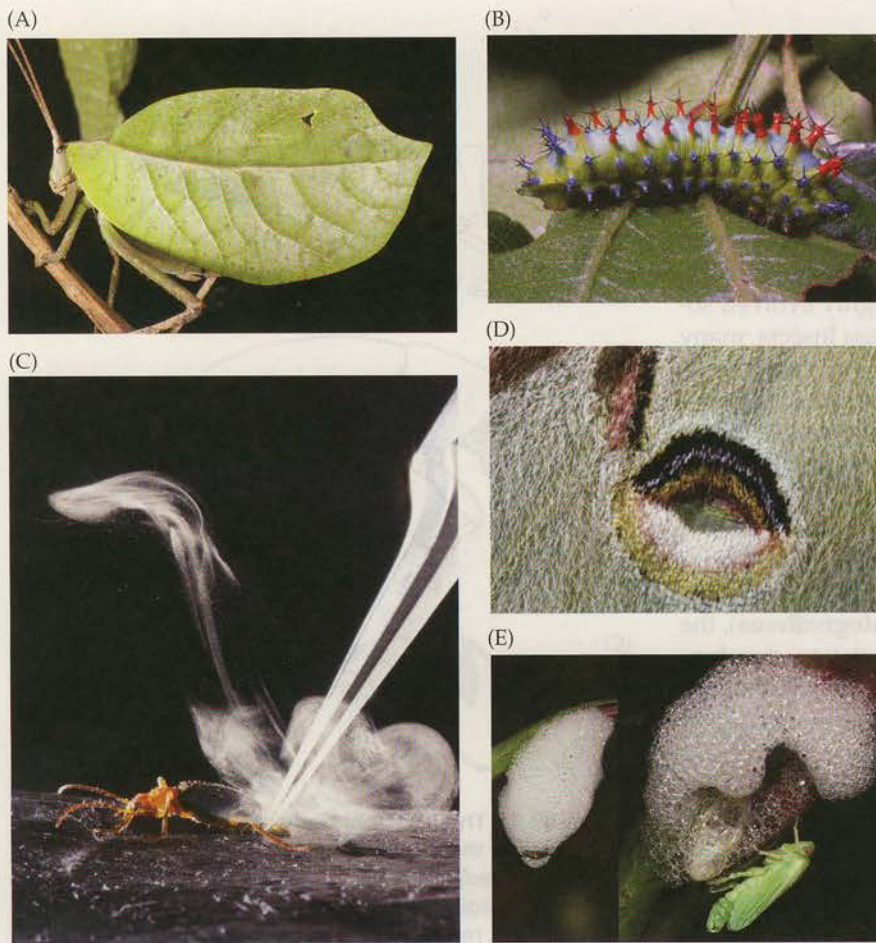


Figure 22.7 Defense, warning coloration, and camouflage in insects. (A) A leaf-mimicking katydid (Orthoptera: Tettigoniidae) from Ecuador is perfectly camouflaged. (B) The bright coloration of the silkmoth caterpillar (Lepidoptera: Saturniidae: *Hyalophora euryalus*), warns potential predators of the defensive hairs on its back. (C) A bombardier beetle (Coleoptera: Carabidae: *Brachinus*) sprays noxious benzoquinones in defense while being “attacked” by forceps. (D) Close-up of an “eye spot” on a luna moth (see Figure 22.6K) (Lepidoptera: Saturniidae). Eyespots attract predators away from the moth’s head and body and encourage predators to focus on their wings. Since butterflies and moths can fly even with slight wing damage, eyespots are a commonly used defense mechanism. (E) A spittlebug (Hemiptera: Cercopoidea) produces a cover of frothed-up plant sap resembling saliva which hides the nymph from the view of predators and parasites.

for cleaning antennae; male genitalia complex; females with ovipositors.

Butterflies and moths are among the best known and most colorful of all the insects. The adults are primarily nectar feeders, and many are important pollinators, some of the best known being the large hawk, or sphinx, moths (Sphingidae). A few tropical species are known to feed on animal blood, and some even drink the tears of mammals. The larvae (caterpillars) feed on green plants. Caterpillars have three pairs of thoracic legs and a pair of soft prolegs on each of abdominal segments 3–6; the anal segment bears a pair of prolegs or claspers. Butterflies can be distinguished from moths by two features: their antennae are always long and slender, ending in a knob (moth antennae are never knobbed), and their wings are typically held together above the body at rest (moths never hold their wings in this position). Over 80% of the described Lepidoptera are moths.

Other common families include Psychidae (bag worms); Cossidae (carpenter worms); Pyralidae (snout moths); Saturniidae (silk moths); Sphingidae (hawk moths); Hesperidae (skippers); Geometridae (inch worms); Arctiidae (tiger moths); Noctuidae (owlet moths); Papilionidae (swallowtails); Nymphalidae (brush-footed butterflies); Pieridae (whites and sulphurs); Lycaenidae (gossamer-winged butterflies); and Riodinidae (metalmarks).²

The Hexapod Body Plan

General Morphology

In Chapter 20 we briefly discussed the various advantages and constraints imposed by the phenomenon of arthropodization, including those associated with the establishment of a terrestrial lifestyle. Departure from the ancestral aquatic environment necessitated the evolution of stronger and more efficient support and locomotory appendages, special adaptations to withstand osmotic and ionic stress, and aerial gas exchange structures. The basic arthropod body plan included many preadaptations to life in a “dry” world. As we have seen, the arthropod exoskeleton inherently provides physical support and protection from predators, and

²One of the best known butterfly taxonomists was the great Russian novelist Vladimir Nabokov (*Lolita*, *Pale Fire*, *The Gift*), who left Saint Petersburg in 1917 to travel around Europe and eventually settled in the United States (first working at the American Museum of Natural History in New York, then at Cornell University). Nabokov was a specialist on the blue butterflies (Polyommata) of the New World and a pioneer anatomist, coining such alliterative anatomical terms as “alula” and “bullula.” Butterflies, real and imaginary, flit through 60 years of Nabokov’s fiction, and many lepidopterists have named butterflies after characters in his life and writings (e.g., species epithets include *lolita*, *humberti*, *ada*, *zembra*, and *vokoban*—a reversal of Nabokov). Nabokov’s descriptions of *Lolita* were patterned after his species descriptions of butterflies (e.g., “her fine downy limbs”).

by incorporating waxes into the epicuticle, the insects, like the arachnids, acquired an effective barrier to water loss. Similarly, within the Hexapoda, the highly adaptable, serially arranged arthropod limbs evolved into a variety of specialized locomotory and food-capturing appendages. Reproductive behavior became increasingly complex, and in many cases highly evolved social systems developed. Within the class Insecta, many taxa underwent intimate coevolution with land plants, particularly angiosperms. The adaptive potential of insects is evident in the many species that have evolved striking camouflage, warning coloration, and chemical defense (Figure 22.7).

Non-insect hexapods (proturans, collembolans, and diplurans—the entognathous hexapods) differ from insects in several important ways. The mouthparts are not fully exposed (i.e., they are **entognathous**), the mandibles have a single point of articulation, development is always simple, the abdomen may have a reduced number of segments, and they never developed flight.

Insects are primitively composed of 20 somites (as in the Eumalacostraca; Chapter 21), although these are not always obvious. The consolidation and specialization of these body segments (i.e., tagmosis) has played a key role in hexapod evolution and has opened the way for further adaptive radiation. The body is always organized into a head, thorax, and abdomen (Figures 22.8 and 22.9), comprising 6, 3, and 11 segments respectively. In contrast to marine arthropods, a true carapace never develops in hexapods. In the head, all body sclerites are more or less fused as a solid head capsule. In the thorax and abdomen, the adult sclerites usually develop embryologically such that they overlap the primary segment articulations, forming secondary segments, and these are the “segments” we typically see when we examine an insect externally (e.g., the tergum and sternum of each adult abdominal secondary segment actually overlap its adjacent anterior primary segment) (Figure 22.10). The primitive (primary) body segmentation can be seen in unsclerotized larvae by the insertions of the segmental muscles and transverse grooves on the body surface.

Most insects are small, between 0.5 and 3.0 cm in length. The smallest are the thrips, feather-winged beetles, and certain parasitic wasps, which are all nearly microscopic. The largest are certain beetles, orthopterans, and stick insects, the latter attaining lengths greater than 56 cm. However, certain Paleozoic species grew to twice that size. To familiarize you with the hexapod body plan and its terminology, we briefly discuss each of the main body regions (tagmata) below.

The hexapod head The hexapod head comprises an acron and six segments, bearing (from anterior to posterior) the eyes, antennae, clypeolabrum, and three pairs of mouth appendages (mandibles, maxillae,

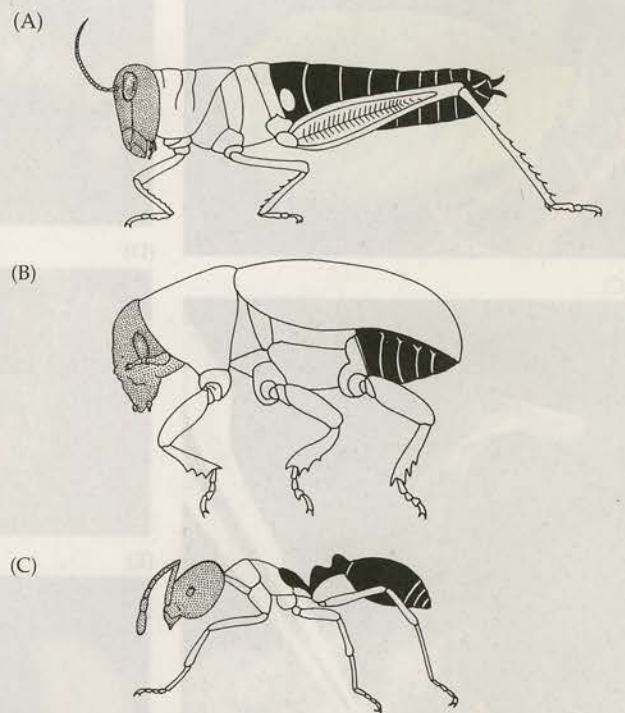


Figure 22.8 The principal body regions of hexapods, illustrated by three kinds of insects. (A) A grasshopper (wings removed). (B) A beetle. (C) An ant. In each case, the stippled region is the head; the white region is the thorax; the black region is the abdomen.

labium) (Figure 22.11). Compound eyes, as well as three **simple eyes (ocelli)** are typically present in adult hexapods. The median (anterior) ocellus is thought to have arisen through the fusion of two separate ocelli. The internal manifestation of the fused exoskeleton of the head forms a variety of apodemes, braces, and struts collectively called the **tentorium**. Externally, the head may also bear lines that may demarcate its original segmental divisions, and others that represent the dorsal (and ventral) ecdysial lines, where the head capsule splits in immature insects and which persist as unpigmented lines in some adults. Still other lines represent inflections of the surface associated with internal apodemes.

The antennae (Figure 22.12) are composed of three regions: the scape, pedicel, and multijointed sensory flagellum. The **scape** and **pedicel** constitute the **proto-pod**; the **flagellum** represents the telopod. Among the entognathous insects, muscles intrinsic to the scape, pedicel and flagellum are retained. But in the class Insecta, the intrinsic muscles of the antennae have been lost except for those in the scape. In addition, in many insects the joints, or **flagellomeres**, of the flagellum may have been secondarily subdivided (or annulated) to produce additional unmuscle joints, and increasing the length and flexibility of the antenna.

The mouth is bordered anteriorly by the clypeolabrum, posteriorly by the labium, and on the sides by

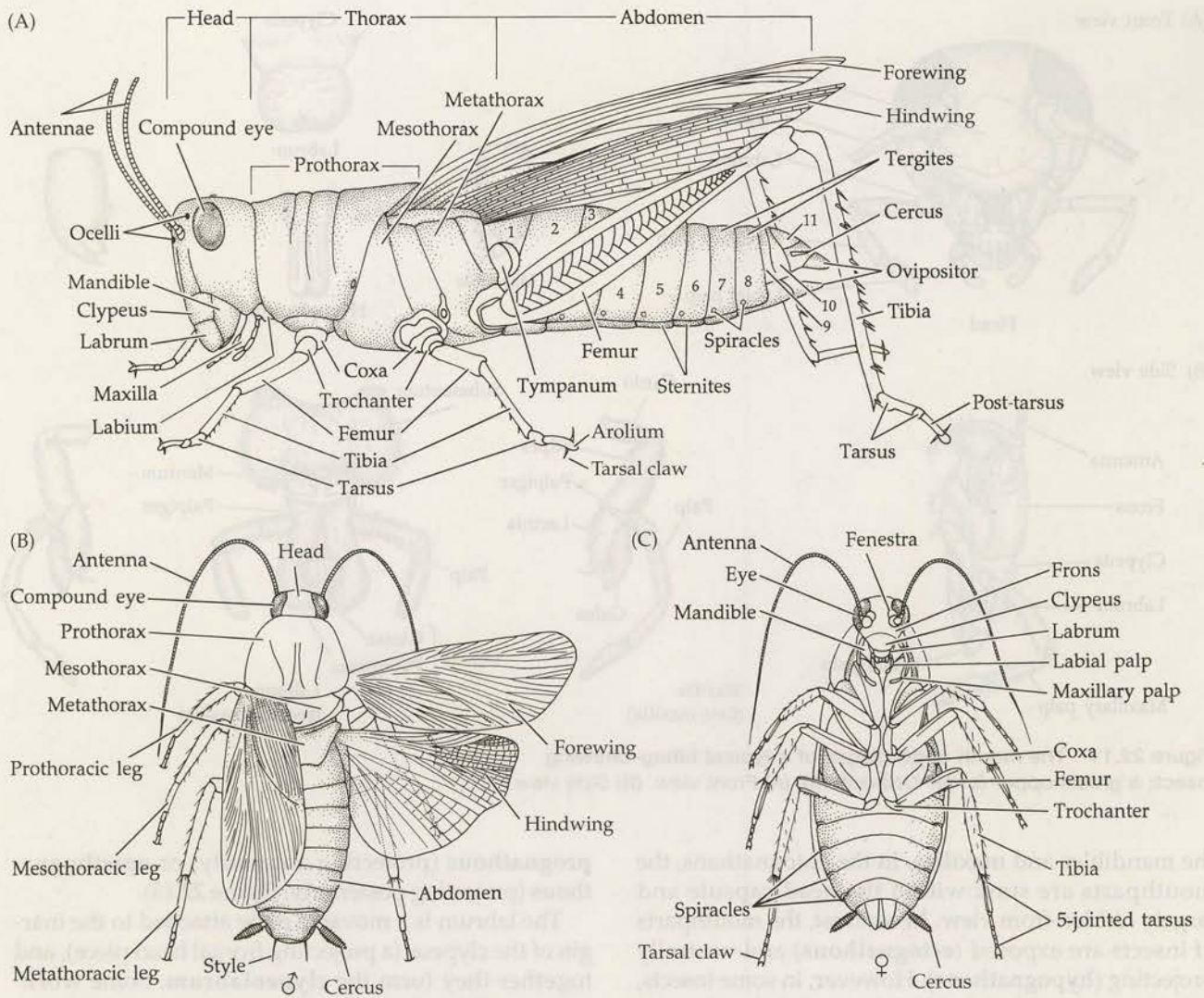


Figure 22.9 General body anatomy of insects. (A) A grasshopper (order Orthoptera). (B,C) Dorsal and ventral views of a cockroach (order Blattodea).

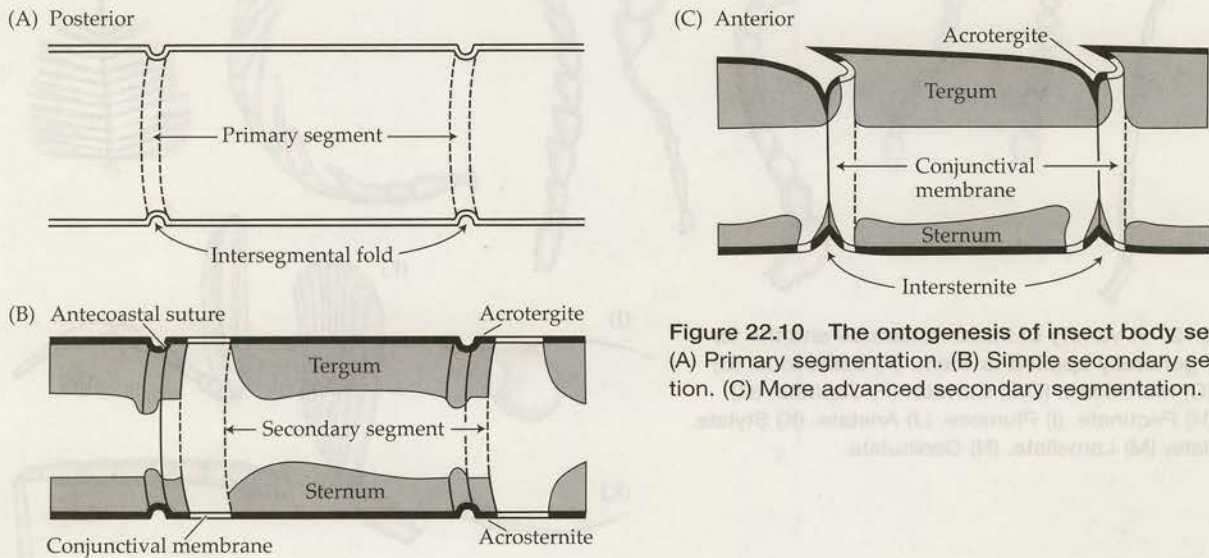
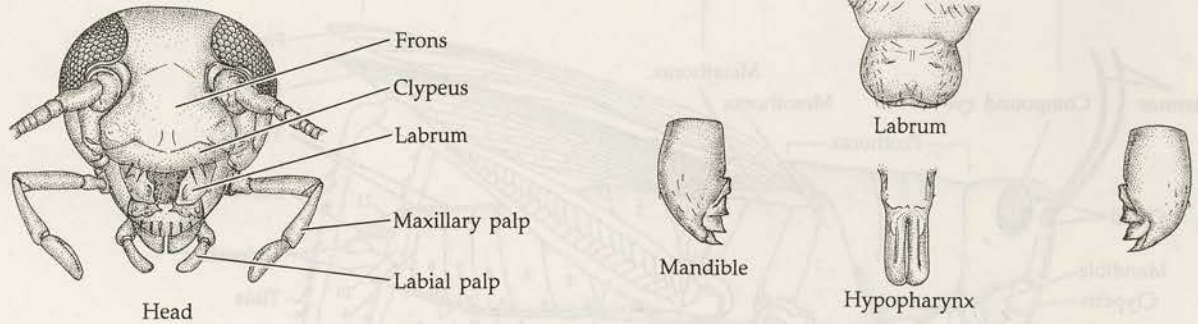


Figure 22.10 The ontogenesis of insect body segments. (A) Primary segmentation. (B) Simple secondary segmentation. (C) More advanced secondary segmentation.

(A) Front view



(B) Side view

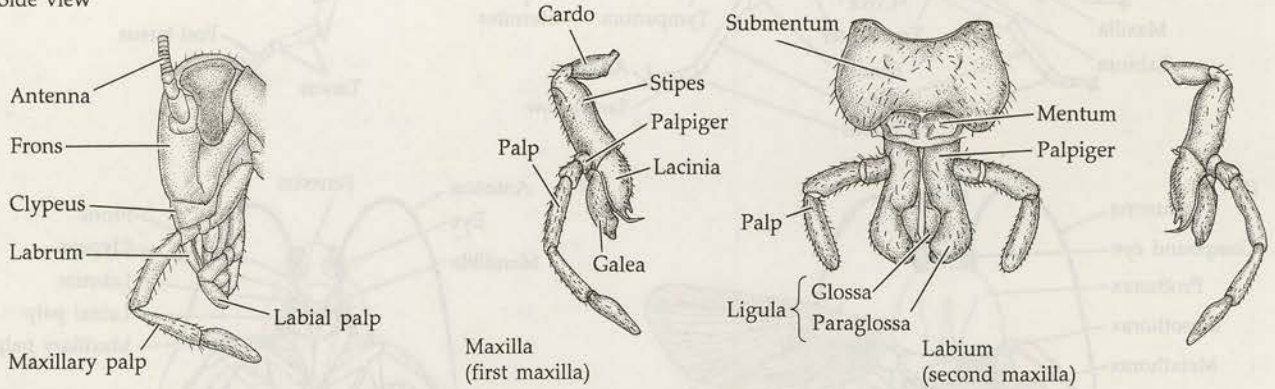


Figure 22.11 The mouth appendages of a typical biting–chewing insect: a grasshopper (order Orthoptera). (A) Front view. (B) Side view.

the mandibles and maxillae. In the entognathans, the mouthparts are sunk within the head capsule and largely hidden from view. In contrast, the mouthparts of insects are exposed (**ectognathous**) and ventrally projecting (**hypognathous**). However, in some insects, the orientation of the head has changed so that they are

prognathous (projecting anteriorly) or **opisthognathous** (projecting posteriorly; Figure 22.13).

The labrum is a movable plate attached to the margin of the clypeus (a projecting frontal head piece), and together they form the **clypeolabrum**. Some workers regard the clypeolabrum to be an independently

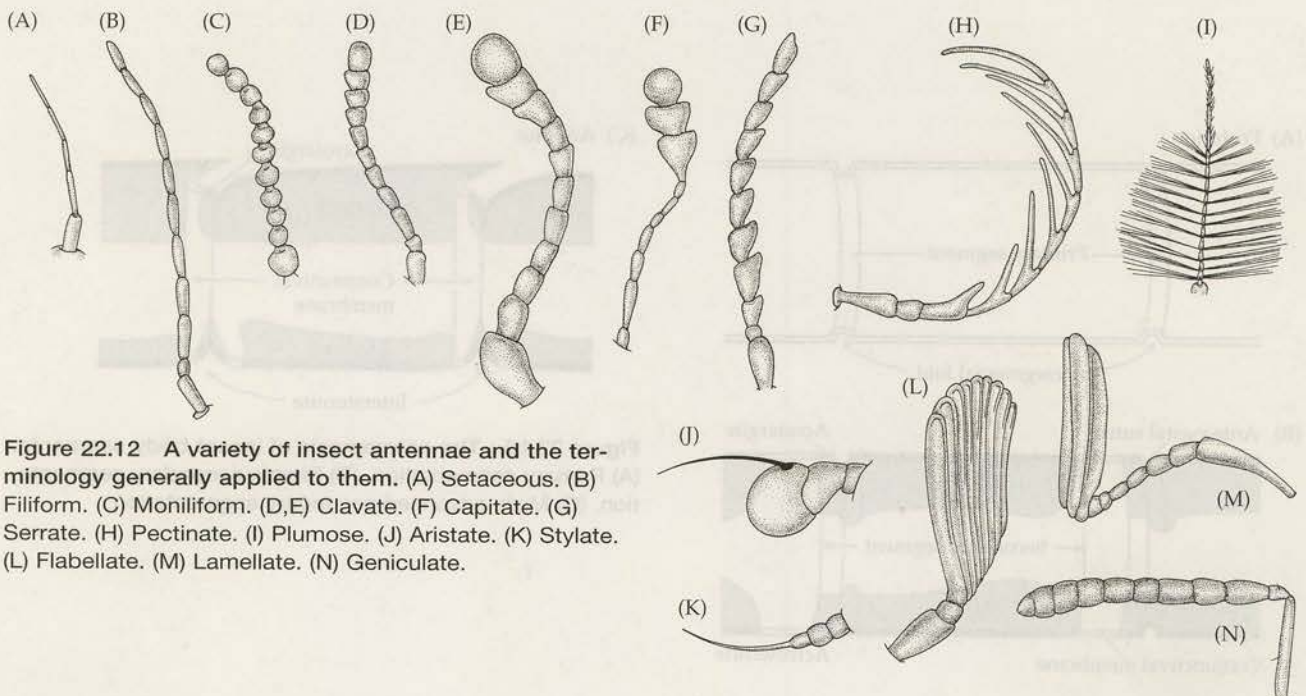


Figure 22.12 A variety of insect antennae and the terminology generally applied to them. (A) Setaceous. (B) Filiform. (C) Moniliform. (D,E) Clavate. (F) Capitate. (G) Serrate. (H) Pectinate. (I) Plumose. (J) Aristate. (K) Styletate. (L) Flabellate. (M) Lamellate. (N) Genuiculate.

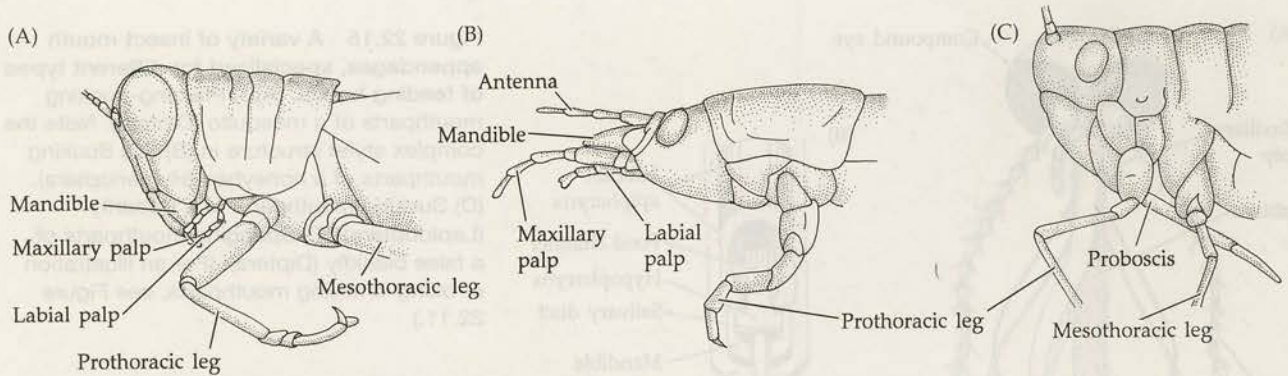


Figure 22.13 Different positions of head and mouthparts relative to the rest of the body. (A) Hypognathous condition (grasshopper). (B) Prognathous condition (beetle larva). (C) Opisthorhynchous condition (aphid).

derived structure of the exoskeleton; others believe it could be the fused appendages of the first or third head segment. The mandibles (Figure 22.14) are strongly sclerotized, usually toothed, and lack a palp. In most insects the mandible is of one article, but in some primitive groups (and fossil taxa) it is composed of several articles. However, the gene *Distal-less (Dll)* is apparently never expressed in the embryogeny of hexapodan mandibles, suggesting that they are fully gnathobasic (i.e., protopodal). The maxillae are generally multi-articulate and bear a palp of 1–7 articles. The labium comprises the fused second maxillae and typically bears two palps. In addition to these appendages, there is a median, unpaired, tongue-like organ called the hypopharynx that projects forward from the back of the preoral cavity. The salivary glands open through the hypopharynx.³

In the past variations in feeding appendages were often used to define the major insect clades, and more recent molecular phylogenetic work has largely corroborated those ideas although a number of cases of convergent evolution in mouthparts have also been revealed. In sucking insects both mandibles and maxillae may be transformed into spear-like structures (stylets), or the mandibles may be absent altogether (Figure 22.15 and 22.24). In most Lepidoptera, the maxillae form an elongate coiled sucking tube, the proboscis. In

some insects (e.g., Hemiptera), the labium is drawn out into an elongate trough to hold the other mouthparts, and its palps may be absent; in others (e.g., Diptera), it is modified distally into a pair of fleshy porous lobes called labellae.

The hexapod thorax The three segments of the thorax are the **prothorax**, **mesothorax**, and **metathorax** (Figure 22.9). Their tergites carry the same prefixes: **pronotum**, **mesonotum**, **metanotum**. In the winged insects (Pterygota), the mesothorax and metathorax are enlarged and closely united to form a rigid **pterothorax**. Wings, when present, are borne on these two segments and articulate with processes on the tergite (notum) and pleura of the somites. The prothorax is sometimes greatly reduced, but in some insects it is greatly enlarged (e.g., beetles) or even expanded into a large shield (e.g., cockroaches). The lateral, pleural sclerites are complex and thought to be derived, at least in part, from subcoxal (protopodal) elements of the ancestral legs that became incorporated into the lateral body wall. The sternites may be simple, or may be divided into multiple sclerites on each segment.

Each of the three thoracic somites bears a pair of legs (Figure 22.9), composed of two parts, a proximal protopod and a distal telopod. The protopod (sometimes

³Study of the *Dll* gene reveals that it was probably primitively expressed in the distal parts of all arthropod appendages. It is also expressed in the endites, or inner lobes, of arthropod limbs (e.g., in the phyllopodous limbs of Branchiopoda and in the maxillae of Malacostraca). In crustaceans and myriapods there is an initial *Dll* expression in the mandibular limb buds that is displaced laterally and continues in the mandibular palp in crustaceans. In insects, no *Dll* expression at all is seen in the mandibles—it has apparently been completely lost. Thus, the mandibles of all three groups are gnathobasic. The palp of the crustacean mandible represents the distal portion of the mandibular limb, altogether lost in hexapods and myriapods. The only real “whole-limb jaws” among the arthropods are those of onychophorans. *Dll* is also expressed in the coxal endites of chelicerates and the pedipalp endites of arachnids. The complete loss of *Dll* expression in hexapod mandibles may be a synapomorphy for the group.

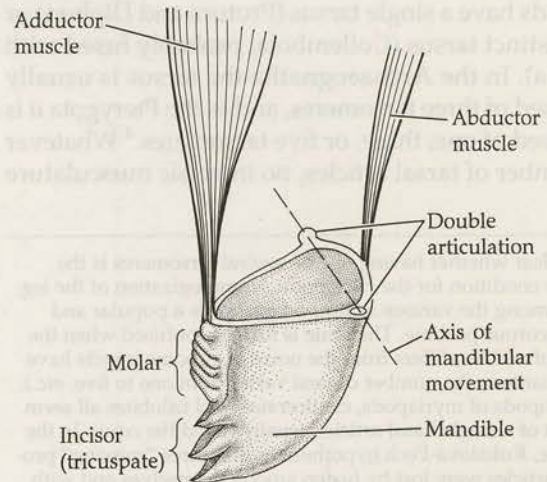


Figure 22.14 The musculature of an insect mandible.

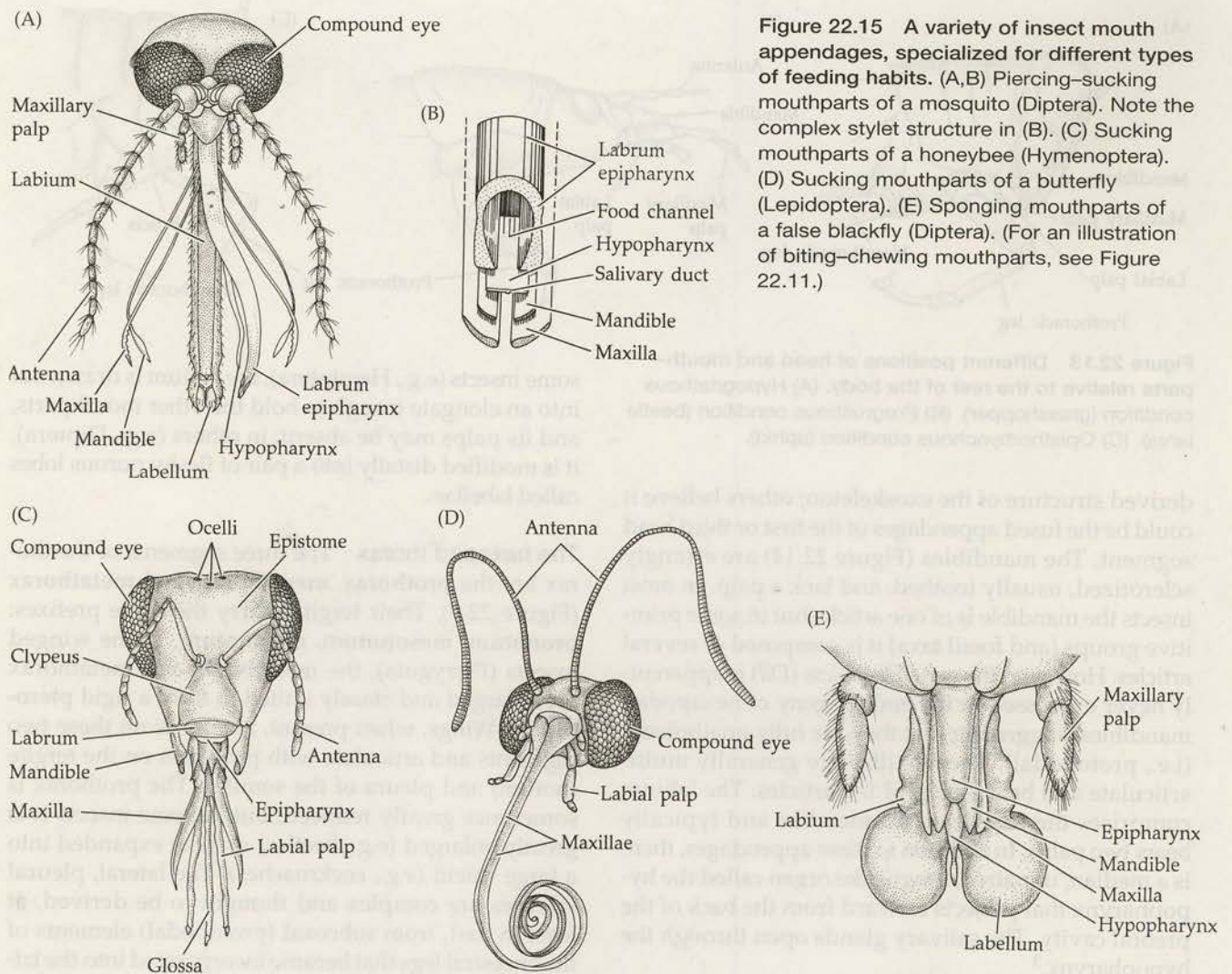


Figure 22.15 A variety of insect mouth appendages, specialized for different types of feeding habits. (A,B) Piercing-sucking mouthparts of a mosquito (Diptera). Note the complex stylet structure in (B). (C) Sucking mouthparts of a honeybee (Hymenoptera). (D) Sucking mouthparts of a butterfly (Lepidoptera). (E) Sponging mouthparts of a false blackfly (Diptera). (For an illustration of biting-chewing mouthparts, see Figure 22.11.)

called a "coxopodite" by entomologists) is composed of two articles (coxa, trochanter), and the telopod is composed of four articles (**femur, tibia, tarsus, pretarsus**) (Figure 22.16). The tarsus is often subdivided into additional pseudoarticles called tarsomeres. The basal hexapods have a single tarsus (Protura and Diplura) or an indistinct tarsus (Collembola; probably fused with the tibia). In the Archaeognatha the tarsus is usually composed of three tarsomeres, and in the Pterygota it is composed of one, three, or five tarsomeres.⁴ Whatever the number of tarsal articles, no intrinsic musculature

⁴It is unclear whether having one or several tarsomeres is the primitive condition for the Hexapoda. Homologization of the leg articles among the various arthropod groups is a popular and often rancorous pastime. The issue is further confused when the number of articles differs from the norm (e.g., some insects have two trochanters, the number of tarsi varies from one to five, etc.). The protopods of myriapods, chelicerates, and trilobites all seem to consist of a single basal article (usually called the coxa). In the latter case, Kukulová-Peck hypothesizes that three "missing" propodal articles were lost by fusion among themselves and with the pleural region. See Chapter 20 for a discussion of ancestral arthropod legs.

occurs in them, and they are thus viewed as subdivisions of a single original article. The whole length of the tarsus is crossed by the tendon of the flexor muscle of the pretarsus, whose fibers usually arise on the tibia (Figure 22.17). The pretarsus is a minute article that usually bears a pair of lateral claws. The pretarsus in Collembola and Protura bears a single median claw. A single claw also occurs in many holometabolous larvae and some pterygote adults. But in most hexapods, the pretarsus bears a pair of lateral claws, and many also have a median **arolium** (which functions as an adhesive pad on smooth surfaces), **unguitractor plate**, or median claw.

In insects, many adult organs derive from clusters of early embryonic cells called **imaginal discs**, which arise from localized invaginations of the ectoderm in the early embryo. The embryonic thorax contains three pairs of leg discs, and as development proceeds, these discs develop a series of concentric rings, which are the presumptive leg articles. The center of the disc corresponds to the distalmost articles (tarsus and pretarsus) of the future leg, while the peripheral rings correspond

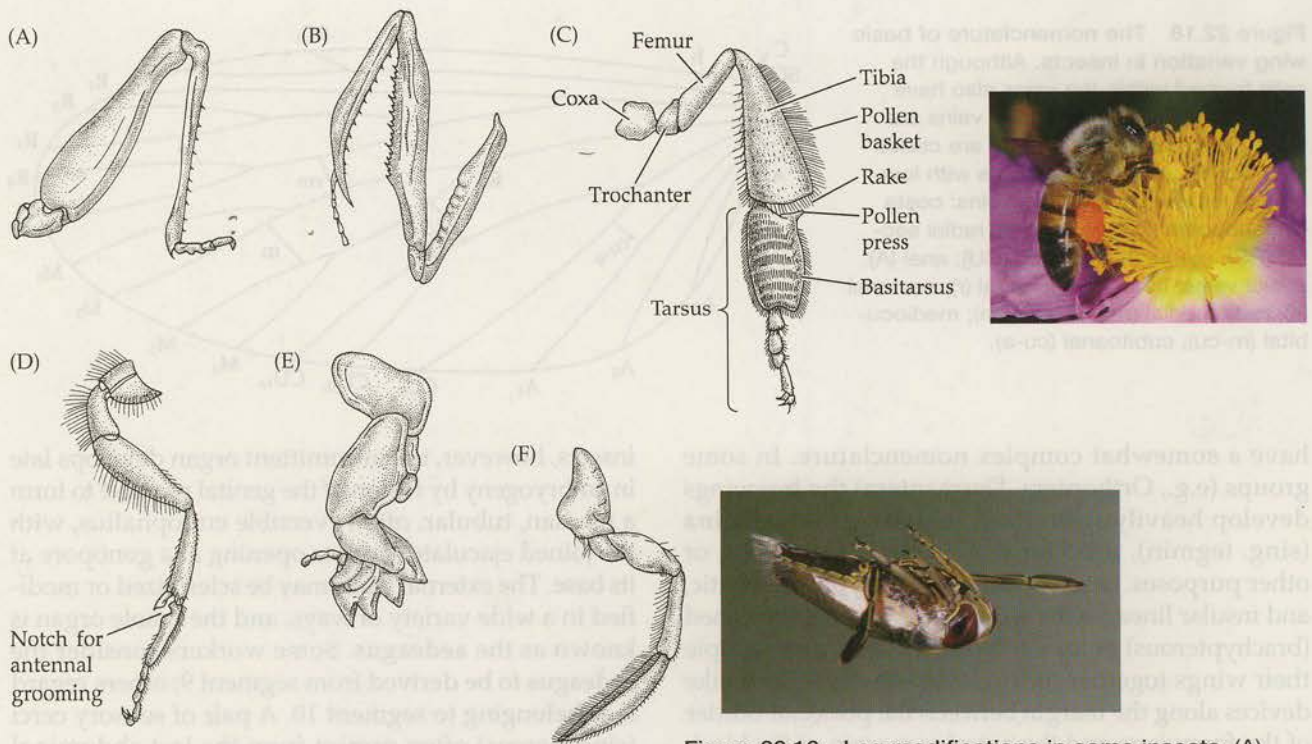


Figure 22.16 Leg modifications in some insects. (A) The hindleg of a grasshopper (Orthoptera), modified for jumping. (B) The raptorial foreleg of a mantid (Mantodea), modified for prey capture. (C) The hindleg of a honeybee (Hymenoptera), modified for collecting and holding pollen (anatomy diagram and photograph). (D) The foreleg of a worker honeybee has a notch for antennal grooming. (E) The foreleg of a mole cricket (Orthoptera), modified for digging. (F) The hindleg of a backswimmer (Hemiptera), modified for swimming (anatomy diagram and photograph). (G) Close-up of insect tarsus with 5 tarsomeres and a pretarsus with 2 lateral claws flanking an arolium.

to its proximal region (coxa, trochanter). During embryogenesis, the leg telescopes out as it subdivides into the component articles. The gene *Distal-less (Dll)* is expressed in the presumptive distal region of the limb, while the gene *Extradenticle (Exd)* is necessary for the development of the proximal portion of the limb. Thus the protopod and telopod of the legs are each under their own genetic control.

Within the Pterygota, most species also have a pair of wings on the second and third thoracic segments. Wing morphology has been more extensively used in insect classification than any other single structure. Wings are often the only remains of insects preserved in fossils. The wings of modern insects develop as evaginations of the integument, with thin cuticular membranes forming the upper and lower surfaces of each wing. Wing **veins**, which contain circulating hemolymph, anastomose and eventually open into the body. The arrangement of veins in insect wings provides important diagnostic characters at all taxonomic levels. The origin and homologization of wing venation has been heavily debated over the decades.

Most workers use a consistent naming system that recognizes six major veins: costa (C), subcosta (SC), radius (R), media (M), cubitus (CU), and anal (A) (Figure 22.18). Areas in the wings that are enclosed by longitudinal and cross veins are called **cells**, and these too

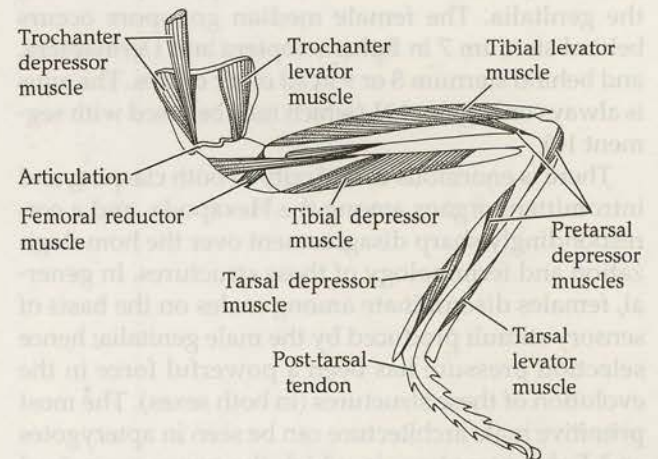
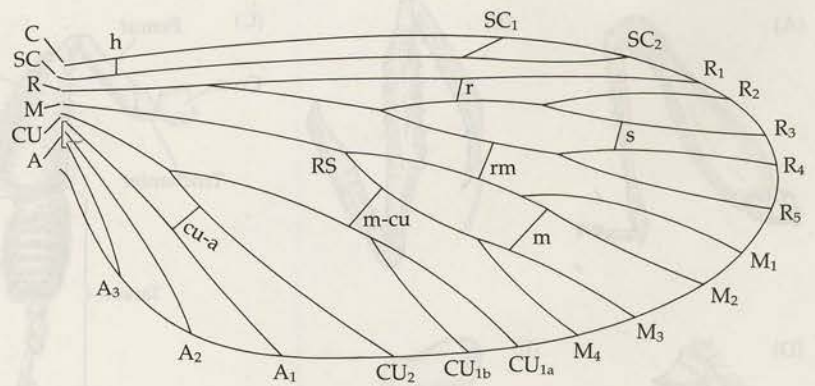


Figure 22.17 The musculature of an insect leg.

Figure 22.18 The nomenclature of basic wing venation in insects. Although the cells formed within the veins also have names, only the names of the veins are given here. Longitudinal veins are coded with capital letters, cross veins with lowercase letters. Longitudinal veins: costa (C); subcosta (SC); radius (R); radial sector (RS); media (M); cubitus (CU); anal (A). Cross veins: humeral (h); radial (r); sectorial (s); radiomedial (rm); medial (m); mediocubital (m-cu); cubitoanal (cu-a).



have a somewhat complex nomenclature. In some groups (e.g., Orthoptera, Dermaptera) the forewings develop heavily sclerotized regions called **tegmina** (sing. *tegmin*), used for protection, stridulation, or other purposes. In many sedentary, cryptic, parasitic, and insular lineages the wings have become shortened (brachypterous) or lost (apterous). Insects often couple their wings together for flight by means of hook-like devices along the margin between the posterior border of the forewings and the anterior margin of the hindwings (e.g., **hamuli** in Hymenoptera; **frenula** in many Lepidoptera). In these insects the coupled wings function together as a single unit.

The hexapod abdomen The abdomen primitively comprises 11 segments, although the first is often reduced or incorporated into the thorax, and the last may be vestigial. Abdominal pleura are greatly reduced or absent. The occurrence of true (though minute) abdominal leglets (sometimes called “prolegs” or “styli”) on the pregenital segments is commonplace among the apterygotes and also occurs in the larvae of many pterygotes (e.g., the legs of caterpillars). In addition, transitory limb buds or rudiments appear fleetingly in the early embryos of some species, presumably harking back to the deep evolutionary past. Abdominal segments 8–9 (or 7–9) are typically modified as the **anogenital tagmata**, or **terminalia**, the exposed parts being the genitalia. The female median gonopore occurs behind sternum 7 in Ephemeroptera and Dermaptera, and behind sternum 8 or 9 in all other orders. The anus is always on segment 11 (which may be fused with segment 10).

There is enormous complexity in both clasping and intromittent organs among the Hexapoda, and a correspondingly sharp disagreement over the homologization and terminology of these structures. In general, females discriminate among males on the basis of sensory stimuli produced by the male genitalia; hence selection pressure has been a powerful force in the evolution of these structures (in both sexes). The most primitive male architecture can be seen in apterygotes and Ephemeroptera, in which the penes are paired and contain separate ejaculatory ducts. In most other

insects, however, the intromittent organ develops late in embryogeny by fusion of the genital papillae to form a median, tubular, often eversible endophallus, with the joined ejaculatory ducts opening at a gonopore at its base. The external walls may be sclerotized or modified in a wide variety of ways, and the whole organ is known as the **aedeagus**. Some workers consider the aedeagus to be derived from segment 9; others regard it as belonging to segment 10. A pair of sensory cerci (sing. *cercus*) often project from the last abdominal segment.

Locomotion

Walking Hexapods rely on their sclerotized exoskeleton for support on land. Their limbs provide the physical support needed to lift the body clear of the ground during locomotion. In order to accomplish this, the limbs must be long enough to hold the body high off the ground, but not so high as to endanger stability. Most hexapods maintain stability by having the legs in positions that suspend the body in a sling-like fashion and keep the overall center of gravity low (Figure 20.19).

The basic structure of arthropod limbs was described in Chapter 20. In hexapods (and crustaceans) the anterior–posterior limb movements take place between the coxae and the body proper (in contrast to most arachnids, in which the coxae are immovably fixed to the body and limb movement occurs at more distal joints). Like the power controlled by the range of gears in an automobile, the power exerted by a limb is greatest at low speeds and least at higher speeds. At lower speeds the legs are in contact with the ground for longer periods of time, thus increasing the power, or force, that can be exerted during locomotion. In burrowing forms the legs are short, and the gait is slow and powerful as the animal forces its way through soil, rotting wood, or other material. Longer limbs reduce the force, but increase the speed of a running gait, as do limbs capable of swinging through a greater angle. Limbs long in length and stride are typical features of the fastest-running insects (e.g., tiger beetles, Carabidae).

One of the principal problems associated with increased limb length is that the field of movement of one

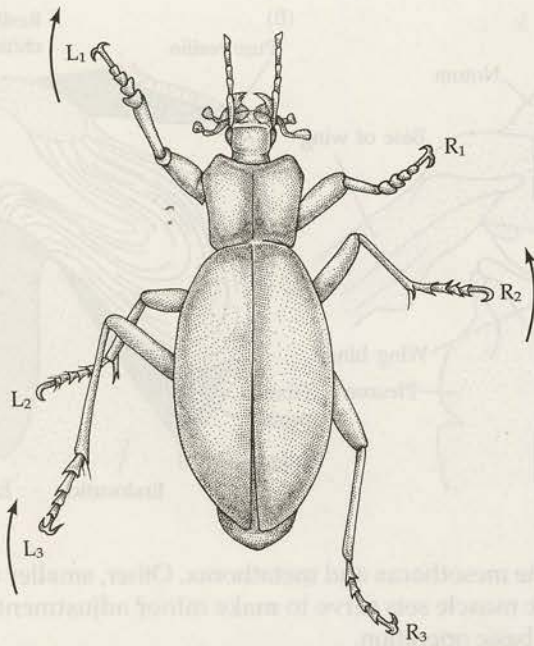


Figure 22.19 A beetle walking. The alternating tripod gait consists of alternate stepping with two sets of three legs; thus the body is always supported by a triad of legs. Here, three legs (L1, R2, and L3) are moving forward while the other three (R1, L2, and R3) are on the ground.

limb may overlap that of adjacent limbs. Interference is prevented by the placement of the tips of adjacent legs at different distances from the body (Figure 22.19). Thus fast-running insects usually have legs of slightly different lengths. Insects usually move their legs in an alternating tripod sequence. Balance is maintained by always having three legs in contact with the ground.

Like many spiders, some insects can walk on water, and they do so in much the same way—by balancing the pull of gravity on their featherweight bodies with the physical principles of buoyancy and surface tension. Insects (and spiders) that walk on water don't get wet because their exoskeletons are coated with waxes that repel water molecules. The water surface, held taut by surface tension, bends under each leg to create a depression, or dimple, that works to push the animal upward in support. Water walking occurs in many insect groups, notably the Hemiptera (e.g., water striders), Coleoptera (e.g., whirligig beetles), and Collembola (some springtails).⁵

Many insects are good jumpers (e.g., fleas, springtails, most orthopterans), but the click beetles (Elateridae) are probably the champions. It has been calculated that a typical click beetle (e.g., *Athous haemorrhoidalis*), when jackknifing into the air to escape a

predator, generates 400 g of force, with a peak deceleration of 2,300 g.

Flight Among the many remarkable advances of insects, flight is perhaps the most impressive. Insects were the first flying animals, and throughout the history of life on Earth no other invertebrates have learned the art of true flight. The wingless insects belong either to groups that have secondarily lost the wings (e.g., fleas, lice, certain scale insects) or to primitive taxa (the apterygotes) that arose prior to the evolution of wings. In three orders, the wings are effectively reduced to a single pair. In beetles, the forewings are modified as a protective dorsal shield (**elytra**). In dipterans, the hindwings are modified as organs of balance (**halteres**). The halteres beat with the same frequency as the forewings, functioning as gyroscopes to assist in flight performance and stability—flies fly very well.

Compared with an insect, an airplane is a simple study in aerodynamics. Planes fly by moving air over a fixed wing surface, the leading edge of which is tilted upward, forcing the air to travel farther (thus faster) over the top of the wing than the bottom, resulting in a vortex that creates a lift. But conventional fixed-wing aerodynamic theory is insufficient to understand insect flight. Insect wings are anything but fixed. Insects, of course, fly by flapping their wings to create vortices, from which they gain lift, but these vortices slip off the wings with each beat, and new vortices are formed with each alternate stroke. Beating insect wings trace a figure eight pattern, and they also rotate at certain crucial moments. Thus, each cycle of flapping creates dynamic forces that fluctuate drastically. By complex actions of wing orientation, insects can hover, fly forward, backward, and sideways, negotiate highly sophisticated aerial maneuvers, and land in any position. To complicate matters even more, in the case of small insects (and most are small, the average size of all insects being just 3–4 mm), the complex mechanics of flight take place at very low Reynolds numbers (see Chapter 4), such that the insect is essentially “flying through molasses.” As a result of these complex mechanics, insect flight is energetically costly, requiring metabolic rates as high as 100 times the resting rate.

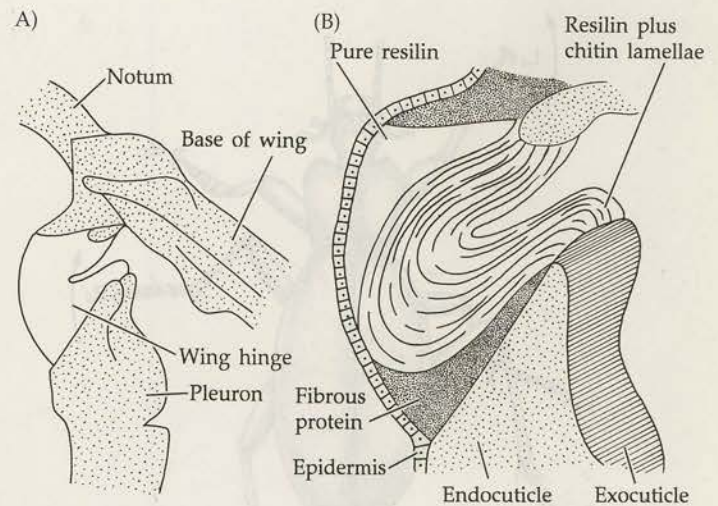
Each wing articulates with the edge of the notum (thoracic tergite), but its proximal end rests on a dorsolateral pleural process that acts as a fulcrum (Figure 22.20). The wing hinge itself is composed in large part of resilin, a highly elastic protein that allows for rapid, sustained movement. The complex wing movements are made possible by the flexibility of the wing itself and by the action of a number of different muscle sets that run from the base of the wing to the inside walls of the thoracic segment on which it is borne. These direct flight muscles serve to raise and lower the wings and to tilt their plane at different angles (somewhat like altering the blade angles on a helicopter) (Figure

⁵On an undisturbed surface, water molecules are attracted to their neighbors beside and below, resulting in a flat skin of molecules that exerts only horizontal tensile forces; it is this “elasticity” of the surface that we call surface tension.

Figure 22.20 A typical insect wing hinge arrangement. This transverse section through the thoracic wall of a grasshopper shows the base of the wing and the wing hinge. (A) Entire hinge area. (B) Enlargement of hinge section.

22.21). However, except in palaeopterans (Odonata and Ephemeroptera), the direct flight muscles are not the main source of power for insect wing movements. Most of the force comes from two sets of indirect flight muscles, which neither originate nor insert on the wings themselves (Figures 22.21 and 22.22).

Dorsal longitudinal muscles run between apodemes at the anterior and posterior ends of each winged segment. When these muscles contract, the segment is shortened, which results in a dorsal arching of the segment roof and a downstroke of the wings. Dorsoventral muscles, which extend from the notum to the sternum (or to basal leg joints) in each wing-bearing segment, are antagonistic to the longitudinal muscles. Contraction of the dorsoventral muscles lowers the roof of the segment. In doing so, it raises the wings. Thus, wing flapping in most insects is primarily generated by rapid changes in the walls and overall shape



of the mesothorax and metathorax. Other, smaller thoracic muscle sets serve to make minor adjustments to this basic operation.

Insects with low wing-flapping rates (e.g., dragonflies, orthopterans, mayflies, and lepidopterans) are limited by the rate at which neurons can repeatedly fire and muscles can execute contractions. However, in insects with high wing-flapping rates (e.g., dipterans, hymenopterans, and some coleopterans), an entirely different regulatory mechanism has evolved. Once

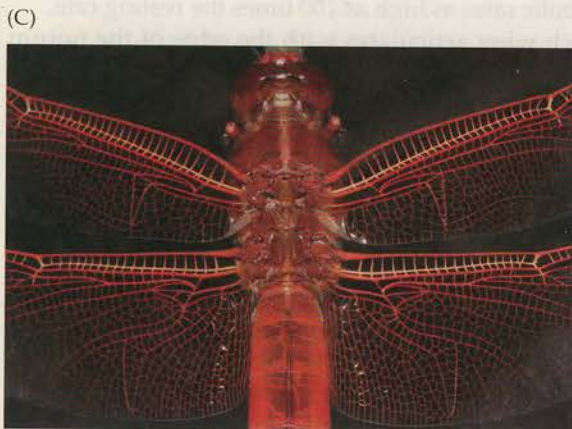
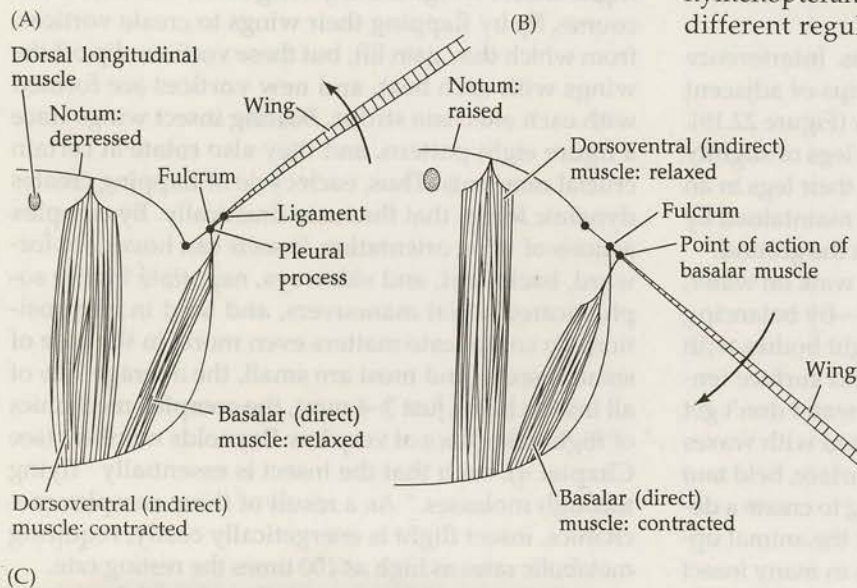


Figure 22.21 Wing movements of a primitive insect such as a dragonfly, in which direct wing muscles cause depression of the wings. Dots represent pivot points, and arrows indicate the direction of wing movement. (A) The dorsoventral muscles contract to depress the notum as the basalar muscles relax, a combination forcing the wings into an upstroke. (B) The dorsoventral muscles relax as the basalar muscles contract, a combination pulling the wings into a downstroke and relaxing (and raising) the notum. (C) Thorax of a dragonfly showing wing attachment to the notum of thoracic segments 2 and 3.

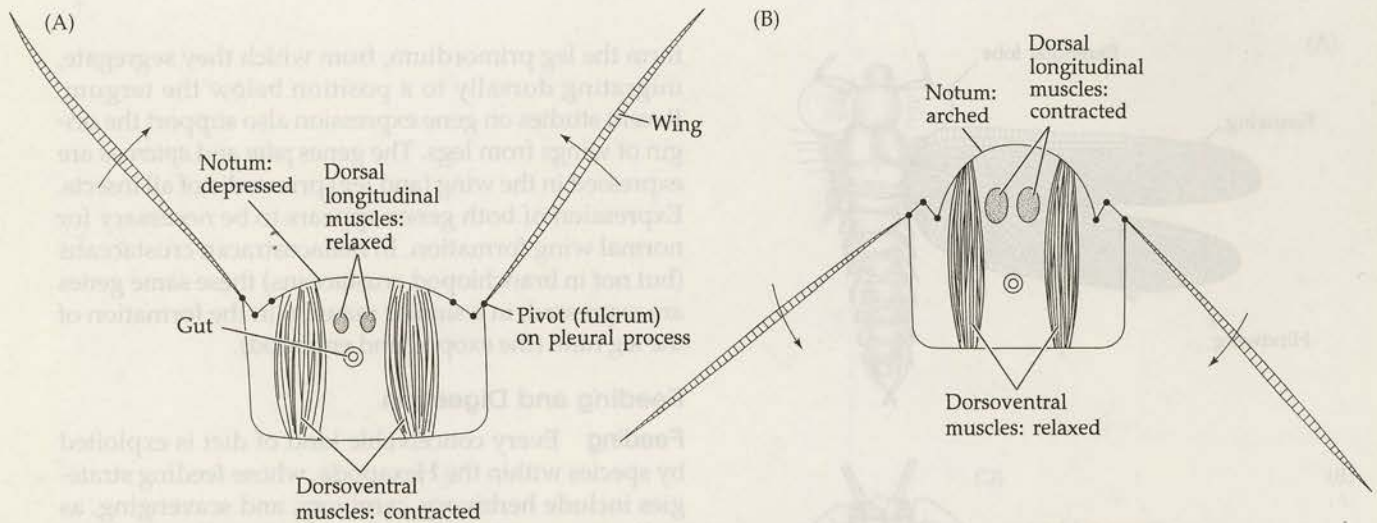


Figure 22.22 Wing movements of an insect such as a fly or hemipteran, in which both upward and downward movements of the wings are produced by indirect flight muscles. In these transverse sections of a thoracic segment, dots represent pivot points, and arrows indicate the direction of wing movement. Only two sets of muscles are shown. (A) The dorsoventral muscles contract, depressing the thoracic notum and forcing the wings into upstroke. (B) The dorsoventral muscles relax as the dorsal longitudinal muscles contract to “pop up” the notum, elevating it and forcing the wings into a downstroke.

flight has been initiated and a high wing-flapping rate attained (up to 100 beats/second), myogenic control takes over. This mechanism exploits the elastic-mechanical properties of the exoskeleton. When one set of indirect muscles contracts, the thorax is deformed. Upon relaxation of the muscles, there is an elastic rebound of the thoracic exoskeleton, which stretches the second set of indirect muscles and thus directly stimulates their contraction. This contraction establishes a second deformation, which in turn stretches and stimulates the first muscle group. Once initiated, this mechanism is nearly self-perpetuating, and the nonsynchronous firing of neurons serves only to keep it in action.

Not all insects utilize wings to travel through the air. Many small and immature insects are effectively dispersed by wind power alone. Some first-instar lepidopterans use silk threads for dispersal (as do spiders and mites). Tiny scale insects are commonly collected in aerial nets. In fact, studies have revealed the existence of “aerial plankton” consisting of insects and other minute arthropods, extending to altitudes as high as 14,000 feet. Most are minute winged forms, but wingless species are also common.

The Origin of Insect Flight

For many decades, two competing views of insect wing origin have dominated. In general, these views can be termed the paranotal lobe hypothesis and the appendage hypothesis. The former holds that wings evolved by way of a gradual expansion of lateral folds of the

thoracic tergites (paranotal lobes), which eventually became articulated and muscled to form wings. The latter hypothesizes that wings evolved from pre-existing articulated structures on the thoracic appendages, such as gills or protopodal exites on the legs. There is also tantalizing evidence from the fossil record suggesting that the first pterygote insects possessed appendages on the prothorax, called “winglets,” that may have been serially homologous to modern wings, implying that the loss of prothoracic proto-wings might have taken place in the early evolutionary history of the Hexapoda.

The paranotal lobe hypothesis was first proposed by Müller in 1873, saw a resurgence of popularity in the middle of the twentieth century, and has lost favor in recent years. It suggests that wings originated as lateral aerodynamic flaps of the thoracic nota that enabled insects to alight right side up when jumping or when blown about by the wind. These stabilizing paranotal lobes later evolved hinged structures and muscles at their bases. The occurrence of fixed paranotal lobes in certain ancient fossil insects has been cited in support of the paranotal lobe hypothesis (Figure 22.23). However, recent studies suggest that these primitive paranotal lobes might have been used for other purposes, such as covering the spiracular openings or gills in amphibious insects, protecting or concealing the insects from predators, courtship displays, or thermo-regulation by absorption of solar radiation.

The appendage hypothesis (also known as the “gill or branchial theory,” “exite theory,” or “leg theory”) also dates back to the nineteenth century, but was resurrected by the great entomologist V. B. Wigglesworth in the 1970s, and was championed by J. Kukulová-Peck since the 1980s. It is the more favored hypothesis of wing origin today, based on recent paleontological work, microscopic anatomy, and molecular developmental biology. It suggests that insect wings are derived from thoracic appendages—from protopodal exites, in Wigglesworth and Kukulová-Peck’s view. These proto-wing appendages might have first

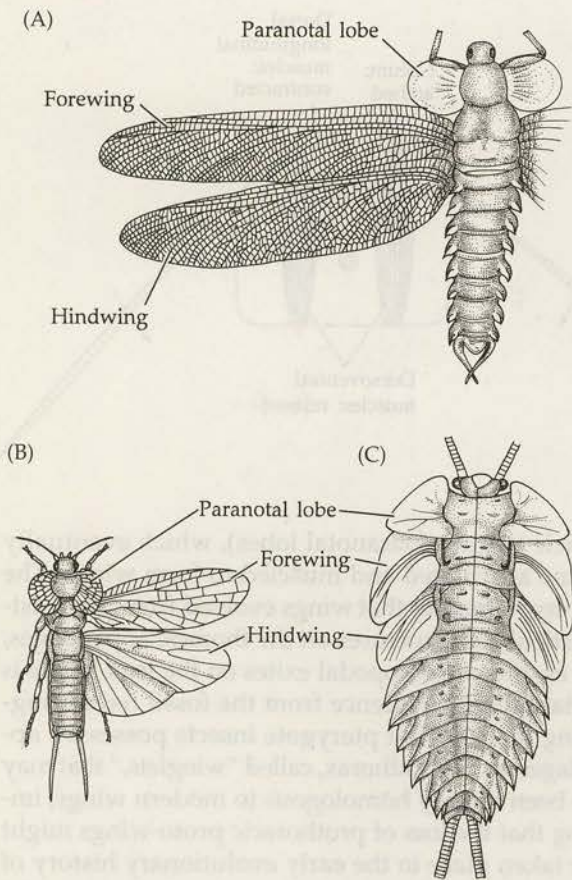


Figure 22.23 Fossil insects with paranotal lobes on the prothorax. (A) *Stenodictya lobata*. (B) *Lemmatophora typa*. (C) Nymphal stage of *Rochdalia parkeri*, a Paleozoic terrestrial palaeodictyopteran. In this species, all three thoracic segments appear to have had “articulated” thoracic lobes.

functioned as aquatic gills or paddles, or as terrestrial gliding structures. The paired abdominal gills of mayflies have been suggested as serial homologues of such “proto-wings.” In Kukalová-Peck’s version of this hypothesis, the first protopodal leg article (the epicoxa) fused with the thoracic pleural membrane early in the evolution of the Arthropoda, as did the second article (the precoxa) in the ancient hexapods, with both migrating dorsally off the leg and onto the body proper. In insects, the epicoxa eventually fused with the tergite, its exite enlarging to form the proto-wing, and eventually the true wing. The precoxa formed the pleural sclerite providing the ventral articulation of the wing. Wing veins might have evolved from cuticular ridges that served to strengthen these structures, and eventually to circulate blood through them.⁶

Kukalová-Peck’s theory of wing evolution finds support in molecular developmental studies, which have shown that the cells that give rise to the wing primordium derive from the same cluster of cells that

form the leg primordium, from which they segregate, migrating dorsally to a position below the tergum. Recent studies on gene expression also support the origin of wings from legs. The genes *pdm* and *apterous* are expressed in the wing (and leg) primordia of all insects. Expression of both genes appears to be necessary for normal wing formation. In malacostracan crustaceans (but not in branchiopod crustaceans) these same genes are expressed, in a similar manner, in the formation of the leg rami (the exopod and endopod).

Feeding and Digestion

Feeding Every conceivable kind of diet is exploited by species within the Hexapoda, whose feeding strategies include herbivory, carnivory, and scavenging, as well as a magnificent array of commensalism and parasitism. This “nutritional radiation” has played a key role in the phenomenal evolution among the Insecta. A comprehensive survey of insect feeding biology alone could easily fill a book this size. Setting aside symbiotic relationships for a moment, in the most general sense insects can be classified as (1) biters–chewers, (2) suckers, or (3) spongers (Figure 22.24).

Biters–chewers, such as the grasshoppers, have the least modified mouthparts, so we describe them first. The maxillae and labium of these insects have well developed leglike palps (Figure 22.24A) that help them hold food in place, while powerful mandibles cut off and chew bite-sized pieces. The mandibles lack palps (in all insects) and typically bear small, sharp teeth that work in opposition as the appendages slide against each other in the transverse (side to side) fashion characteristic of most arthropod jaws. Biting–chewing insects may be carnivores, herbivores, or scavengers. In many plant eaters, the labrum bears a notch or cleft in which a leaf edge may be lodged while being eaten. Some of the best examples of this feeding strategy are seen among the Orthoptera (locusts, grasshoppers, crickets), and most people have witnessed the efficient fashion in which these insects consume their garden plants! Equally impressive are the famous leafcutter ants of the Neotropics, which can denude an entire tree in a few days. Leafcutter ants have a notable feeding adaptation: when cutting leaf fragments, they produce high-frequency vibrations with an abdominal stridulatory organ. This stridulation is synchronized with movements of the mandible, generating complex vibrations. The high vibrational acceleration of the mandible appears to stiffen the material being cut, just as soft material is stiffened with a vibrator for sectioning in a laboratory. Leafcutters don’t eat the leaves they cut; instead, they carry them into an underground nest, where they use them to grow a fungus on which they feed. Several other insect groups have evolved associations with fungi, and in almost every case these relationships are obligate and mutualistic—neither partner can live without the other.

⁶Unspecialized coxal exites can be seen on the legs of some living archaeognathans (bristletails) and in numerous extinct hexapods.

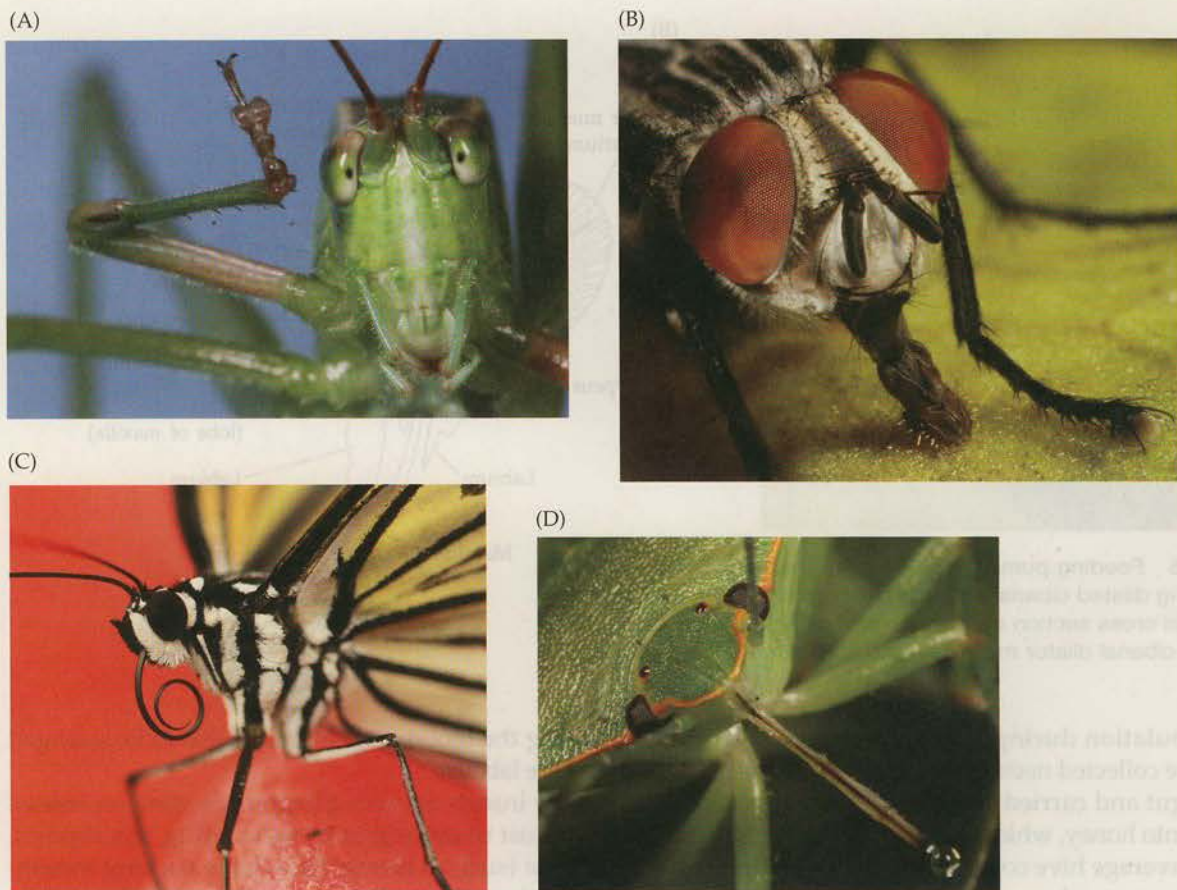


Figure 22.24 Mouthparts specialized for different modes of feeding. (A) Biting-chewing mouthparts of a grasshopper. Note the well developed leglike palps. (B) Sponging mouthparts of a fly. (C) Sucking mouthparts of a butterfly. (D) Piercing mouthparts of a true bug.

In sucking insects the mouthparts are markedly modified for the consumption of liquid foods, generally plant saps or nectars or animal blood or cell fluids (Figure 22.24D). Sucking mouthparts and liquid diets have clearly evolved many times in different insect lines—further testimony to the frequency of evolutionary convergence in arthropods and the developmental adaptability of their appendages. In some sucking insects, such as mosquitoes, feeding is initiated by piercing the victim's epidermal tissue; this mode of feeding is referred to as piercing-sucking. Other insects, such as butterflies and moths that feed on flower nectar, do not pierce anything and are merely suckers.

In all sucking insects the mouth itself is very small and hidden. The mouthparts, instead of being adapted for handling and chewing solid pieces of food, are elongated into a needle-like beak adapted for a liquid diet. Different combinations of mouth appendages constitute the beak in different taxa. True bugs (Hemiptera), which are piercer-suckers, have a beak composed of five elements: an outer troughlike element (the labium) and, lying in the trough, four very sharp stylets (the two mandibles and two maxillae). The stylets are

often barbed to tear the prey's tissues and enlarge the wound. The labrum is in the form of a small flap covering the base of the grooved labium. When piercer-suckers feed, the labium remains stationary, and the stylets do the work of puncturing the plant (or animal) and drawing out the liquid meal.

Different variations of piercing-sucking mouthparts are found in other insect taxa. In mosquitoes, midges, and certain biting flies (e.g., horseflies) there are six long, slender stylets, which include the labrum-epipharynx and the hypopharynx as well as the mandibles and first maxillae (Figure 22.15A). Other biting flies, such as the stable fly, have mosquito-like mouthparts but lack mandibles and maxillae altogether. Fleas (Siphonaptera) have three stylets: the labrum-epipharynx and the two mandibles. Thrips have unusual mouthparts: the right mandible is greatly reduced, making the head somewhat asymmetrical, and the left mandible, first maxillae, and hypopharynx make up the stylets.

Lepidopterans are nonpiercing sucking insects in which the paired first maxillae are enormously elongated, coiled, and fused to form a tube through which flower nectar is sucked (Figure 22.24C); the mandibles are vestigial or absent (Figure 22.15D). The mouthparts of bees are similar: the first maxillae and labium are modified together to form a nectar-sucking tube, but the mandibles are retained and used for

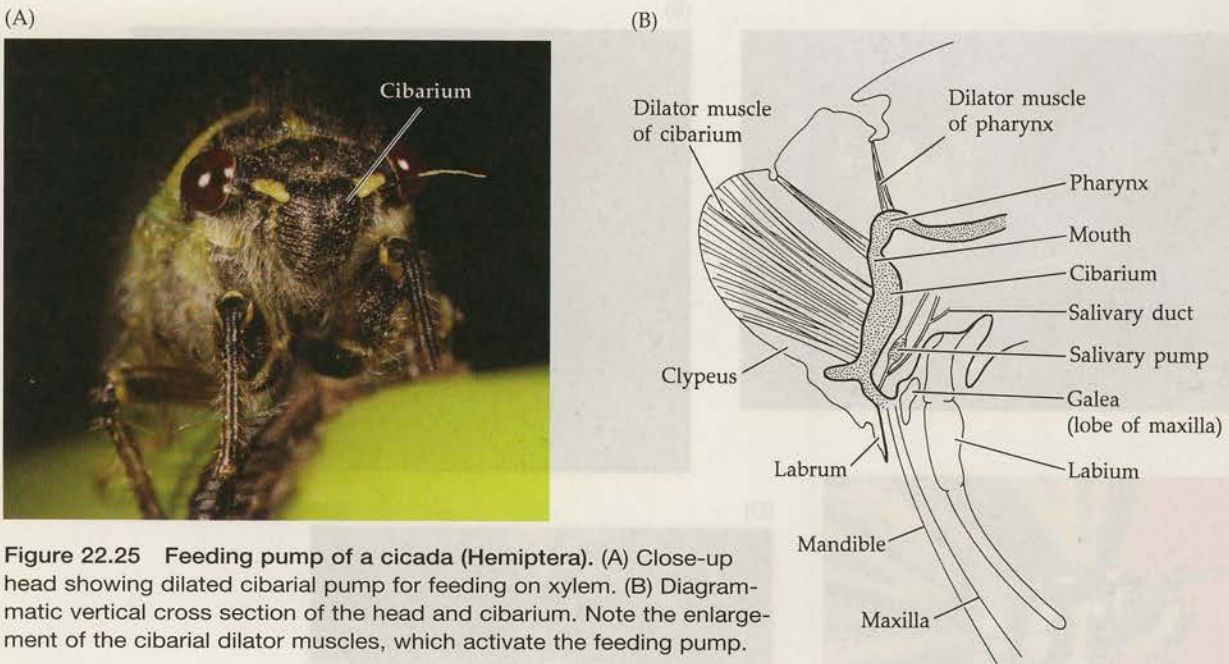


Figure 22.25 Feeding pump of a cicada (Hemiptera). (A) Close-up head showing dilated cibarial pump for feeding on xylem. (B) Diagrammatic vertical cross section of the head and cibarium. Note the enlargement of the cibarial dilator muscles, which activate the feeding pump.

wax manipulation during hive construction (Figure 22.15C). The collected nectar is stored in a special “sac” in the foregut and carried back to the hive where it is converted into honey, which is stored as a food reserve. Bees in an average hive consume about 500 pounds of honey per year—we humans get the leftovers.

Associated with sucking mouthparts are various mechanisms for drawing liquid food into the mouth. Most piercer-suckers rely largely on capillary action, but others have developed feeding “pumps.” Often the pump is developed through elongation of the preoral cavity, or **cibarium**, which by extension of the cuticle around the mouth becomes a semi-closed chamber connecting with the alimentary canal (Figure 22.25). In these cases, cibarial muscles from the clypeus are enlarged to make a powerful pump. In lepidopterans, dipterans, and hymenopterans the cibarial pump is combined with a pharyngeal pump, which operates by means of muscles arising on the front of the head. Specialized salivary glands are also often associated with sucking mouthparts. In some hemipterans a salivary pump forces saliva through the feeding tube and into the prey, softening tissues and predigesting the liquid food. In mosquitoes, saliva carries blood thinners and anticoagulants (and often parasites such as *Plasmodium*, which causes malaria).

In spongers, such as most flies (order Diptera), the labium is typically expanded distally into a **labellum** (Figures 22.15E and 25.24B). Fluid nutrients are transported by capillary action along minute surface channels from the labellae to the mouth. In many spongers, such as houseflies, saliva is exuded onto the food to partly liquefy it. In strict spongers, the mandibles are absent. In biting spongers, such as horseflies, the mandibles serve to slice open a wound in the flesh, thus

exposing the blood and cellular fluids to be sponged up by the labellae.

Many insects are scatophagous, feeding on animal feces. Most of these groups have biting mouthparts, but some (such as certain flies) have sucking mouthparts. Perhaps the most famous of the scatophagous insects are the dung beetles, or tumblebugs (certain beetles in the families Scarabaeidae and Histeridae). These remarkable insects harvest animal dung by biting or slicing off pieces with specialized head or leg structures and working them into a ball. They may roll the dung ball a considerable distance, and eventually bury it in the soil, whereupon females deposit eggs within it. Larvae are thus assured of a ready food supply. Dung balls may even be maneuvered by a pair of dung beetles pushing and pulling in a cooperative effort.

There are many symbiotic insects, and two orders are composed entirely of wingless parasites, most of which spend their entire lives on their host: some Psocodea (lice) and Siphonaptera (fleas). Bird lice are common, and lice are also found on dogs, cats, horses, cattle, and other mammals. Biting lice have broad heads and biting mouthparts used to chew epithelial cells and other structures on the host’s skin. Sucking lice have narrow heads and piercing-sucking mouthparts, which they use to suck blood and tissue fluids from their host, always a mammal. Unlike most arthropod parasites, lice (of both types) spend their entire lives on the bodies of their hosts, and transmission to new hosts is by direct contact. For this reason most lice show a high degree of host specificity. Eggs, or nits, are attached by the female to the feathers or hair of the host, where they develop without a marked metamorphosis. Many lice, particularly those whose diet is chiefly keratin, possess symbiotic intracellular bacteria

that appear to aid in the digestion of their food. These bacteria are passed to the offspring by way of the insects' eggs. Similar bacteria occur in ticks, mites, bedbugs, and some blood-sucking dipterans.

None of the biting lice are known to infest people or to transmit human disease microorganisms, although one species acts as an intermediate host for certain dog tapeworms. The sucking lice, on the other hand, include two genera that commonly infest humans (*Pediculus* and *Phthirus*). The latter genus includes the notorious *P. pubis*, the human pubic "crab" louse (which often occurs on other parts of the body as well). A number of sucking lice are vectors for human disease organisms. The most common reaction to infestation with lice—a condition known as **pediculosis**, or being lousy—is simple irritation and itching caused by the anticoagulant injected by the parasite during feeding. Chronic infestation with lice among certain footloose travelers is manifested by leathery, darkened skin—a condition known as **vagabond's disease**.

Fleas (order Siphonaptera) are perhaps the best known of all insect parasites. Nearly 1,500 species from birds and mammals have been described. Unlike lice, fleas are holometabolous, passing through egg, larval, pupal, and adult stages. Some species of fleas live their entire lives on their host, although eggs are generally deposited in the host's environment and larvae feed on local organic debris. Larvae of domestic fleas, including the rare human flea (*Pulex irritans*), feed on virtually any organic crumbs they find in the household furniture or carpet. Upon metamorphosis to the adult stage, fleas may undergo a quiescent period until an appropriate host appears. A number of serious disease organisms are transmitted by fleas, and at least 8 of the 60 or so species of fleas associated with household rodents are capable of acting as vectors for bubonic plague bacteria.

Other insect orders contain primarily free-living insects, but include various families of parasitic or micro-predatory forms, or groups in which the larval stage is parasitic but the adults are free-living. Most of these "parasites" do not live continuously on a host and have feeding behaviors that fall into a gray zone between true obligate parasitism and predation. Such insects are sometimes classed as intermittent parasites, or micro-predators. Bedbugs (Hemiptera, Cimicidae), for example, are minute flattened insects that feed on birds and mammals. However, most live in the nest or sleeping area of their host, emerging only periodically to feed. The common human bedbugs (*Cimex lectularius* and *C. hemipterus*) hide in bedding, in cracks, in thatched roofs, or under rugs by day and feed on their host's blood at night. They are piercer-suckers, much like the sucking lice. Bedbugs are not known to transmit any human diseases, although when present in large numbers they can be troublesome (in South America, as many as 8,500 bugs have been found in a single

adobe house). Mosquitoes (family Culicidae), on the other hand, are vectors for a large number of disease-causing microorganisms, including *Plasmodium* (responsible for malaria; Figure 3.16), yellow fever, viral encephalitis, dengue, and lymphatic filariasis (with its gross symptom, elephantiasis, resulting from blockage of lymph ducts). Kissing bugs (Hemiptera, Reduviidae, Triatominae) also have a casual host relationship. They live in all kinds of environments, but often inhabit the burrows or nests of mammals, especially rodents and armadillos, as well as birds and lizards. They feed on the blood of these and other vertebrates, including dogs, cats, and people. Their host specificity is low. Several species are vectors of mammalian trypanosomiasis (*Trypanosoma cruzi*, the causative agent of Chagas' disease). The tendency of some species to bite on the face (where the skin is thin) has resulted in the common name.

In the dipteran family Calliphoridae, larvae are saprophagous, coprophagous, wound feeding, or parasitic. The parasitic species include earthworms, locust egg cases, termite colonies, and nestling birds among their hosts, and several parasitize humans and domestic stock (e.g., *Gochliomyia americana*, the tropical American screwworm).

Many insect parasites of plants cause an abnormal growth of plant tissues, called a gall. Some fungi and nematodes also produce plant galls, but most are caused by mites and insects (especially hymenopterans and dipterans). Parasitic adults may bore into the host plant or, more commonly, deposit eggs in plant tissues, where they undergo larval development. The presence of the insect or its larva stimulates the plant tissues to grow rapidly, forming a gall. The adaptive significance (for insects) of galls remains unclear, but one popular theory is that their production interferes with the production of defensive chemicals by the plant, thus rendering gall tissues more palatable. A somewhat similar strategy is used by leaf miners, specialized larvae from several orders (e.g., Coleoptera, Diptera, Hymenoptera) that live entirely within the tissues of leaves, burrowing through and consuming the most digestible tissues.

An interesting predatory strategy is that of New Zealand glowworms (*Arachnocampa luminosa*), which live in caves and in bushes along riverbeds. These larvae of small flies produce a bright bioluminescence in the distal ends of the Malpighian tubules, which lights up the posterior end of the body. (The light peaks at 485 nm wavelength.) Each larva constructs a horizontal web from which up to 30 vertical "fishing lines" descend, each with a regularly spaced series of sticky droplets. Small invertebrates (e.g., flies, spiders, small beetles, hymenopterans) attracted to the light are caught by the fishing lines, hauled up, and eaten. Harvestmen (Opiliones), the main predators of glowworms, use the light to locate their prey!

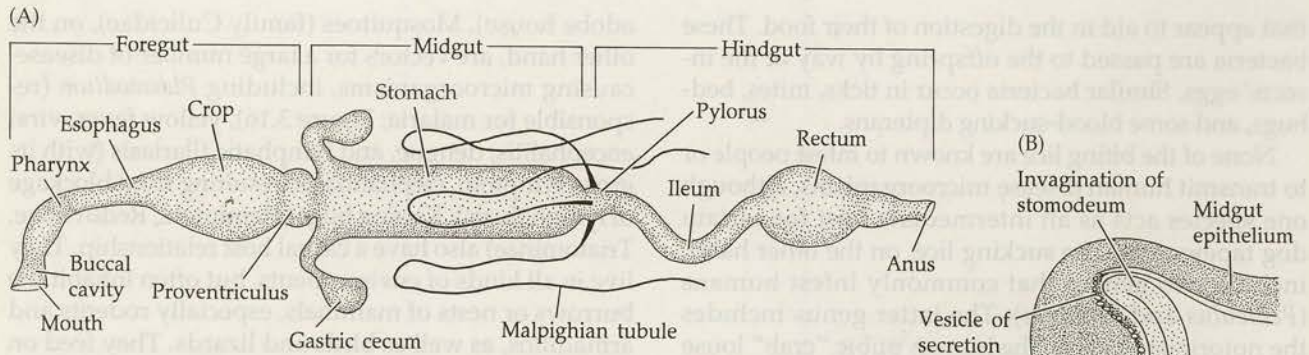


Figure 22.26 Main subdivisions of an insect gut. (A) The entire alimentary canal. (B) The junction of the foregut and midgut in a dipteran. Note the origin of the peritrophic membrane and the fold formed by the stomodeal invagination and the midgut wall.

Digestive system Like the guts of all arthropods, the long, usually straight hexapod gut is divisible into a stomodeal foregut, endodermal midgut, and proctodeal hindgut (Figure 22.26). Salivary glands are associated with one or several of the mouth appendages (Figure 22.27). The salivary secretions soften and lubricate solid food, and in some species contain enzymes that initiate chemical digestion. In larval moths (caterpillars), and in larval bees and wasps, the salivary glands secrete silk used to make pupal cells.

All hexapods, as well as most other arthropods that consume solid foods, produce a **peritrophic membrane** in the midgut (Figure 22.26B). This sheet of thin

chitinous material may line the midgut or pull free to envelop and coat the food particles as they pass through the gut. The peritrophic membrane serves to protect the delicate midgut epithelium from abrasion. It is permeated by microscopic pores that allow passage of enzymes and digested nutrients. In many species, production of this membrane also takes place in the hindgut, where it encapsulates the feces as discrete pellets.

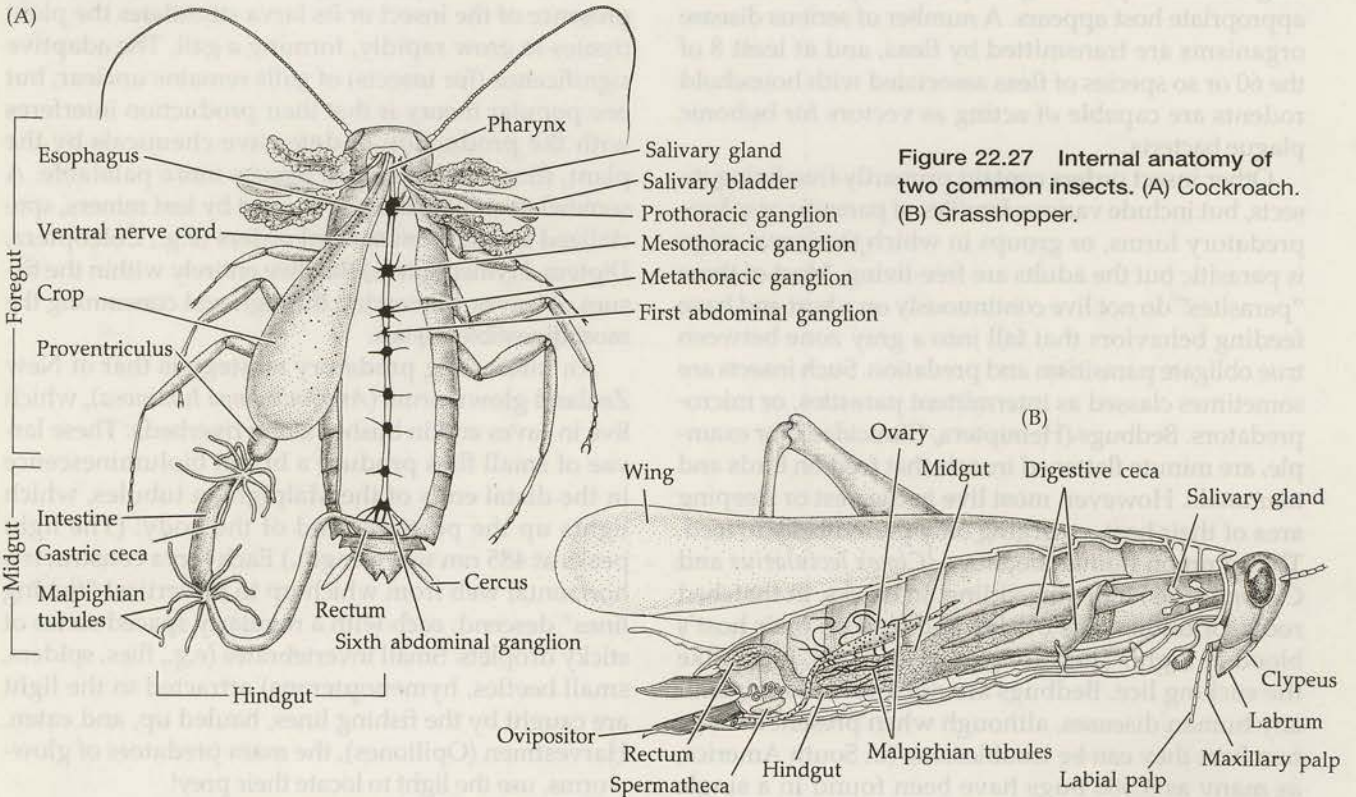


Figure 22.27 Internal anatomy of two common insects. (A) Cockroach. (B) Grasshopper.

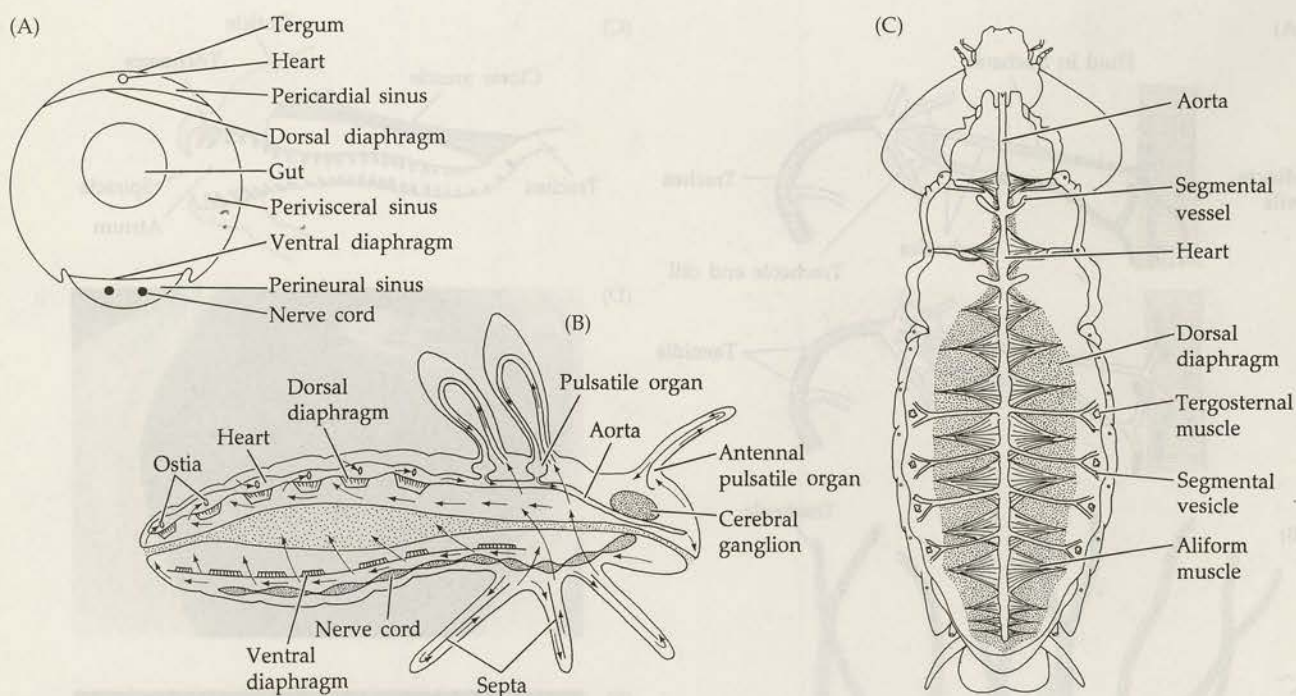


Figure 22.28 The circulatory system of insects. (A) An insect abdomen (cross section). Note the division of the hemocoel into three chambers (a dorsal pericardial sinus, a ventral perineural sinus, and a central perivisceral sinus). These chambers are separated by diaphragms lying on frontal planes. (B) Blood circulation in an insect with a fully developed circulatory system (longitudinal section). Arrows indicate the circulatory course. (C) A cockroach (ventral dissection). Note the dorsal and segmental vessels. The dorsal diaphragm and aliform (heart) muscles are continuous over the ventral wall of the heart and vessels, but they are omitted from the diagram for clarity.

Along with their vast range of feeding habits, insects have evolved a number of specialized digestive structures. The foregut is typically divided into a well defined pharynx, esophagus, crop, and proventriculus (Figures 22.26 and 22.27). The pharynx is muscular, particularly in the sucking insects, in which it commonly forms a **pharyngeal pump**. The crop is a storage center whose walls are highly extensible in species that consume large but infrequent meals. The **proventriculus** regulates food passage into the midgut, either as a simple valve that strains the semifluid foods of sucking insects or as a grinding organ, called a gizzard or gastric mill, that masticates the chunks ingested by biting insects. Well-developed gastric mills have strong cuticular teeth and grinding surfaces that are gnashed together by powerful proventricular muscles.

The midgut (= stomach) of most insects bears gastric ceca that lie near the midgut-foregut junction and resemble those of crustaceans. These evaginations serve to increase the surface area available for digestion and absorption. In some cases the ceca also house mutualistic microorganisms (bacteria and protists). The insect

hindgut serves primarily to regulate the composition of the feces and perhaps to absorb some nutrients. Digestion of cellulose by termites and certain wood-eating roaches is made possible by enzymes produced by protists and bacteria that inhabit the hindgut.

Clusters of fat cells create a **fat body** in the hemocoel of many insects, which is most conspicuous in the abdomen but also extends into the thorax and head. The fat body is a unique organ to the insects and is often likened to the vertebrate liver and the chlorogogen tissue in annelids. The fat body not only stores lipids, proteins and carbohydrates, but also synthesizes proteins. Many insects do not feed during their adult life; instead, they rely on stored nutrients accumulated in the larval or juvenile stages and stored in the fat body.

Circulation and Gas Exchange

The hexapod circulatory system includes a dorsal tubular heart that pumps the hemocoelic fluid (blood) toward the head. The heart narrows anteriorly into a vessel-like aorta, from which blood enters the large hemocoelic chambers, through which it flows posteriorly, eventually returning to the pericardial sinus and then to the heart via paired lateral ostia (Figure 22.28). In most insects the heart extends through the first nine abdominal segments; the number of ostia is variable. Accessory pumping organs, or **pulsatile organs**, often occur at the bases of wings and of especially long appendages, such as the hindlegs of grasshoppers, to assist in circulation and maintenance of blood pressure.

The heart is a rather weak pumping organ, and blood is moved primarily by routine muscular activity of the body and appendages. Hence, circulation is slow and system pressure is relatively low. Like many

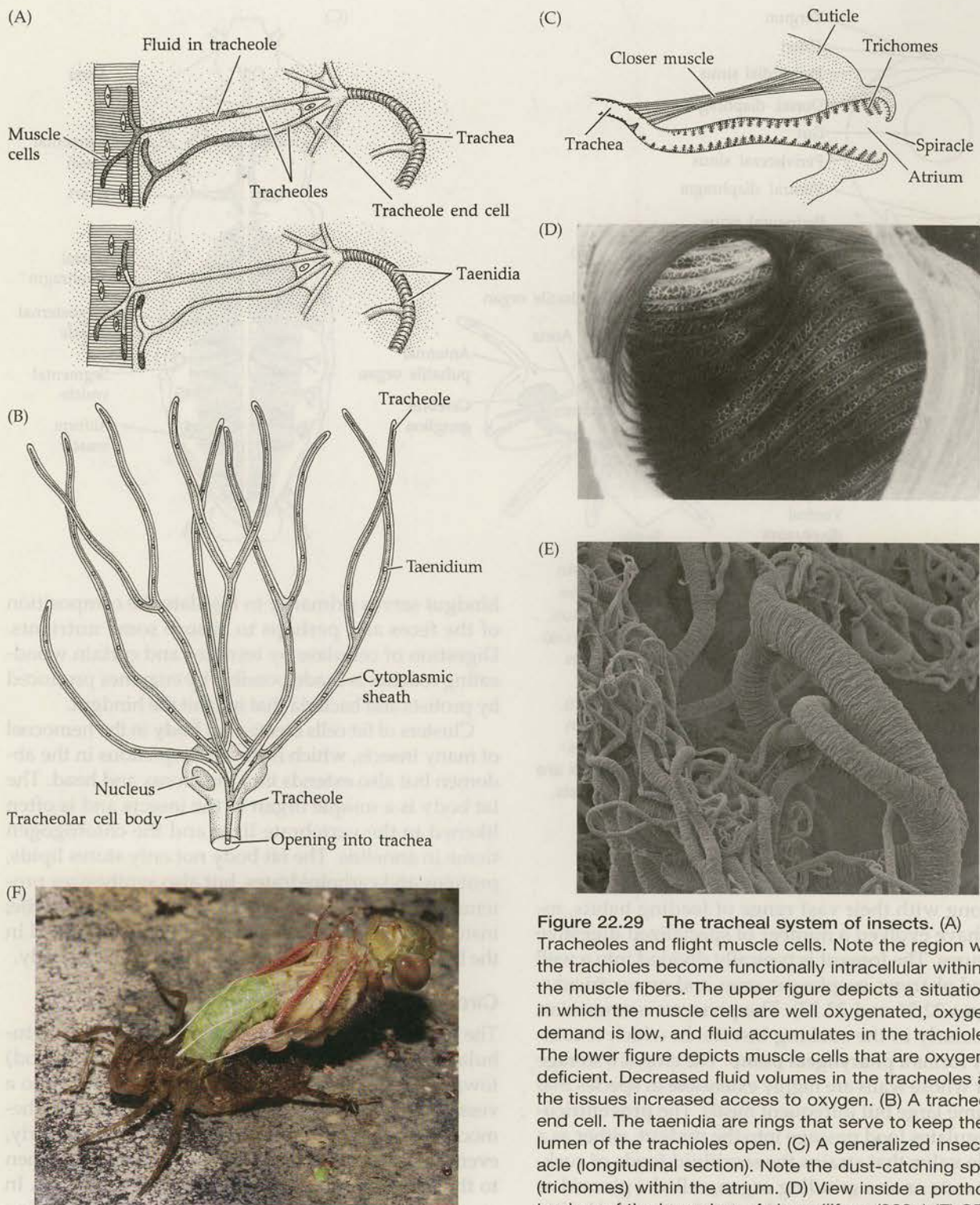


Figure 22.29 The tracheal system of insects. (A) Tracheoles and flight muscle cells. Note the region where the tracheoles become functionally intracellular within the muscle fibers. The upper figure depicts a situation in which the muscle cells are well oxygenated, oxygen demand is low, and fluid accumulates in the tracheoles. The lower figure depicts muscle cells that are oxygen-deficient. Decreased fluid volumes in the tracheoles allow the tissues increased access to oxygen. (B) A tracheole end cell. The taenidia are rings that serve to keep the lumen of the tracheoles open. (C) A generalized insect spiracle (longitudinal section). Note the dust-catching spines (trichomes) within the atrium. (D) View inside a prothoracic trachea of the honeybee, *Apis mellifera*. (960 \times) (E) SEM of trachea and tracheoles of a carabid beetle. (F) Dragonfly nymph molting into an adult. Note the long white tracheae being pulled out of the exuvia by the emerging adult.

arachnids, some hexapods use the hydraulic pressure of the hemocoelic system in lieu of extensor muscles. In this way, for example, butterflies and moths unroll their maxillary feeding tubes.

Many types of hemocytes have been reported from the blood of insects. None functions in oxygen storage or transport, but several are apparently important

in wound healing and clotting. Nutrients, wastes, and hormones can be efficiently carried by this system, but respiratory oxygen cannot (some CO_2 does diffuse into the blood). The active lifestyles of these terrestrial

animals require special structures to carry out the tasks of respiratory gas exchange and excretion. These structures are the tracheal system and the Malpighian tubules, described below.

Desiccation is one of the principal dangers faced by terrestrial invertebrates. Adaptations to terrestrial life always involve some degree of compromise between water loss and gas exchange with the atmosphere. Even though the general body surface of insects may be largely waterproof, the gas exchange surfaces cannot be.

In some minute hexapods, such as Collembola, gas exchange occurs by direct diffusion across the body surface. However, the vast majority of hexapods rely on a tracheal system (Figure 22.29). As explained in Chapter 20, **tracheae** are extensive tubular invaginations of the body wall, opening through the cuticle by pores called spiracles. Up to ten pairs of spiracles can occur on the pleural walls of the thorax and abdomen. Since tracheae are epidermal in origin, their linings are shed with each molt. The cuticular wall of each trachea is sclerotized and usually strengthened by rings or spiral thickenings called **taenidia**, which keep the tube from collapsing but allow for changes in length that may accompany body movements. The tracheae originating at one spiracle commonly anastomose with others to form branching networks penetrating most of the body. In some insects it appears that air is taken into the body through the thoracic spiracles and released through the abdominal spiracles, thus creating a flow-through system.

Each spiracle is usually recessed in an atrium, whose walls are lined with setae or spines (**trichomes**) that prevent dust, debris, and parasites from entering the tracheal tubes. A muscular valve or other closing device is often present and is under control of internal partial pressures of O_2 and CO_2 . In resting insects most of the spiracles are generally closed. Ventilation of the tracheal system is accomplished by simple diffusion gradients, as well as by pressure changes induced by the animal itself. Almost any movement of the body or gut causes air to move in and out of some tracheae. Telescopic elongation of the abdomen is used by some insects to move air in and out of the tracheal tubes. Many insects have expanded tracheal regions called tracheal pouches, which function as sacs for air storage.

Because the blood of hexapods does not transport oxygen, the tracheae must extend directly to each organ of the body, where their ends actually penetrate the tissues. Oxygen and CO_2 thus are exchanged directly between cells and the small ends of the tracheae, the tracheoles. In the case of flight muscles, where oxygen demand is high, the tracheal tubes invade the muscle fibers themselves. **Tracheoles**, the innermost parts of the tracheal system, are thin-walled, fluid-filled channels that end as a single cell, the tracheole end cell (= tracheolar cell) (Figure 22.29). The tracheoles penetrate every organ in the body,

and gas exchange takes place directly between the body cells and the tracheoles. Unlike tracheae, tracheoles are not shed during ecdysis. The tracheoles are so minute (0.2–1.0 μm) that ventilation is impossible, and gas transport here relies on aqueous diffusion. This ultimate constraint on the rate of gas exchange may be the primary reason terrestrial arthropods never achieved extremely large sizes.

In aquatic insects the spiracles are usually nonfunctional, and gases simply diffuse across the body wall directly to the tracheae. A few species retain functional spiracles; they hold an air bubble over each opening, through which oxygen from the surrounding water diffuses. The air bubbles are held in place by secreted waxes and by patches of hydrophobic hairs in densities that may exceed 2 million per square millimeter. Most aquatic insects, particularly larval stages, have **gills**—external projections of the body wall that are covered by thin, unsclerotized cuticle and contain blood, tracheae, or air bubbles (Figure 22.30). The gills contain channels that lead to the main tracheal system. In some aquatic insects, such as dragonfly nymphs, the rectum bears tiny branched tubules called **rectal accessory gills**. By pumping water in and out of the anus, these insects exchange gases across the increased surface area of the thin gut wall. There are analogous examples of hindgut respiratory irrigation in other, unrelated invertebrate groups (e.g., echiurids, holothurians).

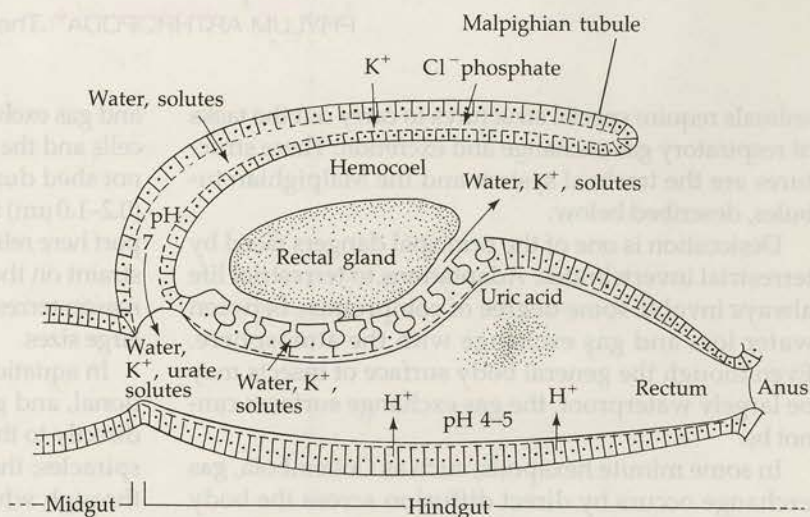
Excretion and Osmoregulation

The problem of water conservation and the nature of the circulatory and gas exchange systems in terrestrial arthropods necessitated the evolution of entirely new structures to remove metabolic wastes. Like the gas exchange surfaces, the excretory system is a site of potential water loss, because nitrogenous wastes initially occur in a dissolved state. These problems are



Figure 22.30 Aquatic nymph of a mayfly, *Paraleptophlebia* (Ephemeroptera), with lateral abdominal gills.

Figure 22.31 A single Malpighian tubule opening into the hindgut at its junction with the midgut. Arrows indicate the flow of materials.



compounded in small terrestrial organisms, such as many hexapods, because of their large surface area-to-volume ratios. And water loss problems are even more severe in flying insects, because flight is probably the most metabolically demanding of all locomotor activities.

In most terrestrial arthropods, the solution to these problems is Malpighian tubules. In the Hexapoda, these unbranched outgrowths of the gut arise near the junction of the midgut and hindgut (Figures 22.26, 22.27, and 22.31). Their blind distal ends extend into the hemocoel and lie among various organs and tissues. Up to several hundred Malpighian tubules may be present.

In the absence of sufficient blood pressure for typical excretory filtration, hexapods use osmotic pressure to achieve the same result. Various ions, especially potassium, are actively transported across the Malpighian tubule epithelium from the blood into the tubule lumen (Figure 22.31). The osmotic gradient maintained by this ion transport mechanism enables water and solutes to move from the body cavity into the tubules, and thence into the gut. Water and other metabolically valuable materials are selectively reabsorbed into the blood across the wall of the hindgut, while the Malpighian filtrate left behind is mixed with the other gut contents. Reabsorption of water, amino acids, salts, and other nutrients may be enhanced by the action of special cells in thickened regions called rectal glands. The soluble potassium urate from the Malpighian tubules has, at this point in the gut, been precipitated out as solid uric acid as a result of the low pH of the hindgut (pH 4–5). Uric acid crystals cannot be reabsorbed into the blood, hence they pass out the gut with the feces. Insects also possess special cells called nephrocytes or pericardial cells that move about in certain areas of the hemocoel, engulfing and digesting particulate or complex waste products.

The hexapod cuticle is sclerotized or tanned to various degrees, adding a small measure of waterproofing. But more importantly, a waxy layer occurs within the epicuticle, which greatly increases resistance to desiccation and frees insects to fully exploit dry

environments. In many terrestrial arthropods (including primitive insects) an eversible coxal sac (not to be confused with the coxal glands of arachnids) projects from the body wall near the base of each leg. It is thought that the coxal sacs assist in maintaining body hydration by taking up water from the environment (e.g., dewdrops). Many insects collect environmental water by various other devices. Some desert beetles (*Tenebrionidae*) collect atmospheric water by “standing on their heads” and holding their bodies up to the moving air so that humidity can condense on the abdomen and be channeled to the mouth for consumption.

Insects that inhabit desert environments have a much greater tolerance of high temperatures and body water loss than do insects in mesic environments, and they are particularly good at water conservation and producing insoluble nitrogenous waste products. They also have behavioral traits, such as nocturnal activity cycles and dormancy periods that enhance water conservation. Upper lethal temperatures for desert species commonly range to 50°C. The spiracles are often covered by setae or depressed below the cuticular surface. Many xeric insects also undergo periods of dormancy (i.e., diapause or aestivation) during some stage of the life cycle, characterized by a lowering of the basal metabolic rate and cessation of movement, which allow them to withstand prolonged periods of temperature and moisture extremes. Some even utilize evaporative cooling to reduce body temperatures. The long-chain hydrocarbons that waterproof the epicuticle also are more abundant in xeric insects.

Nervous System and Sense Organs

The hexapod nervous system conforms to the basic arthropod plan described in Chapter 20 (Figures 22.32 and 22.33). The two ventral nerve cords, as well as the segmental ganglia, are often largely fused. In dipterans, for example, even the three thoracic ganglia are fused into a single mass. The largest number of free ganglia occurs in the primitive wingless insects, which have as many as eight unfused abdominal ganglia. Giant fibers have also been reported from several insect orders.

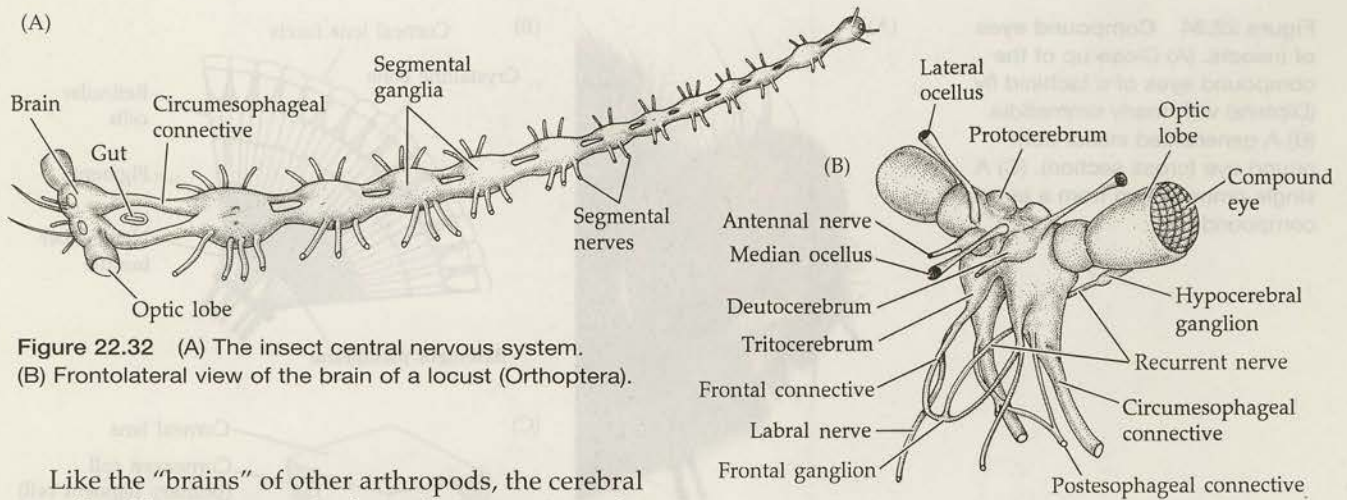


Figure 22.32 (A) The insect central nervous system. (B) Frontolateral view of the brain of a locust (Orthoptera).

Like the “brains” of other arthropods, the cerebral ganglia of insects comprise three distinct regions: the protocerebrum, the deutocerebrum, and the tritocerebrum. The subesophageal ganglion is composed of the fused ganglia of the fourth, fifth, and perhaps the sixth head segments and controls the mouthparts, salivary glands, and some other local musculature.

Insects possess a hypocerebral ganglion between the cerebral ganglion and the foregut. Associated with this ganglion are two pairs of glandular bodies called the **corpora cardiaca** and the **corpora allata** (Figure 22.33). These two organs work in concert with the prothoracic glands and certain neurosecretory cells in the protocerebrum. The whole complex is a major endocrine center that regulates growth, metamorphosis, and other functions (see Chapter 20).

Hexapods typically possess simple ocelli in the larval, juvenile, and often adult stages. When present in adults, they usually form a triad or a pair on the anterodorsal surface of the head. The compound eyes are well developed, resembling those of Crustacea, and are image-forming. Most adult insects have a pair of compound eyes (Figure 22.34), which bulge out to some extent, giving these animals a wide field of vision in

almost all directions. Compound eyes are greatly reduced or absent in parasitic groups and in many cave-dwelling forms. The general anatomy of the arthropod compound eye was described in Chapter 20, but several distinct structural trends are found in hexapod eyes, as we describe below.

The number of ommatidia apparently determines the overall visual acuity of a compound eye; hence large eyes are typically found on active, predatory insects such as dragonflies and damselflies (order Odonata), which may have over 10,000 ommatidia in each eye. On the other hand, workers of some ant species have but a single ommatidium per eye (ants live in a world of chemical communication)! Similarly, larger facets capture more light and are typical of nocturnal insects. In all cases, a single ommatidium consists of two functional elements: an outer light-gathering part composed of a lens and a crystalline cone, and an inner sensory part composed of a rhabdome and sensory cells (Figure 22.34).

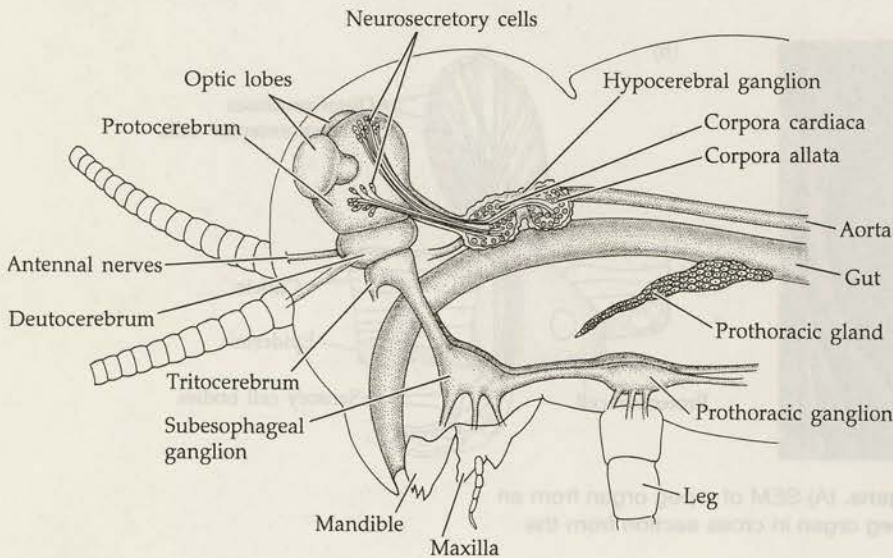
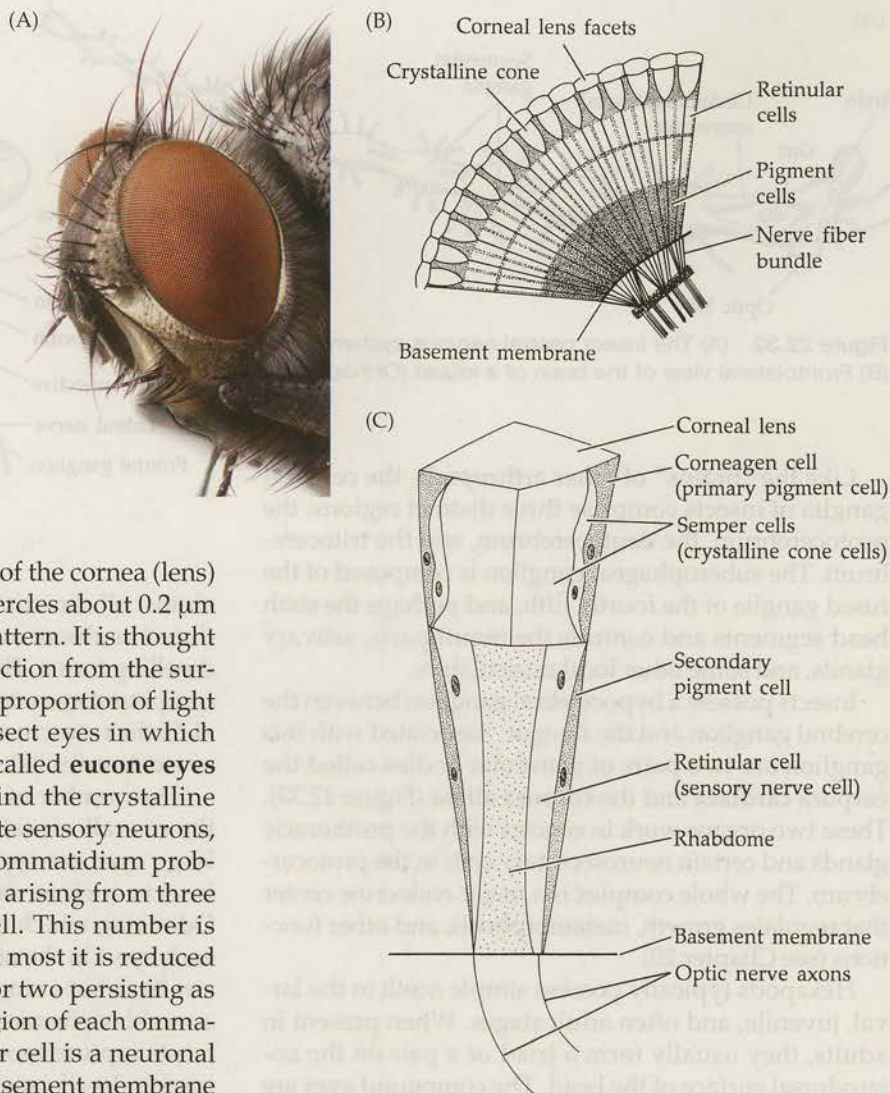


Figure 22.33 Endocrine organs and central nervous system in the head and thorax of a generalized insect. These organs all play roles in the control of molting and metamorphosis.

Figure 22.34 Compound eyes of insects. (A) Close-up of the compound eyes of a tachinid fly (Diptera) with many ommatidia. (B) A generalized insect compound eye (cross section). (C) A single ommatidium from a eucone compound eye.



In some insects the outer surface of the cornea (lens) is covered with minute conical tubercles about $0.2 \mu\text{m}$ tall and arranged in a hexagonal pattern. It is thought that these projections decrease reflection from the surface of the lens, thus increasing the proportion of light transmitted through the facet. Insect eyes in which the crystalline cone is present are called **eucone eyes** (Figure 22.34B). Immediately behind the crystalline cone (in eucone eyes) are the elongate sensory neurons, or reticular cells. Primitively, each ommatidium probably contained eight reticular cells arising from three successive divisions of a single cell. This number is found in some insects today, but in most it is reduced to six or seven, with the other one or two persisting as short basal cells in the proximal region of each ommatidium. Arising from each reticular cell is a neuronal axon that passes out through the basement membrane at the back of the eye into the optic lobe. There is no true optic nerve in insects; the eyes connect directly with the optic lobe of the brain. The rhabdomeres consist of tightly packed microvilli that are about 50 nm in diameter and hexagonal in cross section. The reticular cells

are surrounded by 12 to 18 secondary pigment cells, which isolate each ommatidium from its neighbors.

The general body surface of hexapods, like that of other arthropods, bears a great variety of microscopic

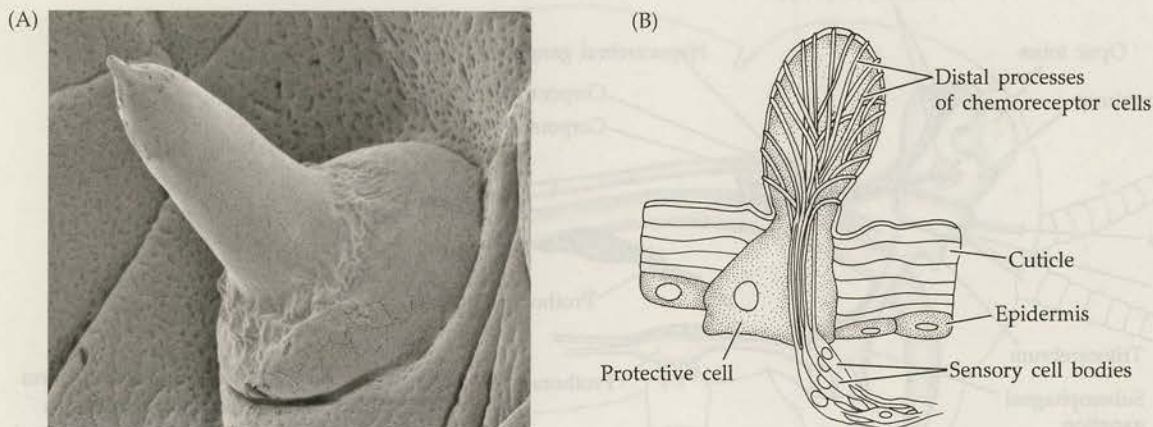


Figure 22.35 Chemosensory peg organs. (A) SEM of a peg organ from an antenna of a beetle. (B) Diagram of a peg organ in cross section from the antenna of a grasshopper.

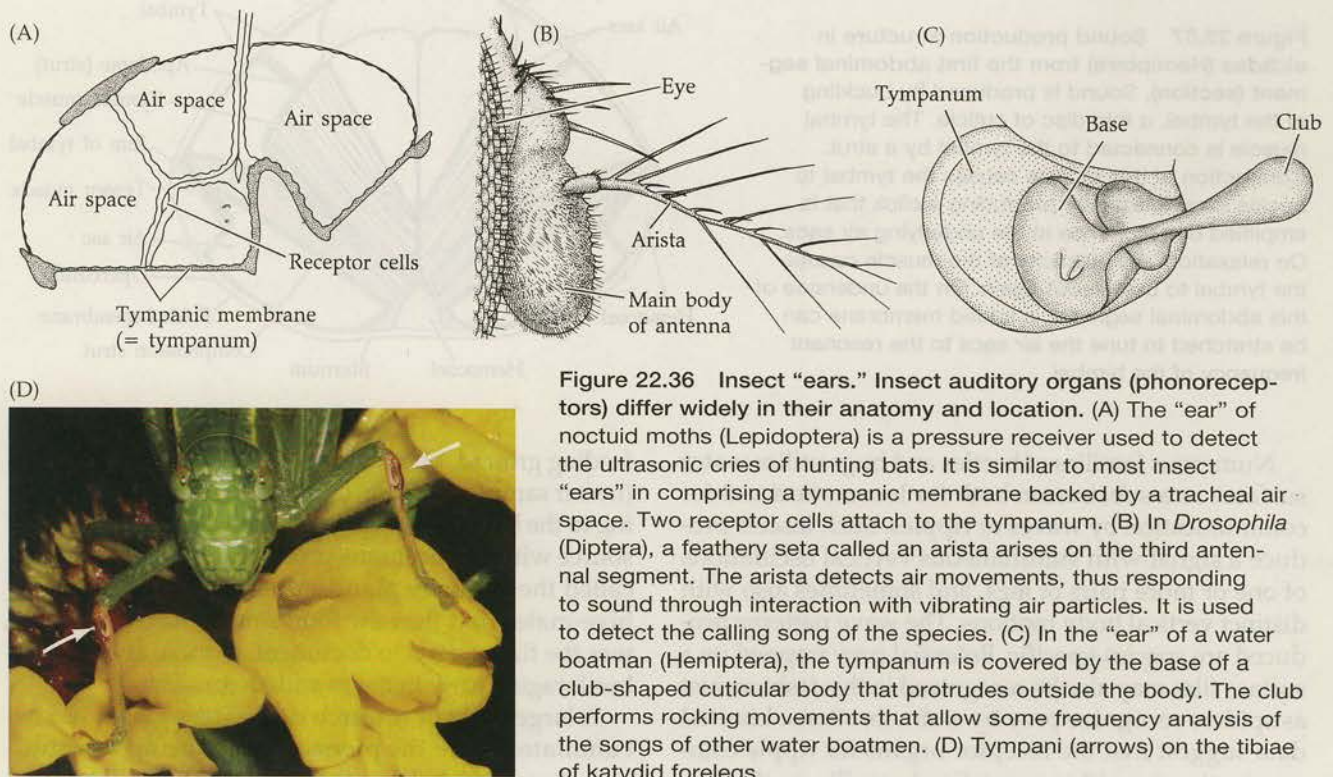


Figure 22.36 Insect “ears.” Insect auditory organs (phonoreceptors) differ widely in their anatomy and location. (A) The “ear” of noctuid moths (Lepidoptera) is a pressure receiver used to detect the ultrasonic cries of hunting bats. It is similar to most insect “ears” in comprising a tympanic membrane backed by a tracheal air space. Two receptor cells attach to the tympanum. (B) In *Drosophila* (Diptera), a feathery seta called an arista arises on the third antennal segment. The arista detects air movements, thus responding to sound through interaction with vibrating air particles. It is used to detect the calling song of the species. (C) In the “ear” of a water boatman (Hemiptera), the tympanum is covered by the base of a club-shaped cuticular body that protrudes outside the body. The club performs rocking movements that allow some frequency analysis of the songs of other water boatmen. (D) Tympani (arrows) on the tibiae of katydid forelegs.

sensory hairs and setae, known collectively as **sensilla** (sing., sensillum). The incredible diversity of these cuticular surface structures has only begun to be explored, primarily by scanning electron microscopy. Sensilla are most heavily concentrated on the antennae, mouthparts, and legs. Most appear to be tactile or chemosensory. Club-shaped or peg-shaped chemosensory setae, usually called **peg organs** and resembling the aesthetascs of crustaceans, are particularly common on the antennae of hexapods (Figure 22.35).

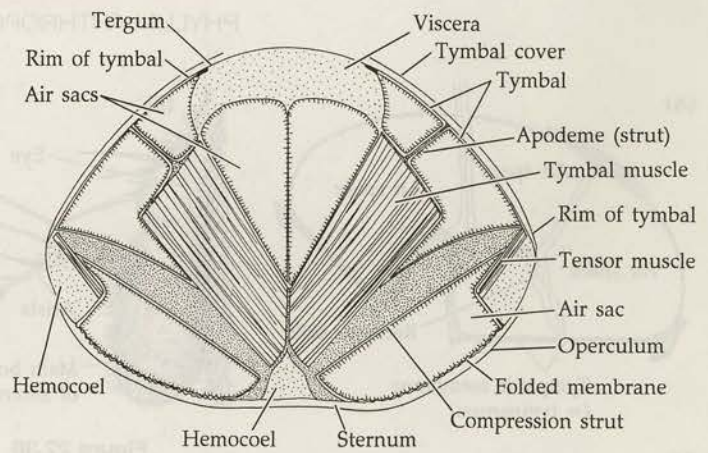
Insects have internal proprioceptors called **chordotonal organs**. These structures stretch across joints and monitor the movement and position of various body parts. Phonoreceptors also occur in most insect orders. These structures may be simple modified body or appendage setae, or antennae, or complex structures called **tympanic organs** (Figure 22.36). Tympanic organs generally develop from the fusion of parts of a tracheal dilation and the body wall, which form a thin tympanic membrane (= tympanum). Receptor cells in an underlying air sac, or attached directly to the tympanic membrane, respond to vibrations in much the same fashion as they do in the cochlea of the human inner ear. Many insects can discriminate among different sound frequencies, but others may be tone-deaf. Tympanic organs may occur on the abdomen, the thorax, or the forelegs. Several insects that are prey to bats have the ability to hear the high frequencies of bat echolocation devices, and they have evolved flight behaviors to avoid these flying mammals. For example, some moths, when they hear a bat’s echolocation

(generally above the range of human ears), will fold their wings and suddenly drop groundward as an evasive maneuver. Praying mantises, whose sonar detection device is buried in a groove on the ventral side of the abdomen, throw out the raptorial forelimbs and elevate the abdomen. These movements cause the insect to “stall” and go into a steep roll, which it pulls out of at the last minute with a “power dive” that effectively avoids bat predators.

Sound communication in insects, like light communication in fireflies (and some ostracods), is a species-specific means of mate communication. Several insect groups (e.g., some orthopterans, coleopterans, dipterans, and hemipterans) possess sound-producing structures. Male flies of the genus *Drosophila* create species-specific mating songs by rapidly vibrating the wings or abdomen. These “love songs” attract conspecific females for copulation. It has been demonstrated that the rhythm of the male’s song is encoded in genes inherited from his mother, on the X chromosome, whereas the song’s “pulse interval” is controlled by genes on autosomal chromosomes.

Cicadas may possess the most complex sound-producing organs in the animal kingdom (Figure 22.37). The ventral metathoracic region of male cicadas bears two large plates, or opercula, that cover a complex system of vibratory membranes and resonating chambers. One membrane, the tymbal, is set vibrating by special muscles, and other membranes in the resonating chambers amplify its vibrations. The sound leaves the cicada’s body through the metathoracic spiracle.

Figure 22.37 Sound production structure in cicadas (Hemiptera) from the first abdominal segment (section). Sound is produced by buckling of the tymbal, a thin disc of cuticle. The tymbal muscle is connected to the tymbal by a strut. Contraction of this muscle causes the tymbal to buckle inward, thereby producing a click that is amplified by resonance in the underlying air sacs. On relaxation, the elasticity of the muscle causes the tymbal to buckle out again. On the underside of this abdominal segment, a folded membrane can be stretched to tune the air sacs to the resonant frequency of the tymbal.



Numerous families of beetles and bugs utilize water surfaces as a substratum both for locomotion and for communication by waves or ripples. Such insects produce a signal with simultaneous vertical oscillations of one or more pairs of legs, and sometimes also with distinct vertical body motions. The wave patterns produced are species-specific. Potential prey trapped on a surface film may also be recognized in this fashion, just as spiders recognize prey by web vibrations. Limited data suggest that the receptor organs for ripple communication are either specialized sensilla on the legs or special proprioceptors between joints of the legs or antennae, perhaps similar to the tarsal organs of scorpions (Chapter 24).

A number of insects are bioluminescent, the most familiar being beetles of the family Lampyridae, known as lightning bugs or fireflies. In the tropics, where they are especially abundant, fireflies are sometimes kept in containers and used as natural flashlights, and women may wrap them in gauze bags worn as glowing hair ornaments. The light of luminescent insects ranges from green through red and orange, depending on the species and the precise chemical nature of the luciferin-luciferase system involved. Light-producing organs are typically composed of clusters of light-producing cells, or **photocytes**, backed by a layer of reflecting cells and covered with a thin, transparent epidermis. The photocytes are richly supplied with tracheae, oxygen being necessary for the chemical reaction. Each species of firefly, and of most other glowing insects, has a distinct flash pattern, or code, to facilitate mate recognition and communication.

One of the most sophisticated communication behaviors among insects may be the famous honeybee "waggle dance." Each day forager bees leave their colony to locate new food sources (e.g., fresh flower blooms). They fly meandering search forays until a good source is located. Then they return to the hive along a straight flight path (a "bee line"); while doing so, they are thought to imprint a navigational "map" from the colony to the food source. Most behaviorists believe that this information is communicated to hive-mates in a complex tail-wagging dance that allows other bees from the hive to fly directly to the new

feeding ground. The forager bee also carries food odors (nectar samples), pollen, and various other odors clinging to the hairs on her body. She can also mark the food source with a pheromone produced in a special gland, called the **Nasnov gland**. All of these clues help her hive-mates find the new food source. Karl von Frisch was the first person to document all these attributes of bee foraging early in the twentieth century.

A large body of research on bee navigation has accumulated since the pioneering "dancing bee studies" of von Frisch. We now know that honeybees (and solitary bees) have outstanding vision. Much of the bee's daily activity, including navigation and flower recognition, relies strongly on ultraviolet vision. Bees appear to utilize a hierarchical series of flight orientation mechanisms; when the primary mechanism is blocked, a bee can switch to a secondary system. The primary navigation system utilizes the pattern of polarized ultraviolet sunlight in the sky. This pattern depends on the location of the sun as determined by two coordinates, the azimuth and the elevation. Bees and many other animals that orient to the sun have a built-in ability to compensate for both hourly changes (elevation) and seasonal changes (azimuth) in the sun's position with time. On cloudy days, when the sun's light is largely depolarized, bees cannot rely on their ultraviolet celestial navigation mechanism and thus may switch to their second-order navigational system: navigation by landmarks (foliage, rocks, and so on) that were imprinted during the most recent flight to the food source. Limited evidence suggests that some form of tertiary backup system may also exist.

Thus, if the honeybee dance model is correct,⁷ honeybees must simultaneously process information concerning time, the direction of flight relative to the sun's azimuth, the movement of the sun, the distance flown, and local landmarks (not to mention complications due to other factors, such as crosswinds), and in doing so reconstruct a straight-line heading to inform

⁷The honeybee dance hypothesis is not without its detractors, and some workers doubt its existence altogether; see the General References section of this chapter for a glimpse at the history of the honeybee dance controversy.

their hive-mates. If recent evidence is correct, bees (like homing pigeons) may also detect Earth's magnetic fields with iron compounds (magnetite) located in their abdomens. Bands of cells in each abdominal segment of the honeybee contain iron-rich granules, and nerve branches from each segmental ganglion appear to innervate these tissues.⁸

In some insects the ocelli are the principal navigation receptors. Some locusts and dragonflies and at least one ant species utilize the ocelli to read compass information from the blue sky. As in bees, the pattern of polarized light in the sky seems to be the main compass cue. In some species, both ocelli and compound eyes may function in this fashion. Many (probably most) insects also see ultraviolet light.

Perhaps the most famous insect navigators are North America's monarch butterflies (*Danaus plexippus*). Each autumn, monarchs migrate up to 4,000 km from breeding grounds in the eastern United States and Canada to over-wintering sites in the mountains of Michoacán, in central Mexico. They make this remarkable journey by orienting with a Sun compass, using the Sun's changing azimuth (and knowledge of the relative time of day) to direct their movements. On cloudy days, when a precise solar azimuth is unobtainable, monarchs still manage to orient towards the south-southwest, suggesting that they also have a backup mechanism of orientation, such as a geomagnetic compass. Monarchs are one of a small group of animal species for which a sun compass orientation mechanism has been shown to exist.

Many insects release noxious quinone compounds to repel attacks. Perhaps best known in this regard are certain Tenebrionidae, many of which stand on their heads to do so. But the champions of this chemical warfare strategy are definitely the bombardier beetles, members of the carabid subfamilies Brachininae and Paussinae, which expel quinone compounds at temperatures reaching 100°C (Figure 22.7C).

Reproduction and Development

Reproduction Hexapods are dioecious, and most are oviparous. A few insects are ovoviviparous, and many can reproduce parthenogenetically. Most insects rely on direct copulation and insemination. Reproductively mature insects are termed adults or **imagos**. Female imagos have one pair of ovaries, formed of clusters of

tubular ovarioles (Figure 22.38A). The oviducts unite as a common duct before entering a genital chamber. Seminal receptacles (spermathecae) and accessory glands also empty into the genital chamber. The genital chamber opens, via a short **copulatory bursa** (= vagina), on the sternum of the eighth, or occasionally the seventh or ninth, abdominal segment. The male reproductive system is similar, with a pair of testes, each formed by a number of sperm tubes (Figure 22.38B). Paired sperm ducts dilate into seminal vesicles (where sperm are stored) and then unite as a single ejaculatory duct. Near this duct, accessory glands discharge seminal fluids into the reproductive tract. The lower end of the ejaculatory duct is housed within a penis, which extends posteroventrally from the ninth abdominal sternite.

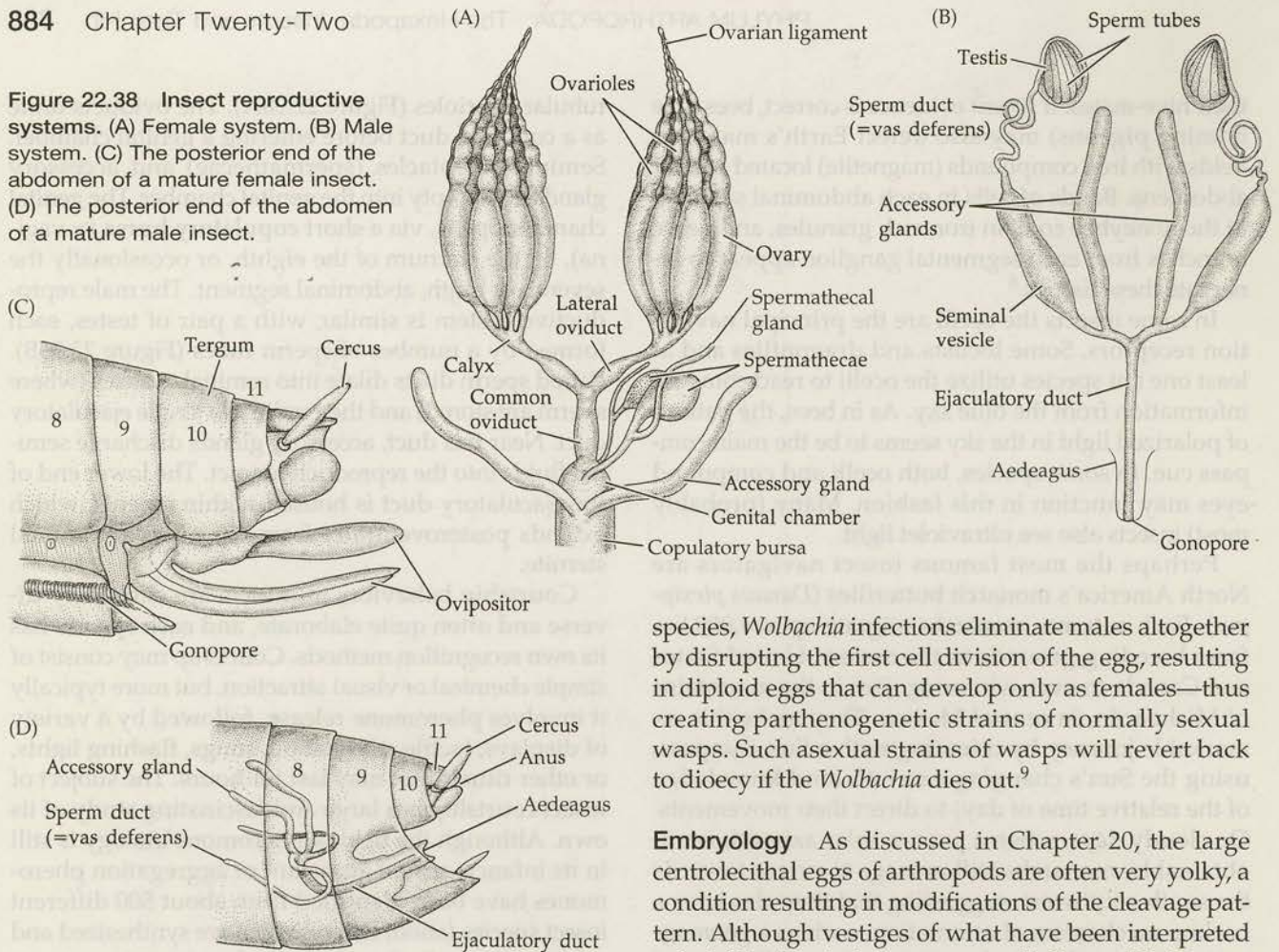
Courtship behaviors in insects are extremely diverse and often quite elaborate, and each species has its own recognition methods. Courtship may consist of simple chemical or visual attraction, but more typically it involves pheromone release, followed by a variety of displays, tactile stimulation, songs, flashing lights, or other rituals that may last for hours. The subject of insect courtship is a large and fascinating study of its own. Although the field of pheromone biology is still in its infancy, sexual attractant or aggregation pheromones have been identified from about 500 different insect species (about half of which are synthesized and sold commercially for pest control purposes).

Most insects transfer sperm directly as the male inserts either his **aedeagus** (Figure 22.38B,D) or a gonopod into the genital chamber of the female. Special abdominal claspers, or other articulated cuticular structures on the male, often augment his copulatory grip. Such morphological modifications are species specific and thus serve as valuable recognition characters, both for insect mates and insect taxonomists. Copulation often takes place in mid-flight. In some of the primitive wingless insects, and in the odonotans, sperm transfer is indirect. In these cases, a male may deposit his sperm on specialized regions of his body to be picked up by the female; or he may simply leave the sperm on the ground, where they are found and taken up by females. In bedbugs (order Hemiptera, family Cimicidae) males use the swollen penis to pierce a special region of the female's body wall; sperm are then deposited directly into an internal organ (**the organ of Berlese**). From there they migrate to the ovaries, where fertilization takes place as eggs are released.

Sperm may be suspended in an accessory gland secretion, or, more commonly, the secretion hardens around the sperm to produce a spermatophore. Females of many insect species store large quantities of sperm within the spermathecae. In some cases sperm from a single mating is sufficient to fertilize a female's eggs for her entire reproductive lifetime, which may last a few days to several years.

⁸Many animals possess magnetotactic capabilities, including some molluscs, hornets, salmon, tuna, turtles, salamanders, homing pigeons, cetaceans, and even bacteria and humans. Magnetotactic bacteria swim to the north in the Northern Hemisphere, to the south in the Southern Hemisphere, and in both directions at the geomagnetic equator. In all these cases, iron oxide crystals in the form of magnetite have been shown to underlie the primary detection devices. However, in honeybees, the iron-containing structures are trophocytes that contain paramagnetic magnetite. These magnetotactic trophocytes surround each abdominal segment and are innervated by the central nervous system.

Figure 22.38 Insect reproductive systems. (A) Female system. (B) Male system. (C) The posterior end of the abdomen of a mature female insect. (D) The posterior end of the abdomen of a mature male insect.



Insect eggs are protected by a thick membrane (the chorion) produced within the ovary. Fertilization occurs as the eggs pass through the oviduct to be deposited. Accessory glands contribute adhesives or secretions that harden over the zygotes. In many species, cuticular extensions around the gonopore of the female form an **ovipositor** (Figure 22.38C), with which she places the eggs in a brooding site that will afford suitable conditions for the young once they hatch (such as in a shallow underground chamber, in a plant stem, or within the body of a host insect). Although 50–100 eggs are usually laid at a time, as few as one and as many as several thousand are deposited by some species. Some insects, such as cockroaches, enclose several eggs at a time in a protective egg case.

Parthenogenesis is common in a variety of insect groups. It is used as an alternative form of reproduction seasonally by a number of insect taxa, particularly those living in unstable environments. In the Hymenoptera (bees, wasps, ants), it is also used as a mechanism for sex determination. In these cases, diploid fertilized eggs become females, and haploid unfertilized eggs develop into males. Infections by the bacterium *Wolbachia*, a frequent parasite of arthropod reproductive systems, are known to affect reproduction in many insect species. In some cases, infections result in infertility, whereas in others they transform males into functional females. But in some wasp

species, *Wolbachia* infections eliminate males altogether by disrupting the first cell division of the egg, resulting in diploid eggs that can develop only as females—thus creating parthenogenetic strains of normally sexual wasps. Such asexual strains of wasps will revert back to dioecy if the *Wolbachia* dies out.⁹

Embryology As discussed in Chapter 20, the large centrolecithal eggs of arthropods are often very yolky, a condition resulting in modifications of the cleavage pattern. Although vestiges of what have been interpreted as holoblastic spiral cleavage are still discernible in some crustaceans, the hexapods show almost no trace of spiral cleavage at all. Instead, most undergo meroblastic cleavage by way of intralecithal nuclear divisions, followed by migration of the daughter nuclei to the peripheral cytoplasm (= periplasm). Cytokinesis does not occur during these early nuclear divisions (up to 13 cycles), which thus generate a syncytium, or plasmodial phase of embryogenesis. The nuclei continue to divide until the periplasm is dense with nuclei, whereupon a syncytial blastoderm exists. Eventually, cell membranes begin to form, partitioning uninucleate cells from one another. At this point the embryo is a periblastula, comprising a yolky sphere containing a few scattered nuclei and covered by a thin cellular layer (Figure 22.39).

Along one side of the blastula a patch of columnar cells forms a germinal disc, sharply marked off from the thin cuboidal cells of the remaining blastoderm (Figure 22.39A). From specific regions of this disc, presumptive endodermal and mesodermal cells begin to proliferate as germinal centers. These cells migrate inward during gastrulation to lie beneath their parental cells, which now form the ectoderm. The mesoderm proliferates inward as a longitudinal gastral groove

⁹*Wolbachia pipientis* are maternally transmitted, gram-negative, obligate intracellular bacteria found in filarial nematodes, crustaceans, arachnids, and at least 20% of all insect species. Many *Wolbachia* increase their prevalence in populations by manipulating host reproductive systems.

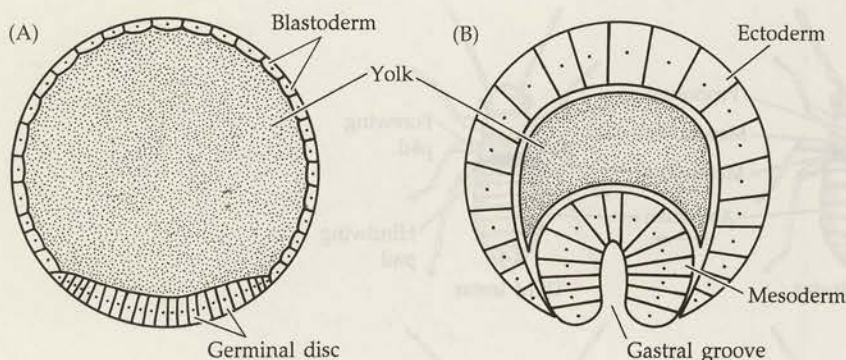


Figure 22.39 Early stages of insect development. (A) The blastoderm (blastula) of a generalized insect, subsequent to cytokinesis (cross section). Note the thickened germinal disc. (B) An early gastrula of a honeybee (cross section). Note the gastral groove and the proliferation of mesoderm.

(Figure 22.39B). The cells of the developing gut usually surround and gradually begin absorbing the central yoky mass of the embryo, and paired coelomic spaces appear in the mesoderm.

As segments begin to demarcate and proliferate, each receives one pair of mesodermal pouches and eventually develops appendage buds. As the mesoderm contributes to various organs and tissues, the paired coelomic spaces merge with the small blastocoel to produce the hemocoelic space. The mouth and anus arise by ingrowths of the ectoderm that form the proctodeal foregut and hindgut, which eventually establish contact with the developing endodermal midgut.

Polyembryony occurs in a number of insect taxa, particularly parasitic Hymenoptera. In this form of development the early embryo splits to give rise to more than one developing embryo. Thus, from two to thousands of larvae may result from a single fertilized egg, which is often deposited in the body of another (host) insect.

Post-embryonic development Within Hexapoda there are three main types of development: **ametabolous** (direct, or amorphic development), **hemimetabolous**, and **holometabolous** (indirect, or complete development). Figure 22.40 depicts these development types. Species in the most primitive wingless hexapod

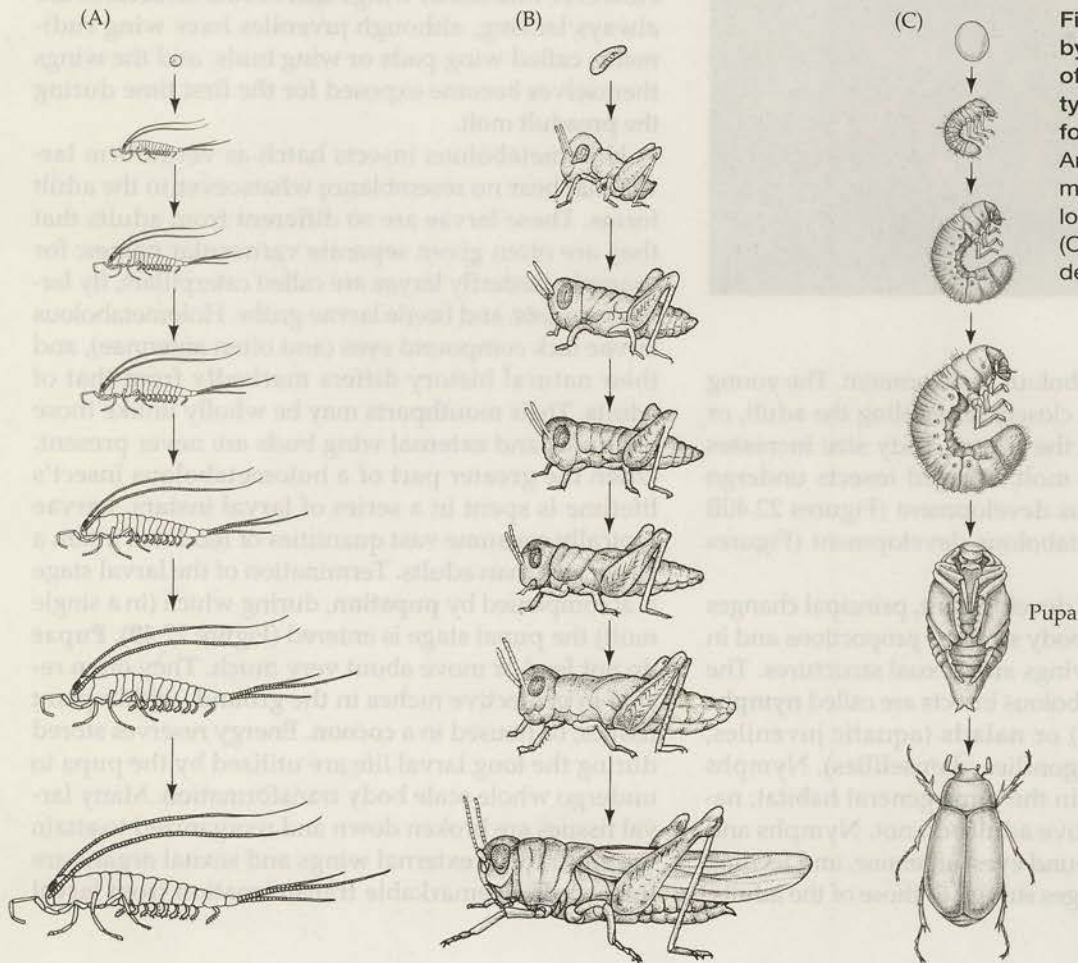


Figure 22.40 Side-by-side comparison of the three main types of development found in hexapods. (A) Ametabolous development, (B) hemimetabolous development, and (C) holometabolous development.

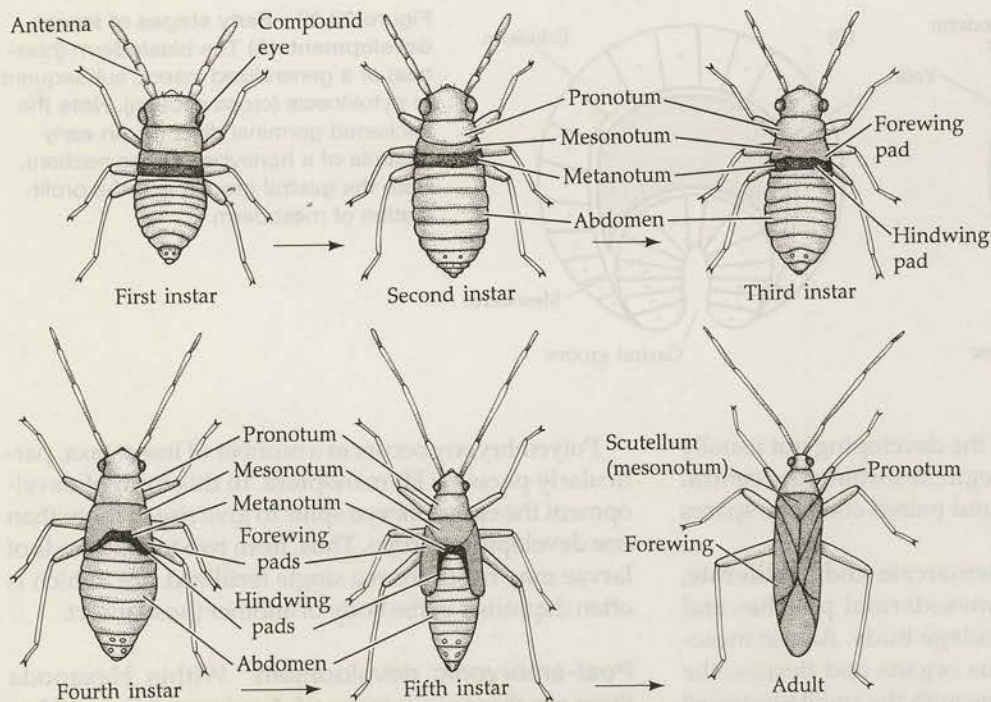


Figure 22.41 Illustrations and photo of the life stages of milkweed bugs (Hemiptera), illustrating the main life stages of hemimetabolous development. Note the wing pads in instars 3–5.



orders undergo ametabolous development. The young hatch out as juveniles closely resembling the adult, or imago, condition but the overall body size increases with each successive molt. Winged insects undergo either hemimetabolous development (Figures 22.40B and 22.41) or holometabolous development (Figures 22.40C and 22.42).

In hemimetabolous development, principal changes during growth are in body size and proportions and in the development of wings and sexual structures. The juveniles of hemimetabolous insects are called **nymphs** (terrestrial juveniles) or **naiads** (aquatic juveniles, such as mayflies, dragonflies, damselflies). Nymphs and adults often live in the same general habitat; naiads and their respective adults do not. Nymphs and naiads possess compound eyes, antennae, and feeding and walking appendages similar to those of the adults.

However functional wings and sexual structures are always lacking, although juveniles have wing rudiments called wing pads or wing buds, and the wings themselves become exposed for the first time during the preadult molt.

Holometabolous insects hatch as vermiform larvae that bear no resemblance whatsoever to the adult forms. These larvae are so different from adults that they are often given separate vernacular names; for example, butterfly larvae are called caterpillars, fly larvae maggots, and beetle larvae grubs. Holometabolous larvae lack compound eyes (and often antennae), and their natural history differs markedly from that of adults. Their mouthparts may be wholly unlike those of adults, and external wing buds are never present. Often the greater part of a holometabolous insect's lifetime is spent in a series of larval instars. Larvae typically consume vast quantities of food and attain a larger size than adults. Termination of the larval stage is accompanied by **pupation**, during which (in a single molt) the pupal stage is entered (Figure 22.43). **Pupae** do not feed or move about very much. They often reside in protective niches in the ground, within plant tissues, or housed in a **cocoon**. Energy reserves stored during the long larval life are utilized by the pupa to undergo whole scale body transformation. Many larval tissues are broken down and reorganized to attain the adult form; external wings and sexual organs are formed. The remarkable transformation from larval

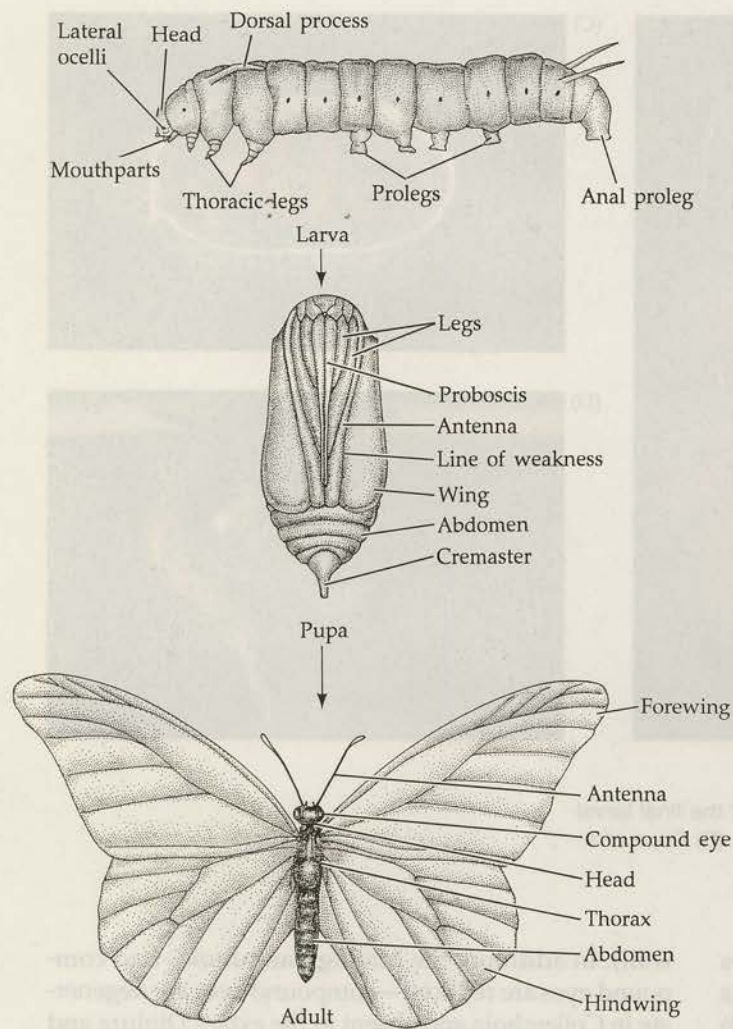


Figure 22.42 Life stages of a butterfly (Lepidoptera), illustrating the main life stages of holometabolous development.

Hexapod Evolution

The hexapods were among the first animals to colonize and exploit terrestrial and freshwater ecosystems. The fossil record is good, with about 1,263 recognized families (by comparison, there are 825 recognized fossil families of tetrapod vertebrates). The oldest known fossil insects are from the Early Devonian, which has led to the hypothesis that hexapods originated in the late Silurian with the earliest terrestrial ecosystems. The remarkable diversification of insects is undoubtedly related to the evolution of wings, and insects are the only group of invertebrates with the ability to fly. Fossil winged insects exist from the Late Mississippian (~324Ma), which suggests a pre-Carboniferous origin of insect flight. However, the description of *Rhyniognatha* (~412Ma) from a mandible, potentially indicative of a winged insect, suggests a late Silurian to Early Devonian origin of winged insects. Divergence time estimates based on a molecular phylogenetic analysis of many nuclear, protein-coding genes (Misof et al. 2014) corroborate an origin of winged insect lineages during this time period, which implies that the ability to fly emerged after the establishment of complex terrestrial ecosystems. Since then, insects have shaped Earth's terrestrial ecosystems, coevolving with another hyperdiverse terrestrial group, the flowering plants, ultimately qualifying the Cenozoic to be called "the age of insects."

By the Carboniferous, various modern insect orders were flourishing, although many were quite unlike today's fauna. Some Carboniferous hexapods are notable for their gigantic size, such as silverfish (Thysanura) that reached 6 cm in length and dragonflies with wingspans of about 70 cm. In addition to the living orders of insects, at least ten other orders arose and radiated in late Paleozoic and early Mesozoic times, then went extinct.

The Permian saw an explosive radiation of holometabolous insects, although many groups went extinct in the great end-Permian extinction event (Chapter 1). In fact, relatively few groups of Paleozoic insects survived into the Mesozoic, and many recent families first appeared in the Jurassic. By the Cretaceous, most modern families were extant, insect sociality had evolved, and many insect families had begun their intimate relationships with angiosperms. Tertiary insects were essentially modern and included many genera indistinguishable from the Recent (Holocene) fauna.

stage to adult stage in holometabolous insects is one of the most impressive achievements of animal evolution (Figure 22.42), and it is on par with the transformation of crustaceans through a series of larval stages to adulthood (Figure 21.33).

The role of ecdysone in initiating molting is described in Chapter 20. This hormone works in conjunction with a second endocrine product in controlling the sequence of events in insect metamorphosis. This second product, juvenile hormone, is manufactured and released by the corpora allata, a pair of glandlike structures associated with the brain (Figure 22.33). When ecdysone initiates a molt in an early larval instar, the accompanying concentration of juvenile hormone in the hemolymph is high. A high concentration of juvenile hormone ensures a larva-to-larva molt. After the last larval instar is reached, the corpora allata ceases to secrete juvenile hormone. Low concentrations of juvenile hormone result in a larva-to-pupa molt. Finally, when the pupa is ready to molt, juvenile hormone is absent from the hemolymph altogether; this deficiency leads to a pupa-to-adult molt.

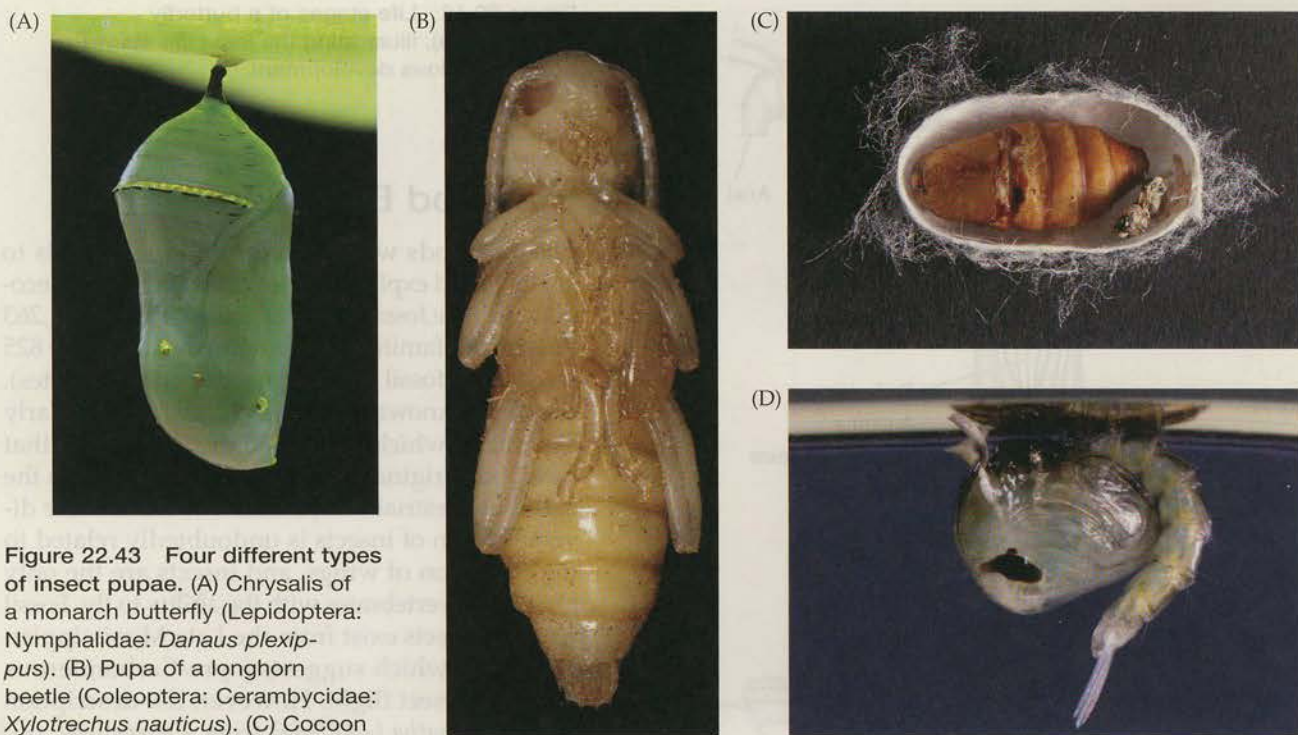


Figure 22.43 Four different types of insect pupae. (A) Chrysalis of a monarch butterfly (Lepidoptera: Nymphalidae: *Danaus plexippus*). (B) Pupa of a longhorn beetle (Coleoptera: Cerambycidae: *Xylotrechus nauticus*). (C) Cocoon of a silkworm moth (Lepidoptera: Saturniidae: *Bombyx mori*) sliced open to reveal the pupa inside. The shed skin (exuviae) of the final larval instar is visible to the right of the pupa inside the cocoon. (D) Pupa of a mosquito (Diptera: Culicidae).

Our current view of the evolutionary relationships of hexapod orders is presented in Figure 22.44. This tree is based on a recent publication (Misof et al. 2014) presenting a molecular phylogenetic analysis of 1,478 single-copy nuclear, protein-coding genes (see Chapter 2 for detailed tree with divergence time estimates.) This is by far the most data rich analysis of the hexapods conducted to date. The results of this analysis support many of the long held views of hexapod evolution but also provide novel support for some parts of the tree that had been difficult to resolve based on smaller molecular sets and by analyses of morphological characters alone.

The hexapods are divided between three entognathous orders and the Insecta. The three entognathous orders (the Collembola, Protura, and Diplura) all have internalized mouthparts. Most current workers regard the Collembola + Protura to be a monophyletic group (called the Ellipura), and this relationship is strongly supported by the most recent analyses. However, whether the Diplura are more closely related to the Collembola + Protura, or to the Insecta (a view persuasively argued by Kukalová-Peck) remains hotly debated and unresolved. Thus, the entognathous hexapods may or may not form a monophyletic group. Among the potential synapomorphies that may unite all three orders is entognathy itself (the overgrowth of the mouthparts by oral folds from the lateral cranial

wall). In addition, the Malpighian tubules and compound eyes are reduced—compound eyes are degenerate in Collembola and absent in the extant Diplura and Protura. However, these reductions could be convergences resulting from small body size. Our evolutionary tree thus depicts an unresolved trichotomy at the base of the Hexapoda, and we treat the entognathous hexapods as a potentially paraphyletic group in our classification.

The monophyly of the Insecta (Archaeognatha, Thysanura, and Pterygota) (Figure 22.44B) is undisputed. The principal synapomorphies of this group include the structure of the antenna, with its lack of muscles beyond the first segment (scape); the presence of a group of special chordotonal organs (vibration sensors) in the second antennal segment (pedicel) called the Johnston's organ; a well developed posterior tentorium (forming a transverse bar); subdivision of the tarsus into tarsomeres; females with ovipositor formed by gonapophyses (limb-base endites) on segments 8 and 9; and long, annulated, posterior terminal filaments (cerci).

The Insecta have traditionally been divided into the wingless insects (Archaeognatha and Thysanura) and the winged insects (Pterygota). However, on the basis of molecular studies and the presence of a dicondylic mandible, the Thysanura (silverfish) are now thought to be the sister group of the Pterygota.

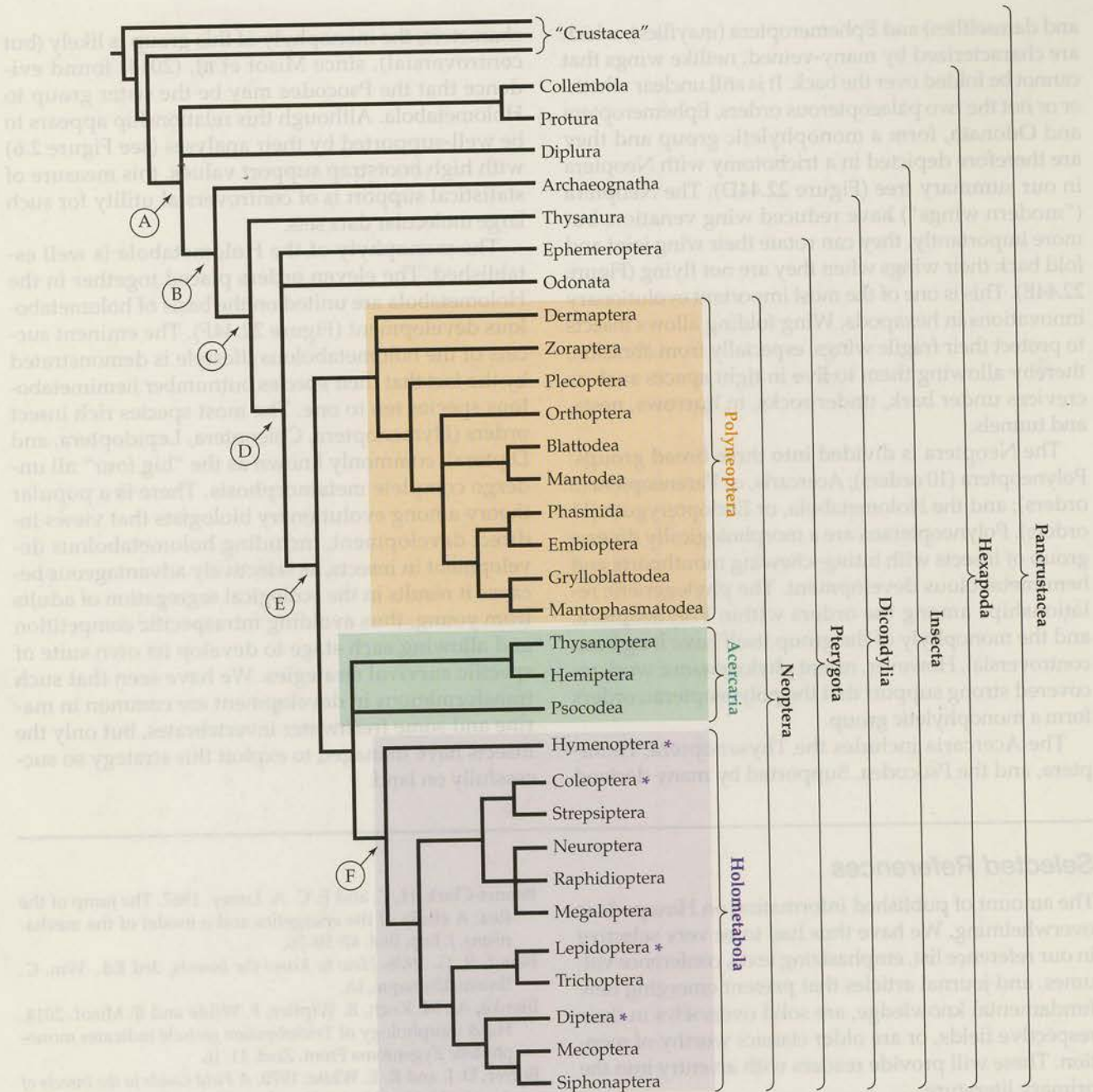


Figure 22.44 Phylogeny of the 31 orders of Hexapoda. Major clades are indicated to the right of the tree. The most recent common ancestor of extant taxa with traits that led to the success of the Hexapods are denoted with circled letters to the left of the tree. These key innovations include: (A) arthropod body subdivided into three tagmata: the head, 3-segmented thorax with one pair of uniramous legs on each segment, and an 11-segmented abdomen (synapomorphies of Hexapoda); (B) the evolution of external mouthparts (an apomorphy of the class Insecta); (C)

the evolution of dicondylic mandibles (an apomorphy of the Dicondylia) (D) the evolution of wings (an apomorphy of Pterygota); (E) the evolution of wing folding (an apomorphy of Neoptera); (F) the evolution of holometabolous development (= indirect development, or complete metamorphosis; an apomorphy of the Holometabola). The most diverse insect orders, commonly known as the "big four," are denoted with asterisks. Crustacea, a paraphyletic group due to its exclusion of the Hexapoda, is shown at the base of the tree.

They are classified together in a lineage known as the Dicondylia (see Figure 22.44C).

The Pterygota are, of course, distinguished by the presence of wings on the mesothorax and metathorax of adults. There is wide agreement that wings evolved

only once in Hexapoda along the branch leading to the Pterygota (Figure 22.44D). However, the Pterygota comprise two groups, Palaeoptera and Neoptera, with fundamentally different wing types. The Palaeoptera ("ancient wings") include the Odonata (dragonflies

and damselflies) and Ephemeroptera (mayflies), which are characterized by many-veined, netlike wings that cannot be folded over the back. It is still unclear whether or not the two palaeopterous orders, Ephemeroptera and Odonata, form a monophyletic group and they are therefore depicted in a trichotomy with Neoptera in our summary tree (Figure 22.44D). The Neoptera (“modern wings”) have reduced wing venation, but more importantly, they can rotate their wing joint and fold back their wings when they are not flying (Figure 22.44E). This is one of the most important evolutionary innovations in hexapods. Wing folding allows insects to protect their fragile wings, especially from abrasion, thereby allowing them to live in tight spaces such as crevices under bark, under rocks, in burrows, nests, and tunnels.

The Neoptera is divided into three broad groups: Polyneoptera (10 orders); Acercaria, or Paraneoptera (3 orders); and the Holometabola, or Endopterygota (11 orders). Polyneopterans are a morphologically diverse group of insects with biting–chewing mouthparts and hemimetabolous development. The phylogenetic relationships among the orders within Polyneoptera, and the monophyly of the group itself have long been controversial. However, recent phylogenomic work recovered strong support that the polyneopteran orders form a monophyletic group.

The Acercaria includes the Thysanoptera, Hemiptera, and the Psocodea. Supported by many derived

characters, the monophyly of this group is likely (but controversial), since Misof et al. (2014) found evidence that the Psocodea may be the sister group to Holometabola. Although this relationship appears to be well-supported by their analyses (see Figure 2.6) with high bootstrap support values, this measure of statistical support is of controversial utility for such large molecular data sets.

The monophyly of the Holometabola is well established. The eleven orders placed together in the Holometabola are united on the basis of holometabolous development (Figure 22.44F). The eminent success of the holometabolous lifestyle is demonstrated by the fact that their species outnumber hemimetabolous species ten to one. The most species rich insect orders (Hymenoptera, Coleoptera, Lepidoptera, and Diptera), commonly known as the “big four” all undergo complete metamorphosis. There is a popular theory among evolutionary biologists that views indirect development, including holometabolous development in insects, as selectively advantageous because it results in the ecological segregation of adults from young, thus avoiding intraspecific competition and allowing each stage to develop its own suite of specific survival strategies. We have seen that such transformations in development are common in marine and some freshwater invertebrates, but only the insects have managed to exploit this strategy so successfully on land.

Selected References

The amount of published information on Hexapoda is overwhelming. We have thus had to be very selective in our reference list, emphasizing texts, conference volumes, and journal articles that present emerging new fundamental knowledge, are solid overviews in their respective fields, or are older classics worthy of mention. These will provide readers with an entry into the primary literature.

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