33 Ecdysozoans: The Molting Animals

Early in animal evolution, the protostomate lineage split into two branches—the lophotrochozoans and the ecdysozoans—as we saw in the previous chapter. The distinguishing feature of the ecdysozoans is an **exoskeleton**, a nonliving covering that provides an animal with both protection and support. Once formed, however, an exoskeleton cannot grow. How, then, can ecdysozoans increase in size? Their solution is to shed, or **molt**, the exoskeleton and replace it with a new, larger one.

Before the animal molts, a new exoskeleton is already forming underneath the old one. When the old exoskeleton is shed, the new one expands and hardens. But until it has hardened, the animal is very vulnerable to its enemies both because its outer surface is easy to penetrate and because it can move only slowly.

The exoskeleton presented new challenges in other areas besides growth. Ecdysozoans cannot use cilia for locomotion, and most exdysozoans have hard exoskeletons that impede the passage of oxygen into the animal. To cope with these challenges, ecdysozoans evolved new mechanisms of locomotion and respiration.

Despite these constraints, the ecdysozoans—the molting animals—have more species than all other animal lineages combined. An increasingly rich array of molecular and genetic evidence, including a set of homeobox genes shared by all ecdysozoans, suggests that molting may have evolved only once during animal evolution.

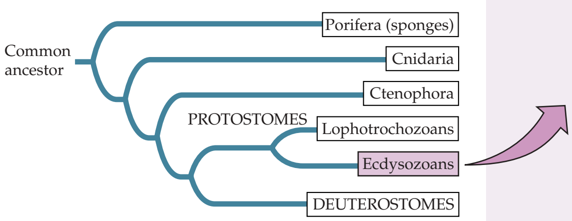
In this chapter, we will review the diversity of the ecdysozoans. We will look at the characteristics of animals in the various ecdysozoan phyla and see how having an exoskeleton has influenced their evolution. The phylogeny we will follow is presented in Figure 33.1. In the first part of the chapter, we will look at several small phyla of wormlike ecdysozoans. Then we will detail the characteristics of the arthropods, an incredibly species-rich group of ecdysozoan phyla with hardened exoskeletons. We will close the chapter with an overview of evolutionary themes found in the evolution of the protostomate phyla, including both the lophotrochozoan and ecdysozoan lineages.

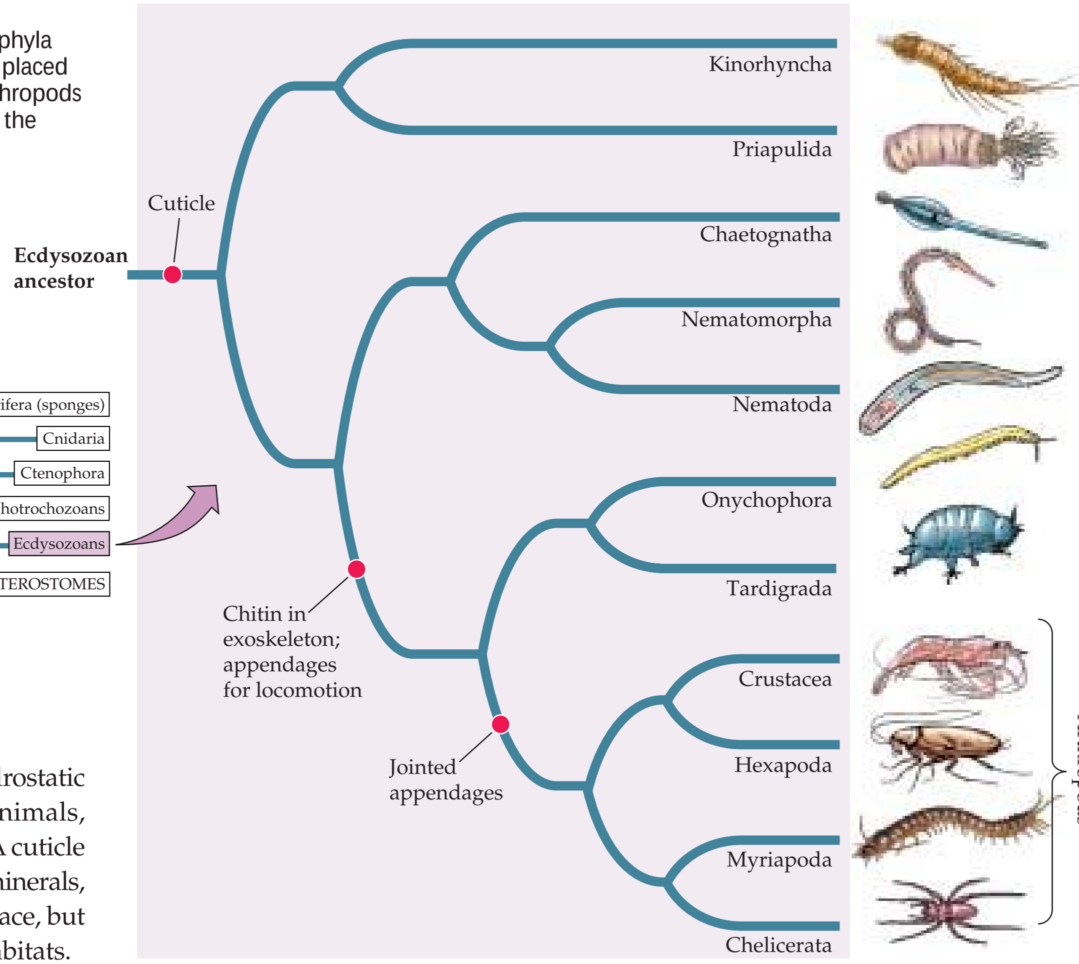
Shedding the Exoskeleton This dragonfly has just gone through a molt, a shedding of the outer exoskeleton. Such molts are necessary in order for the insect to grow larger or to change its form.

Cuticles: Flexible, Unsegmented Exoskeletons

Some ecdysozoans have wormlike bodies covered by exoskeletons that are relatively thin and flexible. Such an exoskeleton, called a **cuticle**, offers the animal some protection, but does not provide body support. The action of circular and longitudinal muscles on fluids in

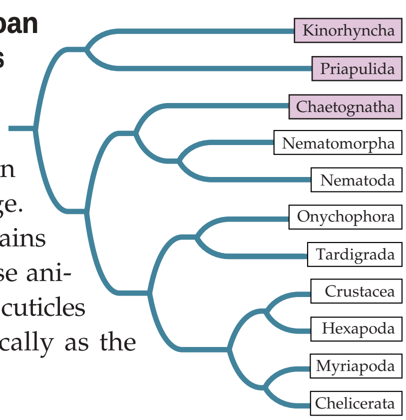
33.1 A Current Phylogeny of the Ecdysozoans Those ecdysozoan phyla with jointed appendages are often placed in a single phylum, Arthropoda. Arthropods are the most numerous animals on the planet.





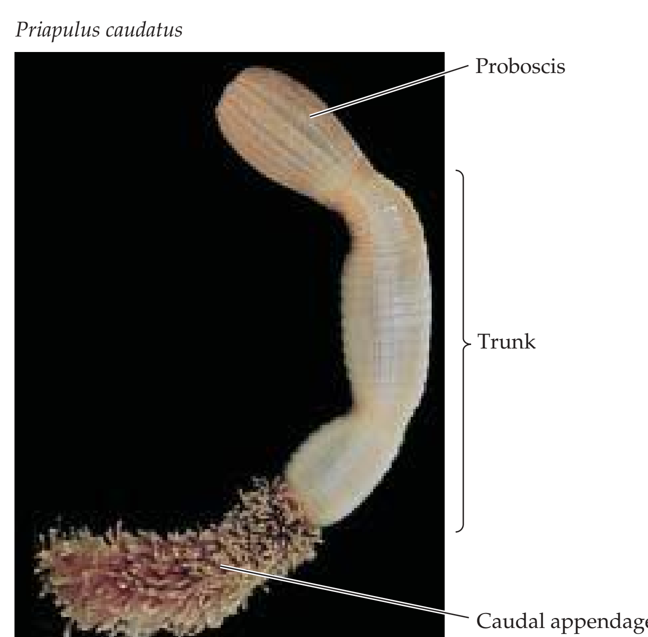
the body cavity provides a hydrostatic skeleton for many of these animals, which can move only slowly. A cuticle allows the exchange of gases, minerals, and water across the body surface, but restricts the animal to moist habitats.

Some marine ecdysozoan phyla have few species

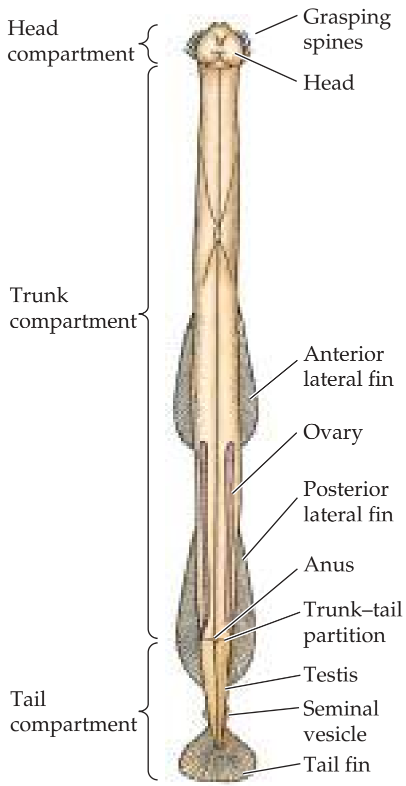


Several phyla of marine wormlike animals branched off early within the ecdysozoan lineage. Each of these phyla contains only a few species. These animals have relatively thin cuticles that are molted periodically as the animals grow to full size.

PRIAPULIDS AND KINORHYNCHS. The 16 species of **priapulids** (phylum **Priapulida**) are cylindrical, unsegmented, wormlike animals that range in size from half a millimeter to 20 centimeters in length (Figure 33.2). They burrow in fine marine sediments and prey on soft-bodied invertebrates, such as polychaete worms. They capture prey with a toothed pharynx, a muscular organ that is everted through the mouth and then withdrawn into the body together with the grasped prey. Fertilization is external, and most species have a larval form that lives in the mud.



33.2 A Priapulid Priapulids are marine worms that live, usually as burrowers, on the ocean floor. They capture prey with a toothed pharynx that everts through the proboscis. They take their name from Priapus, the Greek god of procreation, who was typically portrayed with an oversize penis.



33.3 An Arrow Worm Arrow worms have a three-part body plan. Their fins and grasping spines are adaptations for a predatory lifestyle.

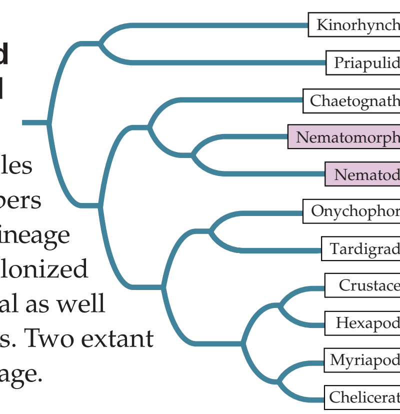
About 150 species of **kinorhynchs** (phylum **Kinorhyncha**) have been described. They are all less than 1 millimeter in length and live in marine sands and muds. Their bodies are divided into 13 segments, each with a separate cuticular plate. These plates are periodically molted during growth. Kinorhynchs feed by ingesting sediments and digesting the organic material found within them, which may include living algae as well as dead matter. Kinorhynchs have no distinct larval stage; fertilized eggs develop directly into juveniles, which emerge from their egg cases with 11 of the 13 body segments already formed.

ARROW WORMS. The phylogeny of the **arrow worms** (phylum **Chaetognatha**) is uncertain. Recent evidence indicates that these animals may in fact belong among the deuterostomes; however, this placement is still in question, and we continue to include them among the ecdysozoans.

The arrow worms body plan is based on a coelom divided into head, trunk, and tail compartments (Figure 33.3). Most arrow worms swim in the open sea, but a few live on the sea floor. Their abundance as fossils indicates that they were common more than 500 million years ago. The 100 or so living species of arrow worms are small enough—less than 12 cm long—that their gas exchange and excretion requirements are met by diffusion through the body surface, and they lack a circulatory system. Wastes and nutrients are moved around the body in the coelomic fluid, which is propelled by cilia that line the coelom. There is no distinct larval stage. Miniature adults hatch directly from eggs that are fertilized internally following elaborate courtship.

Arrow worms are stabilized in the water by means of one or two pairs of lateral fins and a tail fin. They are major predators of small organisms in the open oceans, ranging in size from small protists to young fish as large as the arrow worms themselves. An arrow worm typically lies motionless in the water until water movement signals the approach of prey. The arrow worm then darts forward and grasps the prey with the stiff spines adjacent to its mouth.

Tough cuticles evolved in some unsegmented worms



Tough external cuticles evolved in some members of another ecdysozoan lineage whose descendants colonized freshwater and terrestrial as well as marine environments. Two extant phyla represent this lineage.

HORSEHAIR WORMS. About 320 species of horsehair worms (phylum **Nematomorpha**) have been described. As their name implies, horsehair worms are extremely thin, and they range from a few millimeters up to a meter in length (Figure 33.4). Most adult horsehair worms live in fresh water among leaf litter and algal mats near the edges of streams and ponds. The larvae of horsehair worms are internal par-

Paragordius sp.

33.4 Horsehair Worms These worms get their name from their hair- or threadlike shape. They can grow to be up to a meter long.

asites of terrestrial and aquatic insects and freshwater crayfish. The horsehair worm's gut is greatly reduced, has no mouth opening, and is probably nonfunctional. These worms may feed only as larvae, absorbing nutrients from their hosts across the body wall, but many continue to grow after they have left their hosts, suggesting that adult worms may also absorb nutrients from their environment.

ROUNDWORMS. Roundworms (phylum **Nematoda**) have a thick, multilayered cuticle secreted by the underlying epidermis that gives their body its shape (Figure 33.5*a*). As a roundworm grows, it sheds its cuticle four times.

Roundworms exchange oxygen and nutrients with their environment through both the cuticle and the intestine, which is only one cell layer thick. Materials are moved through the gut by rhythmic contraction of a highly muscular organ, the *pharynx*, at the worm's anterior end. Roundworms move by contracting their longitudinal muscles.

Roundworms are one of the most abundant and universally distributed of all animal groups. About 25,000 species have been described, but the actual number of living species may be more than a million. Countless roundworms live as scavengers in the upper layers of the soil, on the bottoms of lakes and streams, in marine sediments (Figure 33.5*c*), and as parasites in the bodies of most kinds of plants and animals. The topsoil of rich farmland contains up to 3 billion nematodes per acre.

Many roundworms are predators, preying on protists and other small animals (including other roundworms). Many roundworms live parasitically within their hosts. The largest known roundworm, which reaches a length of 9 meters, is a parasite in the placentas of female sperm whales. The roundworms that are parasites of humans (causing serious tropical diseases such as trichinosis, filariasis, and elephantiasis), domestic animals, and economically important plants have been studied intensively in an effort to find ways of controlling them. One soil-inhabiting nematode, *Caenorhabitis elegans*, is a "model organism" in the laboratories of geneticists and developmental biologists.

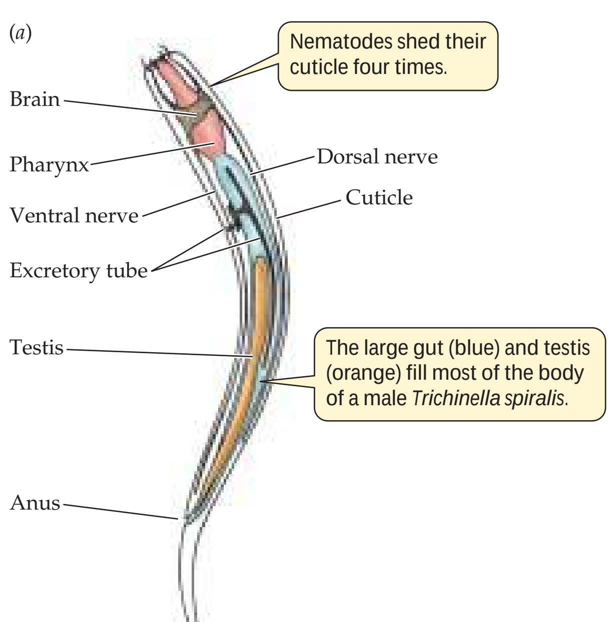
The structure of parasitic roundworms is similar to that of free-living species, but the life cycles of many parasitic species have special stages that facilitate the transfer of individuals among hosts. *Trichinella spiralis*, the species that causes the human disease trichinosis, has a relatively simple life cycle. A person may become infected by eating the flesh of an animal (usually a pig) containing larvae of *Trichinella* encysted in its muscles. The larvae are activated in the digestive tract, emerge from their cysts, and attach to the person's intestinal wall, where they feed. Later, they bore through the intestinal wall and are carried in the bloodstream to muscles, where they form new cysts (Figure 33.5*b*). If present in great numbers, these cysts cause severe pain or death.

Arthropods and Their Relatives: Segmented External Skeletons

In Precambrian times, the cuticle of some wormlike ecdysozoan lineages became thickened by the incorporation of layers of protein and a strong, flexible, waterproof polysaccharide called **chitin**. This rigid body covering may originally have had a protective function, but eventually it acquired both support and locomotory functions as well.

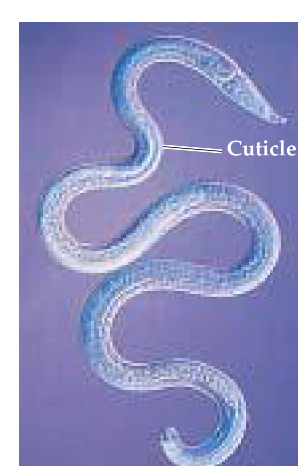
A rigid body covering precludes wormlike movement. To move, the animal requires extensions of the body that can be

(*a*)



(*b*)

(*c*)

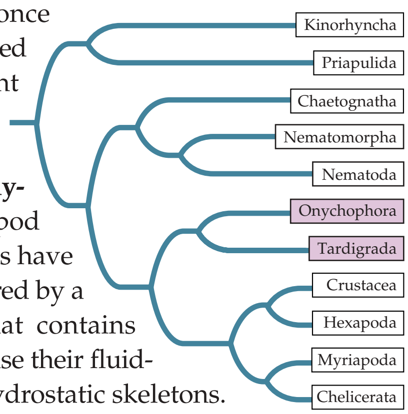


33.5 Roundworms (*a*) The body plan of *Trichinella spiralis*, a roundworm that causes trichinosis. (*b*) A cyst of *Trichinella spiralis* in the muscle tissue of a host. (*c*) This free-living roundworm moves through marine sediments.

manipulated by muscles. Such **appendages** evolved several times in the late Precambrian, leading to the lineages collectively called the **arthropods** ("jointed foot"). Divisions among the arthropod lineages are ancient and have been the subject of much research in the past decade. These phylogenetic relationships are being examined daily in the light of a wealth of new information, much of it concerning gene expression. There is currently no consensus on an exact phylogeny, but most researchers agree that these important animal groups are monophyletic, and some taxonomists consider them as members of a single phylum: **Arthropoda**.

Before presenting one current view of arthropod phylogeny, let's look at some arthropod relatives that have segmented bodies but unjointed legs, and at an early arthropod lineage that disappeared but left an important fossil record.

Some relatives of the arthropods have unjointed legs



Although they were once thought to be closely related to annelid worms, recent molecular evidence links the 110 species of **onychophorans** (phylum **Onychophora**) to the arthropod lineages. Onychophorans have soft bodies that are covered by a thin, flexible cuticle that contains chitin. Onychophorans use their fluid-filled body cavities as hydrostatic skeletons. Their soft, fleshy, unjointed, claw-bearing legs are formed by outgrowths of the body (Figure 33.6*a*). These animals are probably similar in appearance to ancestral arthropods. Fertilization is internal, and the large, yolky eggs are brooded with the body of the female.

Like the onychophorans, **water bears** (phylum **Tardigrada**) have fleshy, unjointed legs and use their fluid-filled body cavities as hydrostatic skeletons (Figure 33.6*b*). Water bears are extremely small (0.1–0.5 mm in length), and they lack circulatory systems and gas exchange organs. The 600 extant species of water bears live in marine sands and on temporary water films on plants. When these films dry out, the water bears also lose water and shrink to small, barrel-shaped objects that can survive for at least a decade in a dormant state. They have been found at densities as high as 2 million per square meter of moss.

Jointed legs appeared in the trilobites

The **trilobites** (phylum **Trilobita**) were among the earliest arthropods. They flourished in Cambrian and Ordovician seas, but disappeared in the great Permian extinction at the close of the Paleozoic era (245 mya). Because their heavy exoskeletons provided ideal material for fossilization, they left behind an abundant record of their existence (Figure 33.7).

Trilobites were heavily armored, and their body segmentation and appendages followed a relatively simple, repetitive plan. But their appendages were jointed, and some of them were modified for different functions. This specialization of appendage function became a theme as the evolution of the arthropod lineage continued.

Modern arthropods dominate Earth's fauna

Arthropod appendages have evolved an amazing variety of forms, and they serve many functions, including walking and swimming, gas exchange, food capture and manipulation, copulation, and sensory perception. The pattern of segmentation is similar among most arthropods because their development is governed by a common cascade of regula-

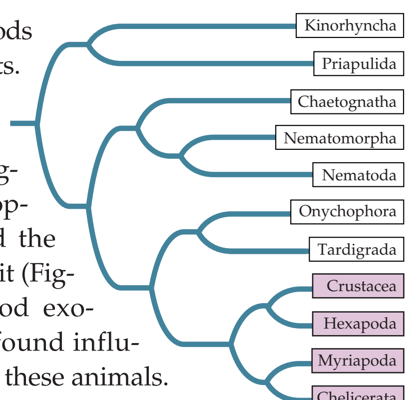
(*a*) *Peripatus* sp.

(*b*) *Echiniscus springer* 50 µm

33.6 Unjointed Legs (*a*) Onychophorans, also called "velvet worms," have unjointed legs and use the body cavity as a hydrostatic skeleton. (*b*) The appendages and general anatomy of water bears superficially resemble those of onychophorans.

33.7 A Trilobite The relatively simple, repetitive segments of the now-extinct trilobites are illustrated by a fossil trilobite from the shallow seas of the Devonian period, some 400 million years ago.

tory genes (see Figure 19.15), including homeotic genes that determine the kinds of appendages that are borne on each segment.



The bodies of arthropods are divided into segments. Their muscles are attached to the inside of the exoskeleton. Each segment has muscles that operate that segment and the appendages attached to it (Figure 33.8). The arthropod exoskeleton has had a profound influence on the evolution of these animals. Encasement within a rigid body covering provides support for walking on dry land, and the waterproofing provided by chitin keeps the animal from dehydrating in dry air. Aquatic arthropods were, in short, excellent candidates to invade terrestrial environments. As we will see, they did so several times.

There are four major arthropod phyla living today: the crustaceans, hexapods (insects), myriapods, and chelicerates. Collectively, the arthropods (including both terrestrial and marine species) are the dominant animals on Earth, both in numbers of species (about 1.5 million described) and number of individuals (estimated at some 10^{18} individuals, or a billion billion).

Crustaceans: Diverse and Abundant

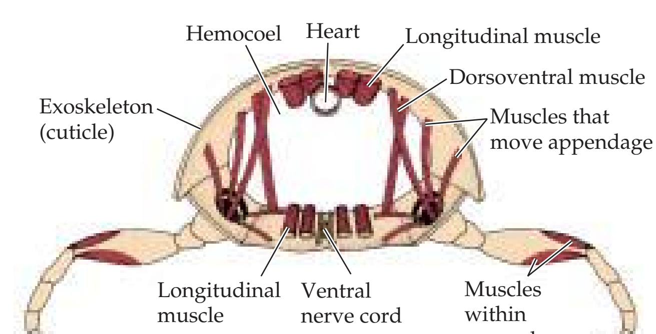
Crustaceans (phylum **Crustacea**) are the dominant marine arthropods today. The most familiar crustaceans belong to the class Malacostraca, which includes shrimp, lobsters, crayfish, and crabs (decapods; Figure 33.9*a*); and sow bugs (isopods; Figure 33.9*b*). Also included among the crustaceans are a variety of small species, many of which superficially resemble shrimp. The individuals of one group alone, the copepods (class Copepoda; Figure 33.9*c*), are so numerous that they may be the most abundant of all animals.

Barnacles (class Cirripedia) are unusual crustaceans that are sessile as adults (Figure 33.9*d*). With their calcareous shells, they superficially resemble mollusks but, as the zoologist Louis Agassiz remarked more than a century ago, a barnacle is "nothing more than a little shrimp-like animal, standing on its head in a limestone house and kicking food into its mouth."

Most of the 40,000 described species of crustaceans have a body that is divided into three regions: *head*, *thorax*, and *abdomen*. The segments of the head are fused together, and the head bears five pairs of appendages. Each of the multiple thoracic and abdominal segments usually bears one pair of appendages. In some cases, the appendages are branched, with different branches serving different functions. In many species, a fold of the exoskeleton, the *carapace*, extends dorsally and laterally back from the head to cover and protect some of the other segments (Figure 33.10*a*).

The fertilized eggs of most crustacean species are attached to the outside of the female's body, where they remain during their early development. At hatching, the young of some species are released as larvae; those of other species are released as juveniles that are similar in form to the adults. Still other species release eggs into the water or attach them to an object in the environment. The typical crustacean larva, called a **nauplius**, has three pairs of appendages and one central eye (Figure 33.10*b*). In many crustaceans, the nauplius larva develops within the egg before it hatches.

There is a growing recognition among researchers that a crustacean lineage may have been ancestral to all present-day arthropods. Therefore, the phylum Crustacea, as we recognize it here, may be paraphyletic (see Chapter 25). Molecular evidence points especially to a link between the crustaceans and another important lineage, the hexapods.



33.8 Arthropod Exoskeletons Are Rigid and Jointed This cross section through a thoracic segment of a generalized arthropod illustrates the arthropod body plan, which is characterized by a rigid exoskeleton with jointed appendages.

(*a*) *Opisthopus transversus*

(*b*) *Ligia occidentalis*

(*c*) *Cyclops* sp.

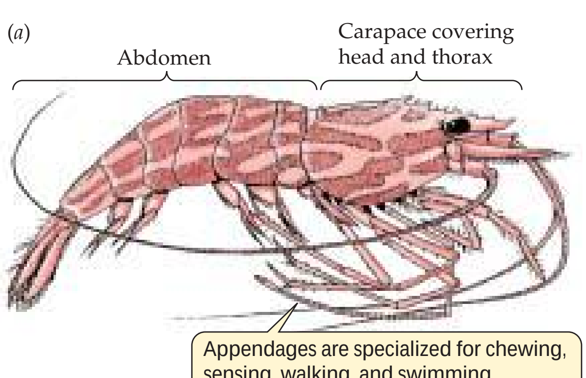
(*d*) *Lepas pectinata*

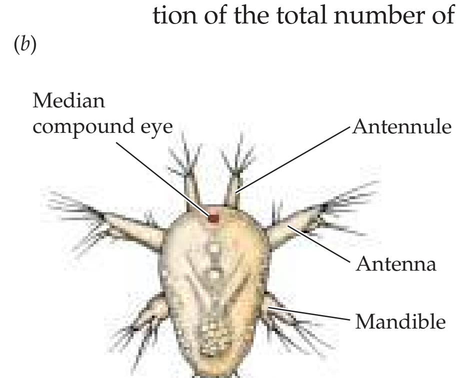
33.9 Crustacean Diversity (*a*) This mottled pea crab is a decapod crustacean. Its pigmentation depends on the food it ingests. (*b*) This isopod is found on the beaches of the California coast. (*c*) This microscopic freshwater copepod is only about 30 μm long. (*d*) Gooseneck barnacles attach to a substratum and feed by protruding and retracting feeding appendages from their shells.

Insects: Terrestrial Descendants of Marine Crustaceans

During the Devonian, more than 400 million years ago, arthropods made the leap from the marine environment onto land. Of the several groups who successfully colonized the terrestrial habitat, none is more prominent today than the six-legged individuals of the phylum **Hexapoda**—the insects.

Insects are found in most terrestrial and freshwater habitats, and they utilize nearly all species of plants and many species of animals as food. Some are internal parasites of plants and animals; others suck their host's blood or consume surface body tissues. The 1.4 million species of insects that have been described are believed to be only a small fraction of the total number of species living today.





33.10 Crustacean Structure (*a*) The bodies of crustaceans are divided into three regions, each of which bears appendages. (*b*) A nauplius larva has one compound eye and three pairs of appendages.

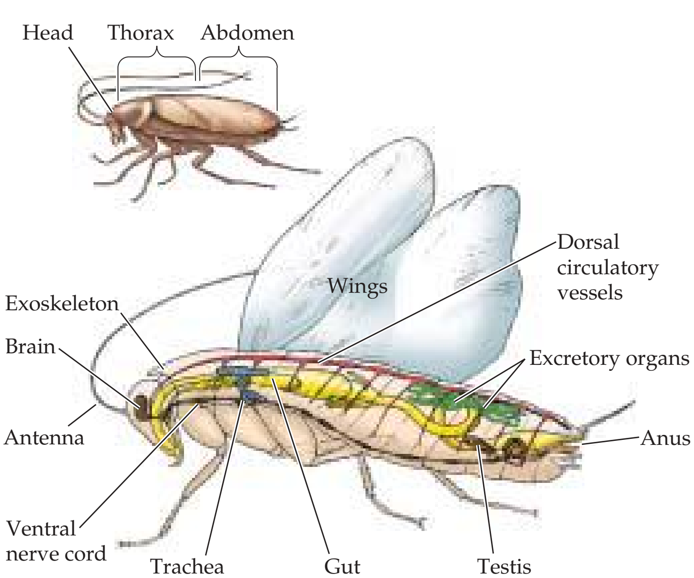
Very few insect species live in the ocean. In freshwater environments, on the other hand, they are sometimes the dominant animals, burrowing through the substratum, extracting suspended prey from the water, and actively pursuing other animals. Insects were the first animals to achieve the ability to fly, and they are important pollinators of flowering plants.

Insects, like crustaceans, have three basic body regions: head, thorax, and abdomen. They have a single pair of antennae on the head and three pairs of legs attached to the thorax (Figure 33.11). Unlike the other arthropods, insects have no appendages growing from their abdominal segments (see Figure 21.5).

An insect exchanges gases by means of air sacs and tubular channels called *tracheae* (singular, trachea) that extend from external openings inward to tissues throughout the body. The adults of most flying insects have two pairs of stiff, membranous wings attached to the thorax. However, flies have only one pair of wings, and in beetles the forewings form heavy, hardened wing covers.

Wingless insects include springtails and silverfish (Figure 33.12). Of the modern insects, they are probably the most similar in form to insect ancestors. Apterygote insects have a simple life cycle, hatching from eggs as miniature adults.

Development in the winged insects (Figure 33.13) is complex. The hatchlings do not look like adults, and they undergo substantial changes at each molt. The immature stages of insects between molts are called **instars**. A substantial change that occurs between one developmental stage and another is called **metamorphosis**. If the changes between its instars are gradual, an insect is said to have **incomplete metamorphosis**.



33.11 Structure of an Insect This diagram of a generalized insect illustrates its three-part body plan. The middle region, the thorax, bears three pairs of legs and, in most groups, two pairs of wings.

Hydropodura aquatica

33.12 Wingless Insects The wingless insects have a simple life cycle. They hatch looking like miniature adults, then grow by successive moltings of the cuticles as these springtails are doing.

In some insect groups, the larval and adult forms appear to be completely different animals. The most familiar example of such **complete metamorphosis** occurs in members of the order Lepidoptera, in which the larval caterpillar transforms itself into the adult butterfly (see Figure 1.1). During complete metamorphosis, the wormlike larva transforms itself during a specialized phase, called the **pupa**, in which many larval tissues are broken down and the adult form develops. In many of these groups, the different life stages are specialized for living in different environments and using different food sources. In many species, the larvae are adapted for feeding and growing, and the adults are specialized for reproduction and dispersal.

Entomologists divide the winged insects into about 29 different orders. We can make sense of this bewildering variety by recognizing three major lineages:

- Winged insects that cannot fold their wings against the body
- Winged insects that can fold their wings and that undergo incomplete metamorphosis
- Winged insects that can fold their wings and that undergo complete metamorphosis

Because they can fold their wings over their backs, flying insects belonging to the second and third lineages can tuck their wings out of the way upon landing and crawl into crevices and other tight places.

33.13 The Diversity of Insects (*a*) Unlike most flying insects, this dragonfly cannot fold its wings over its back. (*b*) The Mexican bush katydid represents the order Orthoptera. (c) Harlequin bugs are "true" bugs (order Hemiptera); (*d*) These mating mantophasmatodeans represent a recently discovered Hemipteran lineage found only in the Cape region of South Africa. (*e*) A predatory diving beetle (order Coleoptera). (*f*) The California dogface butterfly is a member of the Lepidoptera. (*g*) The flies, including this Mediterranean fruit fly, comprise the order Diptera. (*h*) Many genera in the order Hymenoptera, such as honeybees, are social insects. ▶

(*a*) *Anax imperator*

(*b*) *Scudderia mexicana*

(*c*) *Murgantia histrionica*

(*d*) *Timema* sp.

(*e*) *Dytiscus marginalis*

(*f*) *Colias eurydice*

(*g*) *Ceratitis capitata*

(*h*) *Apis mellifera*

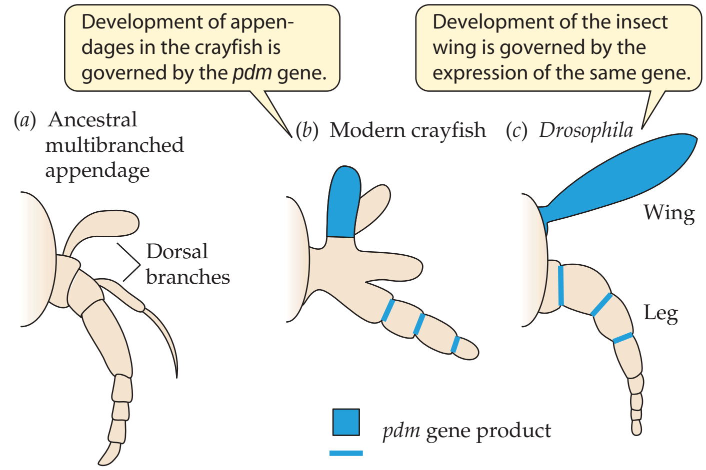
The only surviving members of the lineage whose members cannot fold their wings against the body are the orders Odonata (dragonflies and damselflies, Figure 33.13*a*) and Ephemeroptera (mayflies). All members of these two orders have aquatic larvae that transform themselves into flying adults after they crawl out of the water. Although many of these insects are excellent flyers, they require a great deal of open space in which to maneuver. Dragonflies and damselflies are active predators as adults, but adult mayflies lack functional digestive tracts and live only long enough to mate and lay eggs.

The second lineage, whose members can fold their wings and have incomplete metamorphosis, includes the orders Orthoptera (grasshoppers, crickets, roaches, mantids, and walking sticks; Figure 33.13*b*), Isoptera (termites), Plecoptera (stone flies), Dermaptera (earwigs), Thysanoptera (thrips), Hemiptera (true bugs; Figure 33.13*c*), and Homoptera (aphids, cicadas, and leafhoppers). In these groups, hatchlings are sufficiently similar in form to adults to be recognizable. They acquire adult organ systems, such as wings and compound eyes, gradually through several juvenile instars. Remarkably, a new insect order in this lineage, the Mantophasmatodea, was first described in 2002 (Figure 33.13*d*). These small insects are common in the Cape Region of southern Africa, an area of exceptional species richness and endemism for many animal and plant groups.

Insects belonging to the third lineage undergo complete metamorphosis. About 85 percent of all species of winged insects belong to this lineage. Familiar examples are the orders Neuroptera (lacewings and their relatives), Coleoptera (beetles; Figure 33.13*e*), Trichoptera (caddisflies), Lepidoptera (butterflies and moths; Figure 33.13*f*), Diptera (flies; Figure 33.13*g*), and Hymenoptera (sawflies, bees, wasps, and ants; Figure 33.13*h*).

Members of several orders of winged insects, including the Phthiraptera (lice) and Siphonaptera (fleas), are parasitic. Although descended from flying ancestors, these insects have lost the ability to fly.

Molecular data suggest that the lineage leading to the insects separated from the lineage leading to modern crustaceans about 450 million years ago, about the time of the appearance of the first land plants. These ancestral forms penetrated a terrestrial environment that was ecologically empty, which in part accounts for their remarkable success. But this success of the insects is also due to their wings, which arose only once early during insect evolution. Homologous genes control the development of insect wings and crustacean appendages, suggesting that that the insect wing evolved from a dorsal branch of a crustacean limb (Figure 33.14). The dorsal limb branch of crustaceans is used for respiration and osmoregulation. This finding suggests that the insect wing evolved from a gill-like structure that had a respiratory function.



33.14 Origin of Insect Wings The insect wing may have evolved from an ancestral appendage similar to that of modern crustaceans. (*a*) A diagram of the ancestral, multibranched arthropod limb. (*b*, *c*) The *pdm* gene, a Hox gene, is expressed throughout the dorsal limb branch and walking leg of the thoracic limb of a crayfish (*a*) and in the wings and legs of *Drosophila* (*b*).

Arthropods with Two Body Regions

Insects and most crustaceans have tripartite body plans, with a head, thorax, and abdomen. In two other arthropod lineages, evolution resulted in a body plan with two regions—a head and a trunk.

Myriapods have many legs

Centipedes, millipedes, and the two other groups of animals comprise the phylum **Myriapoda**. Centipedes and millipedes have a well-formed head and a long, flexible, segmented trunk that bears many pairs of legs (Figure 33.15). Centipedes, which have one pair of legs per segment, prey on insects and other small animals. Millipedes, which have two pairs of legs per segment, scavenge and eat plants. More than 3,000 species of centipedes and 10,000 species of millipedes have been described; many more species probably remain unknown. Although most myriapods are less than a few centimeters long, some tropical species are ten times that size.

Most chelicerates have four pairs of walking legs

In the body plan of **chelicerates** (phylum **Chelicerata**), the anterior region (head) bears two pairs of appendages modified to form mouthparts. In addition, many chelicerates have four pairs of walking legs. The 63,000 described chelicerate species are usually placed in three classes: Pycnogonida, Merostomata, and Arachnida; most of them belong to Arachnida.

The **pycnogonids** (class **Pycnogonida**), or sea spiders, are a poorly known group of about 1,000 marine species (Figure 33.16*a*). Most are small, with leg spans less than 1 cm, but some deep-sea species have leg spans up to 60 cm. A few py-

(*a*) *Scolopendra heros*

(*b*) *Harpaphe haydeniana*

33.15 Myriapods
(*a*) Centipedes have powerful jaws for capturing active prey. (*b*) Millipedes, which are scavengers and plant eaters, have smaller jaws and legs. They have two pairs of legs per segment, in contrast to the one pair on each segment of centipedes.

cnogonids feed on algae, but most are carnivorous, feeding on a variety of small invertebrates.

The class **Merostomata** contains the horseshoe crabs (order Xiphosura), with five living species, and the extinct giant water scorpions (order Eurypterida). Horseshoe crabs, which have changed very little during their long fossil history, have a large horseshoe-shaped covering over most of the body. They are common in shallow waters along the eastern coasts of North America and Southeast Asia, where they scavenge and prey on bottom-dwelling invertebrates. Periodically they crawl into the intertidal zone in large numbers to mate and lay eggs (Figure 33.16*b*).

Arachnids (class **Arachnida**) are abundant in terrestrial environments. Most arachnids have a simple life cycle in which miniature adults hatch from internally fertilized eggs and begin independent lives almost immediately. Some arachnids retain their eggs during development and give birth to live young.

The most species-rich and abundant arachnids are the spiders, scorpions, harvestmen, mites, and ticks (Figure 33.17). The 30,000 described species of mites and ticks live in soil, leaf litter, mosses, and lichens, under bark, and as parasites of plants, invertebrates, and vertebrates. They are vectors for wheat and rye mosaic viruses, and they cause mange in domestic animals and skin irritation in humans.

Spiders are important terrestrial predators. Some have excellent vision that enables them to chase and seize their prey. Others spin elaborate webs made of protein threads in which they snare prey. The threads are produced by modified abdominal appendages connected to internal glands that secrete the proteins, which dry on contact with air. The webs of different groups of spiders are strikingly varied, and this variation enables the spiders to position their snares in many different environments. Spiders also use protein threads to construct safety lines during climbing and as homes, mating

(*a*) *Decalopoda sp.*

(*b*) *Limulus polyphemus*

33.16 Minor Chelicerate Phyla (*a*) Although they are not spiders, it is easy to see why sea spiders were given their common name. (*b*) This spawning aggregation of horseshoe crabs was photographed on a sandy beach in Delaware.

(*a*) *Phidippus formosus*

(*b*) *Pseudouroctonus minimus*

(*c*) *Hadrobunus maculosus*

(*d*) *Brevipalpus phoenicis*

33.17 Arachnid Diversity (*a*) The black jumping spider's bite produces an inflammatory reaction on mammalian skin. (*b*) Scorpions are nocturnal predators. (*c*) Harvestmen, also called daddy longlegs, are scavengers. (*d*) Mites are blood-sucking, external parasites on vertebrates.

structures, protection for developing young, and means of dispersal.

Themes in the Evolution of Protostomes

We end this chapter by reviewing some of the evolutionary trends we have seen in the animal groups we have discussed so far. Most of protostomate evolution took place in the oceans. Early protostomes used their fluid-filled body cavities as hydrostatic skeletons. Segmentation permitted different parts of the body to be moved independently of one another. Thus species in some protostomate lineages gradually evolved the ability to change their shape in complex ways and to move rapidly over and through the substratum or through the water.

During much of animal evolution, the only food in the water consisted of dissolved organic matter and very small organisms. Consequently, many different lineages of animals, including lophophorates, mollusks, tunicates, and some crustaceans, evolved feeding structures designed to filter small prey from water, as well as structures for moving water through or over their prey-collecting devices. Animals that feed in this manner are abundant and widespread in marine waters today.

Because water flows readily, bringing food with it, sessile lifestyles also evolved repeatedly during lophotrochozoan and ecdysozoan evolution. Most phyla today have at least some sessile members. Being sessile presents certain challenges. For example, sessile animals cannot come together to mate. Some species eject both eggs and sperm into the water; others retain their eggs within their bodies and extrude only their sperm, which are carried by the water to other individuals. Species whose adults are sessile often have motile larvae, many of which have complicated mechanisms for locating suitable sites on which to settle.

A sessile animal gains access to local resources, but forfeits access to more distant resources. Many colonial sessile pro-

33.1 Anatomical Characteristics of the Major Protostomate Phyla

PHYLUM	BODY CAVITY	DIGESTIVE TRACT	CIRCULATORY SYSTEM
Lophotrochozoans			
Platyhelminthes	None	Dead-end sac	None
Rotifera	Pseudocoelom	Complete	None
Bryozoa	Coelom	Complete	None
Brachiopoda	Coelom	Complete in most	Open
Phoronida	Coelom	Complete	Closed
Nemertea	Coelom	Complete	Closed
Annelida	Coelom	Complete	Closed or open
Mollusca	Reduced coelom	Complete	Open except in cephalopods
Ecdysozoans			
Chaetognatha	Coelom	Complete	None
Nematomorpha	Pseudocoelom	Greatly reduced	None
Nematoda	Pseudoceolom	Complete	None
Crustacea	Hemocoel	Complete	Open
Hexapoda	Hemocoel	Complete	Open
Myriapoda	Hemocoel	Complete	Open
Chelicerata	Hemocoel	Complete	Open

Note: All protostomes have bilateral symmetry.

tostomes, however, are able to grow in the direction of better resources or into sites offering better protection. Individual members of colonies, if they are directly connected, can share resources. The ability to share resources enables some individuals to specialize for particular functions, such as reproduction, defense, or feeding. The nonfeeding individuals derive their nutrition from their feeding associates.

Predation may have been the major selective pressure for the development of hard, external body coverings. Such coverings evolved independently in many lophotrochozoan and ecdysozoan lineages. In addition to providing protection, they became key elements in the development of new systems of locomotion. Locomotory abilities permitted prey to escape more readily from predators, but also allowed predators to pursue their prey more effectively. Thus, the evolution of animals has been, and continues to be, a complex "arms race" among predators and prey.

Although we have concentrated on the evolution of greater complexity in animal lineages, many lineages whose members have remained simple have been very successful. Cnidarians are common in the oceans; roundworms are abundant in most aquatic and terrestrial environments. Parasites have lost complex body plans but have evolved complex life cycles.

The characteristics of the major existing phyla of protostomate animals are summarized in Table 33.1. Many major evolutionary trends were shared by protostomes and deuterostomes, the lineage that includes the chordates, the group to which humans belong. We will consider the evolution of diversity among the deuterostomes in the next chapter.

Chapter Summary

- The ecdysozoan lineage is characterized by a nonliving external covering—an exoskeleton, or cuticle. **Review Figure 33.1**
- An animal with an exoskeleton grows by periodically shedding its exoskeleton and replacing it with a larger one, a process called molting.

Cuticles: Flexible, Unsegmented Exoskeletons

- Members of several phyla of marine worms with thin cuticles are descendants of an early split in the ecdysozoan lineage. **Review Figure 33.3**
- Tough cuticles are found in members of two phyla, the horsehair worms and the roundworms.
- Roundworms (phylum Nematoda) are one of the most abundant and universally distributed of all animal groups. Many are parasites. **Review Figure 33.5**

Arthropods and Their Relatives: Segmented External Skeletons

- Animals with rigid exoskeletons lack cilia for locomotion. To move, they have appendages that can be manipulated by muscles. **Review Figure 33.8**
- Although there is currently no consensus on an exact phylogeny, most researchers agree that the arthropod groups are monophyletic.
- Onychophorans and tardigrades have soft, unjointed legs. They are probably similar to ancestral arthropods.
- Trilobites flourished in Cambrian and Ordovician seas, but they became extinct at the close of the Paleozoic era.

Crustaceans: Species-Rich and Abundant

- The segments of the crustacean body are divided among three regions: head, thorax, and abdomen. **Review Figure 33.10**
- The most familiar crustaceans are shrimp, lobsters, crayfish, crabs, sow bugs, and sand fleas. Copepod crustaceans may be the most abundant animals on the planet.
- Recent molecular evidence indicates that the crustacean lineage may be ancestral to all the arthropods.

Insects: Terrestrial Descendants of Marine Crustaceans

- About 1.4 million species of insects (phylum Hexapoda) have been described, but that number is a small fraction of the total number of existing species. Although few species are found in marine environments, they are among the dominant animals in virtually all terrestrial and many freshwater habitats.
- Like crustaceans, insects have three body regions (head, thorax, abdomen). They bear a single pair of antennae on the head and three pairs of legs attached to the thorax. No appendages grow from their abdominal segments. **Review Figure 33.11**
- Wingless insects look like miniature adults when they hatch. Hatchlings of some winged insects resemble adults, but others undergo substantial changes at each molt.

▶ The winged insects can be divided into three major subgroups. Members of one subgroup cannot fold their wings back against the body. Members of the other two subgroups can.

▶ The wings of insects probably evolved from the dorsal branches of multibranched ancestral appendages. **Review Figure 33.14**

Arthropods with Two Body Regions

▶ Individuals of the remaining arthropod phyla generally have segmented bodies with two distinct regions, head and trunk.

▶ Myriapods (centipedes and millipedes) have many segments and many pairs of legs.

▶ Most chelicerates (phylum Chelicerata) have four pairs of legs.

▶ Arachnids—scorpions, harvestmen, spiders, mites, and ticks—are abundant in terrestrial environments.

Themes in the Evolution of Protostomes

▶ Most evolution of protostomes took place in the oceans.

▶ Early animals used fluid-filled body cavities as hydrostatic skeletons. Subdivision of the body cavity into segments allowed better control of movement.

▶ During much of animal evolution, the only food in the water consisted of dissolved organic matter and very small organisms.

▶ Flowing water brings food with it, allowing many aquatic animals to obtain food while being sessile.

▶ Predation may have been the major selective pressure for the development of hard, external body coverings.

See Web/CD Activities 33.1 and 33.2 for a concept review of this chapter.

Self-Quiz

1. The outer covering of ecdysozoans
   a. is always hard and rigid.
   b. is always thin and flexible.
   c. is present at some stage in the life cycle but not always among adults.
   d. ranges from very thin to hard and rigid.
   e. prevents the animals from changing their shapes.
2. The primary support for members of several small phyla of marine worms is
   a. their exoskeletons.
   b. their internal skeletons.
   c. their hydrostatic skeletons.
   d. the surrounding sediments.
   e. the bodes of other animals within which they live.
3. Roundworms are abundant and diverse because
   a. they are both parasitic and free-living and eat a wide variety of foods.
   b. they are able to molt their exoskeletons.
   c. their thick cuticle enables them to move in complex ways.
   d. their body cavity is a pseudocoelom.
   e. their segmented bodies enable them to live in many different places.
4. The arthropod exoskeleton is composed of a
   a. mixture of several kinds of polysaccharides.
   b. mixture of several kinds of proteins.
   c. single complex polysaccharide called chitin.
   d. single complex protein called arthropodin.
   e. mixture of layers of proteins and a polysaccharide called chitin.
5. Which phyla are arthropod relatives with unjointed legs?
   a. Trilobita and Onychophora
   b. Onychophora and Tardigrada
   c. Trilobita and Tardigrada
   d. Onychophora and Chelicerata
   e. Tardigrada and Chelicerata
6. The members of which crustacean group are probably the most abundant of all animals?
   a. Decapoda
   b. Amphipoda
   c. Copepoda
   d. Cirripedia
   e. Isopoda
7. The body plan of insects is composed of which of the three following regions?
   a. Head, abdomen, and trachea
   b. Head, abdomen, and cephalothorax
   c. Cephalothorax, abdomen, and trachea
   d. Head, thorax, and abdomen
   e. Abdomen, trachea, and mantle
8. Insects that hatch from eggs into juveniles that resemble miniature adults are said to have
   a. instars.
   b. neopterous development.
   c. accelerated development.
   d. incomplete metamorphosis.
   e. complete metamorphosis.
9. Which of the following groups of insects cannot fold their wings back against the body?
   a. Beetles
   b. True bugs
   c. Earwigs
   d. Stone flies
   e. Mayflies
10. Factors that may have contributed to the remarkable evolutionary diversification of insects include
    a. the terrestrial environments penetrated by insects lacked any other similar organisms.
    b. insects evolved the ability to fly.
    c. some lineages of insects evolved complete metamorphosis.
    d. insects evolved effective means of delivering oxygen to their internal tissues.
    e. All of the above

For Discussion

1. Segmentation has arisen several times during animal evolution. What advantages does segmentation provide? Given these advantages, why do so many unsegmented animals survive?
2. The British biologist J. B. S. Haldane is reputed to have quipped that "God was unusually fond of beetles." Beetles are, indeed, the most species-rich lineage of organisms. What features of beetles have contributed to the evolution and survival of so many species?
3. In Part Four of this book, we pointed out that major structural novelties have arisen infrequently during the course of evolution. Which of the features of protostomes do you think are major evolutionary novelties? What criteria do you use to judge whether a feature is a major as opposed to a minor novelty?
4. There are more described and named species of insects than of all other animal lineages combined. However, only a very few species of insects live in marine environments, and those species are restricted to the intertidal zone or the ocean surface. What factors may have contributed to the inability of insects to be successful in the oceans?