The Smaller Ecdysozoan Phyla

13

13.1 Evolutionary Perspective

Learning Outcomes

1. Describe the unifying features that define the clade Ecdysozoa.
2. Describe one common function of the cuticle in ecdysozoan phyla covered in this chapter.

"Beauty is in the eye of the beholder"—the Western philosopher, Plato, said it first around 300 B.C. He was probably not thinking about nematodes when he made that statement. For some zoologists, however, it applies. What phylum of animals has representatives that live at the freezing point in Arctic ice (Cryonema)? What phylum has members that live in sulfide-rich marine sediments (Stilbonematinae), in millipede guts (Zalophora), on beer coasters in Germany (Panagrellus), or in the placentas of sperm whales (Placentonema)? In what phylum can one count over 200 species in a few cubic centimeters of marine mud or 90,000 individuals in a single rotting apple? What phylum is composed of decomposers and predators in aquatic sediment and soil? What phylum has parasitic members that have killed and maimed across all other animal phyla? The answer to all of these questions is the phylum Nematoda. The nematode structure that you will study in this chapter is deceptively simple—this is an introductory textbook. A lifetime of detailed study, however, could never uncover the endless variation found within this highly diverse phylum.

Nematoda is just one of the eight phyla covered in chapters 13 through 15 that are members of the clade Ecdysozoa. Members of these phyla are united by common molecular features and a single morphological character—they all possess a nonliving, secreted cuticle (L. cutis, skin) that is molted periodically as they grow (figure 13.1). Molting of the cuticle is called ecdysis (Gr. ektysis, getting out). Chapter 13 describes members of the phylum Nematoda and four other smaller ecdysozan phyla: Nematomorpha, Loricifera, Kinorhyncha, and Priapulida. Chapters 14 and 15 describe the largest animal phylum, Arthropoda, and two smaller phyla, Tardigrada and Onychophora. These three phyla comprise the ecdysozoan clade Panarthropoda. Phylogenetic relationships within the ecdysozoan phyla are discussed at the end of chapters 13 and 15.
Ecdysozoans are united by molecular characteristics and the presence of a secreted, non-living cuticle. The cuticle is molted to accommodate growth—a process called ecdysis. Chapters 13 through 15 cover the ecdysozoan phyla. The Gordian worm, Gordius robustus, is a member of the ecdysozoan phylum Nematomorpha.

The function of the cuticle is somewhat different in the phyla covered in chapters 13 through 15. The arthropods have a reduced coelom (chapters 14 and 15) and the cuticle forms an armor-like exoskeleton. This exoskeleton provides support and protection and is jointed for mobility. It is one of the major reasons for the success of the phylum. The cuticles of the phyla described in chapter 13 are composed of either collagen or chitin—an important taxonomic difference that will be discussed at the end of this chapter. The phyla in chapter 13 are also pseudocoelomate (see figure 7.11). One of the major functions of the pseudocoelom interacting with the cuticle (see chapter 7) is to act as a hydrostatic skeleton. Body movements occur as a result of contractions of body wall musculature acting on the fluid or gel within the pseudocoelom. The tough cuticle prevents tearing of the body wall with changes in pseudocoelomic pressure. The pseudocoelom also serves as a vehicle for the distribution of nutrients, respiratory gases, and metabolic wastes. The pseudocoelom is of little phylogenetic significance. It is present in phyla scattered through Lophotrochozoa and Ecdysozoa.

**FIGURE 13.1**
Ecdysozoan Phylogeny. Ecdysozoans are united by molecular characteristics and the presence of a secreted, non-living cuticle. The cuticle is molted to accommodate growth—a process called ecdysis. Chapters 13 through 15 cover the ecdysozoan phyla. The Gordian worm, Gordius robustus, is a member of the ecdysozoan phylum Nematomorpha.

Ecdysozoa is composed of eight phyla: Nematoda, Nematomorpha, Kinorhyncha, Priapulida, Loricifera, Arthropoda, Tardigrada, and Onychophora. The latter three comprise a clade called Panarthropoda. The cuticle of arthropods is their exoskeleton, and in pseudocoelomate ecdysozoans, it aids in the function of the pseudocoelom as a hydrostatic skeleton.

**What morphological feature unites all members of the clade Ecdysozoa?**

### 13.2 Phylum Nematoda (Roundworms)

**Learning Outcomes**

1. Explain how the body wall and pseudocoelom of a nematode influence locomotion of a nematode.
2. Contrast the life cycles of common nematode parasites with the life cycles of digenetic flukes.

Nematodes (nem'a-todes) (Gr. nematos, thread) or roundworms are some of the most abundant animals on earth—some 5 billion may be in every acre (4,046 m²) of fertile garden soil. Zoologists estimate that the number of roundworm species may be as high as 500,000. Roundworms feed
The nematode worm *Caenorhabditis elegans* is a 1-mm-long soil resident. The worms are very easy to maintain in the laboratory and grow from fertilized egg to an adult in just three days. The somatic cell number in all adults is constant for the entire animal and for each given organ in all individuals of the species. This constancy of cell number is called eutely (Gr. *euteia*, thrift). All 959 adult somatic cells arise from the zygote in virtually the same way for every *C. elegans*. Using a microscope to follow all the cell divisions starting immediately after a zygote forms, researchers have been able to construct the entire ancestry of every cell in the adult body, the nematode’s cell lineage. This is possible because *C. elegans* is transparent at all stages of its development, making it possible for researchers to trace the lineage of every cell, from the zygote to the adult worm. A half day after the first cell division, the nematode is a larva of 558 cells. Further rounds of cell division and the death of precisely 113 cells sculpt the 959-celled adult worm. A cell lineage diagram like the one in the figure is a type of fate map, a representation of the fate of various parts of a developing embryo. The much simplified fate map shown to the right indicates the development of the major tissues of the nematode’s body.

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on every conceivable source of organic matter—from rotting substances to the living tissues of other invertebrates, vertebrates, and plants. They range in size from microscopic to several meters long. Many nematodes are parasites of plants or animals; most others are free living in marine, freshwater, or soil habitats. Some nematodes play an important role in recycling nutrients in soils and bottom sediments.

Except in their sensory structures, nematodes lack cilia, a characteristic they share with arthropods. Also in common with some arthropods, the sperm of nematodes are amoeboid.

**Taxonomy within the phylum Nematoda** is a subject of intensive study. Two classes have been recognized based upon morphological studies: Secernentea and Adenophorea. Molecular studies suggest that these class designations do not accurately reflect nematode phylogeny. Additional information on nematode phylogeny is presented at the end of this chapter.

**Characteristics of the phylum Nematoda include:**

1. Triploblastic, bilateral, vermiform (resembling a worm in shape; long and slender), unsegmented, pseudocoelomate
2. Body round in cross section and covered by a layered collagenous cuticle; molting usually accompanies growth in juveniles
3. Complete digestive tract; mouth usually surrounded by lips bearing sense organs
4. Most with unique excretory system composed of one or two renette cells or a set of collecting tubules
5. Body wall has only longitudinal muscles
**Structure and Function**

A nematode body is slender, elongate, cylindrical, and tapered at both ends (figure 13.2a and b). Much of the success of nematodes is due to their outer, noncellular, collagenous cuticle (figure 13.2c) that is continuous with the foregut, hindgut, sense organs, and parts of the female reproductive system. The collagenous cuticle may be smooth, or it may contain spines, bristles, papillae (small, nipplelike projections), warts, or ridges, all of which are of taxonomic significance. Three primary layers make up the cuticle: cortex, matrix layer, and basal layer. The cuticle maintains internal hydrostatic pressure, provides mechanical protection, and, in parasitic species of nematodes, resists digestion by the host. The cuticle is usually molted four times during maturation.

Beneath the cuticle is the epidermis, or hypodermis, which surrounds the pseudocoelom (figure 13.2d). The epidermis may be syncytial, and its nuclei are usually in the four epidermal cords (one dorsal, one ventral, and two lateral) that project inward. The longitudinal muscles are the principal means of locomotion in nematodes. Contraction of these muscles results in undulatory waves that pass from the anterior to the posterior end of the animal, creating characteristic thrashing movements. Nematodes lack circular muscles and therefore cannot crawl as do worms with more complex musculature.

Some nematodes have lips surrounding the mouth, and some species bear spines or teeth on or near the lips (figure 13.3). In others, the lips have disappeared. Some roundworms have head shields that afford protection. Sensory organs include amphids, phasmids, or ocelli. **Amphids** are anterior depressions in the cuticle that contain modified cilia and function in chemoreception. **Phasmids** are near the anus and also function in chemoreception. The presence or

**FIGURE 13.2**

*Phylum Nematoda.* Internal anatomical features of an (a) female and (b) male *Rhabditis.* (c) Section through a nematode cuticle, showing the various layers. (d) Cross section through the region of the muscular pharynx of a nematode. The hydrostatic pressure in the pseudocoelom maintains the rounded body shape of a nematode and also collapses the intestine, which helps move food and waste material from the mouth to the anus.
Mouthparts of nematodes are adapted for various purposes. (a) Head of the rhabditiform larval stage of the hookworm (*Necator*). Adult hookworms have toothlike plates that are used to attach to the intestinal wall of their host (see figure 13.8). (b) Head of the threadworm *Strongyloides*. This nematode tunnels through the intestinal mucosa of its host (humans or other mammals depending on the species of threadworm).

The absence of these organs are taxonomically important. Paired ocelli (eyes) are present in aquatic nematodes.

The nematode pseudocoelom is a spacious, fluid-filled cavity that contains the visceral organs and forms a hydrostatic skeleton. All nematodes are round because the body muscles contracting against the pseudocoelomic fluid generate an equal outward force in all directions (see figure 13.2d).

Depending on the environment, nematodes are capable of feeding on a wide variety of foods; they may be carnivores, herbivores, omnivores, or saprobes (saprotrophs) that consume decomposing organisms, or parasitic species that feed on blood and tissue fluids of their hosts.

Nematodes have a complete digestive system consisting of a mouth, which may have teeth, jaws, or stylets (sharp, pointed structures); buccal cavity; muscular pharynx; long, tubular intestine where digestion and absorption occur; short rectum; and anus. Hydrostatic pressure in the pseudocoelom and the pumping action of the pharynx push food through the alimentary canal.

Nematodes accomplish osmoregulation and excretion of nitrogenous waste products (ammonia, urea) with two unique systems. The glandular system is in aquatic species and consists of ventral gland cells, called renettes, posterior to the pharynx (figure 13.4a). Each gland absorbs wastes from the pseudocoelom and empties them to the outside through an excretory pore. Parasitic nematodes have tubular excretory system that develops from the renette system (figure 13.4b). In this system, the renettes unite to form a large canal, which opens to the outside via an excretory pore.

The nervous system consists of an anterior neural ring (see figures 13.2b and 13.4a). Nerves extend anteriorly and posteriorly; many connect to each other via commissures.

Certain neuroendocrine secretions are involved in growth, molting, cuticle formation, and metamorphosis.

**Reproduction and Development**

Most nematodes are dioecious and dimorphic, with the males being smaller than the females. The long, coiled gonads lie free in the pseudocoelom.

The female system consists of a pair of convoluted ovaries (figure 13.5a). Each ovary is continuous with an oviduct whose proximal end is swollen to form a seminal receptacle. Each oviduct becomes a tubular uterus; the two uteri unite to form a vagina that opens to the outside through a genital pore.

The male system consists of a single testis, which is continuous with a vas deferens that eventually expands into a seminal vesicle (figure 13.5b). The seminal vesicle connects to the cloaca. Males are commonly armed with a posterior flap of tissue called a bursa. The bursa aids the male in the transfer of sperm to the female genital pore during copulation.

After copulation, hydrostatic forces in the pseudocoelom (see figure 13.2d) move each fertilized egg to the gonopore (genital pore). The number of eggs produced varies with the species; some nematodes produce only several hundred, whereas others may produce hundreds of thousands daily. Some nematodes give birth to larvae (ovoviviparity). External factors, such as temperature and moisture, influence the development and hatching of the eggs. Hatching produces a larva (some parasitologists refer to it as a juvenile) that has most adult structures. The larva (juvenile) undergoes four molts, although in some species, the first one or two molts may occur before the eggs hatch.
Some Important Nematode Parasites of Humans

Parasitic nematodes show a number of evolutionary adaptations to their way of life. These include a high reproductive potential, life cycles that increase the likelihood of transmission from one host to another, an enzyme-resistant cuticle, resistant eggs, and encysted larvae. Nematode life cycles are not as complicated as those of cestodes or trematodes because only one host is usually involved. Discussions of the life cycles of five important human parasites follow.

Ascaris lumbricoides: The Giant Intestinal Roundworm of Humans

As many as 800 million people throughout the world may be infected with Ascaris lumbricoides. Adult Ascaris (Gr. askaris, intestinal worm) live in the small intestine of humans. They produce large numbers of eggs that exit with the feces (figure 13.6). A first-stage larva develops rapidly in the egg, molts, and matures into a second-stage larva, the infective stage. When a human ingests embryonated eggs, they hatch in the intestine. The larvae penetrate the intestinal wall and are carried via the circulation to the lungs. They molt twice in the lungs, migrate up the trachea, and are swallowed. The worms attain sexual maturity in the intestine, mate, and begin egg production (figure 13.7).

Enterobius vermicularis: The Human Pinworm

Pinworms (Enterobius; Gr. enteron, intestine + bios, life) are the most common roundworm parasites in the United States. Adult Enterobius vermicularis become established in the lower
region of the large intestine. At night, gravid females migrate out of the rectum to the perianal area, where they deposit eggs containing a first-stage larva (figure 13.8) and then die. The females and eggs produce an itching sensation. When a person scratches the itch, the hands and bedclothes are contaminated with the eggs. When the hands touch the mouth and the eggs are swallowed, the eggs hatch. The larvae molt four times in the small intestine and migrate to the large intestine. Adults mate, and females soon begin egg production.

Necator americanus: The New World Hookworm

The New World or American hookworm, *Necator americanus* (L. necator, killer), is found in the southern United States. The adults live in the small intestine, where they hold onto the intestinal wall with teeth and feed on blood and tissue fluids (figure 13.9). Individual females may produce as many as 10,000 eggs daily, which pass out of the body in the feces.

An egg hatches on warm, moist soil and releases a small rhabditiform (the first- and second-stage juveniles of some nematodes) larva. It molts and becomes the infective filariform (the infective third-stage larva of some nematodes) larva. Humans become infected when the filariform larva penetrates the skin, usually between the toes. (Outside defecation and subsequent walking barefoot through the immediate area maintains the life cycle in humans.) The larva burrows through the skin to reach the circulatory system. The rest of its life cycle is similar to that of *Ascaris* (see figure 13.6).

Trichinella spiralis: The Porkworm

Adult *Trichinella* (Gr. trichinos, hair) spiralis live in the mucosa of the small intestine of humans and other carnivores and omnivores (e.g., the pig). In the intestine, adult females give birth to young larvae that then enter the circulatory system and are carried to skeletal (striated) muscles of the same host (figure 13.10). The young larvae encyst in the skeletal muscles and remain infective for many years. The disease this nematode causes is called trichinosis. Another host must ingest infective meat (muscle) to continue the life cycle. Humans
most often become infected by eating improperly cooked pork products. Once ingested, the larvae excyst in the stomach and make their way to the small intestine, where they molt four times and develop into adults.

**Wuchereria spp.: The Filarial Worms**

In tropical countries, over 250 million humans are infected with filarial (L. filium, thread) worms. Two examples of human filarial worms are *Wuchereria bancrofti* and *W. malayi*. These elongate, threadlike nematodes live in the lymphatic system, where they block the vessels. Because lymphatic vessels return tissue fluids to the circulatory system, when the filarial nematodes block these vessels, fluids and connective tissue tend to accumulate in peripheral tissues. This fluid and connective tissue accumulation causes the enlargement of various appendages, a condition called *elephantiasis* (figure 13.11).

In the lymphatic vessels, filarial nematode adults copulate and produce larvae called *microfilariae* (figure 13.12). The microfilariae are released into the bloodstream of the human host and migrate to the peripheral circulation at night. When a mosquito feeds on a human, it ingests the microfilariae. The microfilariae migrate to the mosquito's thoracic muscles, where they molt twice and become infective. When the mosquito takes another meal of blood, the mosquito's proboscis injects the infective third-stage larvae into the blood of...
Development in thoracic musculature (1st- and 2nd-stage larvae)

Discharged into head and proboscis (3rd-stage larvae) and passed to host during feeding

FIGURE 13.12
Life Cycle of Wuchereria spp. (See text for details.)
Source: Redrawn from Centers for Disease Control, Atlanta, GA.

the human host. The final two molts take place as the larvae enter the lymphatic vessels.

A filarial worm prevalent in the United States is Dirofilaria immitis, a parasite of dogs. Because the adult worms live in the heart and large arteries of the lungs, the infection is called heartworm disease. Once established, these filarial worms are difficult to eliminate, and the condition can be fatal. Prevention with heartworm medicine is thus advocated for all dogs.

SECTION REVIEW 13.2
Members of the phylum Nematoda are the roundworms. They are bilaterally symmetrical and pseudocoelomate. They have longitudinal muscles along their body wall, and a complete digestive tract. They feed on a wide variety of foods. Nematodes are dioecious. After copulation, eggs are usually released to the outside of the body where they hatch. Some nematodes are ovoviviparous. Important nematode parasites include Ascaris lumbricoides, Enterobius vermicularis, Necator americanus, Trichinella spiralis, and Wuchereria spp.

Many parasitic nematodes are intestinal parasites whose eggs are released with feces of their host. How does this observation regarding nematode life cycles inform control measures directed at nematode parasites?

13.3 Other Ecdysozoan Phyla

LEARNING OUTCOME
1. Characterize members of the phyla Nematomorpha, Kinorhyncha, Priapulida, and Loricifera.

Members of the remaining four phyla are a diverse group of ecdysozoans. The primary morphological feature they share with all ecdysozoans is the cuticle. Two other characteristics common to all phyla covered in this chapter are the pseudocoelom and a collar-shaped neural ring ("brain") around the pharynx. The former is of no taxonomic significance as it is present in multiple phyla scattered through the Lophotrochozoa and Ecdysozoa. The neural ring (see figures 13.2b and 13.4a) is an important synapomorphy for the phyla discussed in this chapter. Phylogenetic relationships of these groups will be discussed in the final section of this chapter.

Phylum Nematomorpha

Nematomorphs (nem"a-to-mor'fs) (Gr. nema, thread + morphe, form) are a small group (about 250 species) of elongate worms commonly called either horsehair worms or Gordian worms. The hairlike nature of these worms is so striking that they were formerly thought to arise spontaneously from the hairs of a horse's tail in drinking troughs or other stock-watering places. The adults are free living, but the juveniles are all parasitic in arthropods. They have a worldwide distribution and can be found in both running and standing water. The nematomorph body is extremely long and thread-like and has no distinct head (figure 13.13). The body wall has a thick collagenous cuticle, a cellular epidermis, longitudinal cords, and a muscle layer of longitudinal fibers. The nervous system contains an anterior nerve ring and a ventral cord.

Nematomorphs have separate sexes; two long gonads extend the length of the body. After copulation, the eggs are deposited in water. A small larva with a protrusible proboscis armed with spines hatches from the egg. Terminal stylets are also present on the proboscis. The larva must quickly enter an arthropod (e.g., a beetle, cockroach) host, either by penetrating the host or by being eaten. Lacking a digestive system, the larva feeds by absorbing material directly across its body wall. Once mature, the worm leaves its host only when the arthropod is near water. Sexual maturity is attained during the free-living adult phase of the life cycle.

Phylum Kinorhyncha

Kinorhynchs (kin'o-rinks) are small (less than 1 mm long), elongate, bilaterally symmetrical worms found exclusively in marine environments, where they live in mud and sand. Because they have no external cilia or locomotor appendages, they simply burrow through the mud and sand with their snouts. In fact, the phylum takes its name (Kinorhyncha, Gr. kinein, motion + rhynchos, snout) from this method
Phylum Nematomorpha. This adult nematomorph (*Gordius robustus*) is about 25 cm long and emerged from its cricket host after a rain. These worms tend to twist and turn upon themselves, giving the appearance of complicated knots—thus, the name "Gordian worms." (Legend has it that King Gordius of Phrygia tied a formidable knot—the Gordian knot—and declared that whoever might undo it would be the ruler of all Asia. No one could accomplish this until Alexander the Great cut through it with his broadsword.)

The phylum Kinorhyncha contains about 150 known species.

The body surface of a kinorhynch is devoid of cilia and is composed of 13 or 14 definite units called *zonites* (figure 13.14). The head of a kinorhynch is zonite 1 and is called the *introvert*. It bears the mouth and oral cone, and it is retractable. When it is retracted, the anterior end is covered by chitinous spines on the neck (zonite 2). These spines are called *scalids* and some are modified into plate-like *placids*. Scalids grip the substrate during burrowing. The trunk consists of the remaining 11 or 12 zonites and terminates with the anus. Each trunk zonite bears a pair of lateral spines and one dorsal spine.

**Evolutionary Insights**

**What Are Worms?**

If the ancestral animal was worm-like, as many phylogenetic schemes postulate, it would follow that a wide variety of worms might evolve from a vermiform (*L. vermis*, a worm, worm-like) ancestor, and that ultimately some of these worms might give rise to non-worms. There are other schemes that read the sequence in the opposite direction and derive at least some worms from non-worms.

**Gold Mine Treasure: A New Worm**

Single-cell organisms are now known to live deep in the earth, more than 9,000 feet below the surface in extreme conditions. Until now, it was thought that these conditions were too extreme for multicellular organisms such as worms.

Geoscientists have recently reported their discovery of a small multicellular worm (nematode) in the shaft of a gold mine in Africa. The nematode, *Halicephalobus mephisto*, is only 0.5 mm long. This nematode feeds on bacteria and can tolerate temperatures above 38°C.
The body wall consists of a chitinous cuticle, epidermis, and two pairs of muscles: dorsolateral and ventrolateral. The pseudocoelom is large and contains amoeboid cells. A complete digestive system is present, consisting of a mouth, buccal cavity, muscular pharynx, esophagus, stomach, intestine (where digestion and absorption take place), and anus. Most kinorhynchs feed on diatoms, algae, and organic matter. A pair of protonephridia is in zonite 11. The nervous system consists of a neural ring that encircles the pharynx and single ventral nerve cord with a ganglion (a mass of nerve cells) in each zonite. Some species have eyespots and sensory bristles. Kinorhynchs are dioecious with paired gonads. Several spines that may be used in copulation surround the male gonopore. The young hatch into larvae that do not have all of the zonites. As the larvae grow and molt, the adult morphology appears. Once adulthood is attained, molting no longer occurs.

Phylum Priapulida

The priapulids (pri'a-pyu-lids) (Gr. priapos, phallus + ida, pleural suffix; from Priapos, the Greek god of reproduction, symbolized by the penis) are a small group (only 16 species) of marine worms found in cold waters. They live buried in the mud and sand of the seafloor, where they feed on small annelids and other invertebrates.

The priapulid body is cylindrical and ranges in length from 2 mm to about 8 cm (figure 13.15). The anterior part of the body is an introvert (proboscis), which priapulids can draw into the longer, posterior trunk. The introvert functions in burrowing, and spines surround it. A thin chitinous cuticle that bears spines covers the muscular body, and the trunk bears superficial annuli. A straight digestive tract is suspended in a large pseudocoelom that acts as a hydrostatic skeleton. In some species, the pseudocoelom contains amoeboid cells that probably function in gas transport. The nervous system consists of a nerve ring around the pharynx and a single midventral nerve cord. The sexes are separate but not superficially distinguishable. A pair of gonads is suspended in the pseudocoelom and shares a common duct with the protonephridia. The duct opens near the anus, and gametes are shed into the sea. Fertilization is external, and the eggs eventually sink to the bottom, where the larvae develop into adults. The cuticle is repeatedly molted throughout life. The most commonly encountered species is Priapulus caudatus.

Phylum Loricifera

The phylum Loricifera (lor'a-sif-er-ah) (L. lorica, clothed in armor + fero, to bear) is a recently described animal phylum. Its first members were identified and named in 1983. Loriciferans live in spaces between marine gravel. A characteristic species is Nanaloricus mysticus. It is a small, bilaterally symmetrical worm with a spiny head called an introvert, a thorax, and an abdomen surrounded by a cuticular lorica (figure 13.16). Loriciferans can retract both the introvert and thorax into the anterior end of the lorica. The introvert bears

**FIGURE 13.15**
Phylum Priapulida. Internal anatomy of the priapulid Priapulus caudatus, with the introvert withdrawn into the body.

**FIGURE 13.16**
Phylum Loricifera. Dorsal view of the anatomy of an adult male Nanaloricus mysticus.
eight oral styles that surround the mouth. The loric cuticle is periodically molted. A pseudocoelom is present and contains a short digestive system, neural ring that encircles the pharynx, and several ganglia. Loriciferans are dioecious with paired gonads. Zoologists have described about 22 species.

Section Review 13.3
Members of the phylum Nematomorpha are long and threadlike. They have separate sexes. Larvae are parasites in arthropods, and adults are freeliving in freshwater. Members of the phylum Kinorhyncha live in marine sediments. Their bodies are divided into zonites. Zonite 2 contains scalids and placids. The introvert is retractable. Kinorhynchs are dioecious and larvae molt into the adult form. Members of the phylum Priapulida have an introvert that is used in burrowing in marine sediments. Their cuticle bears spines and superficial annuli. Sexes are separate and gametes are shed into the sea. Members of the phylum Loricifera live in marine sediments. They possess a retractable introvert and are surrounded by a protective outer case called the lorica. Loriciferans are dioecious.

Adult nematomorphs are aquatic, but sometimes they are observed on sidewalks or lawns following a rain. How can you explain these observations?

13.4 Further Phylogenetic Considerations
LEARNING OUTCOMES
1. Describe the relationships of the ecdysozoan phyla and controversies associated with this phylogeny.
2. Describe phylogeny within the Nematoda.

The advent of molecular techniques revolutionized our interpretations of the phylogenetic relationships of animals described in chapters 13 through 15. As described earlier, these phyla are characterized by a secreted cuticle that is shed through ecdysis. The importance of this unifying character has been confirmed by molecular analyses many times. The relationships within the Ecdysozoa are more contentious. Ideally, a combination of morphological and molecular data will eventually sort out the uncertainties that exist. One interpretation of ecdysozoan phylogeny is shown in figure 13.17 and described below.

Some molecular studies have resulted in taxonomists concluding that there are two clades within the Ecdysozoa. The Arthropoda, Tardigrada, and Onychophora are covered in chapters 14 and 15 and comprise the clade Panarthropoda.

FIGURE 13.17
One Interpretation of Ecdysozoan Phylogeny. Some molecular data suggest that Ecdysozoa is comprised of two clades, Cycloneuralia and Panarthropoda. The position of the Loricifera is uncertain, although loriciferans are usually thought to be more closely related to the kinorhynchs and priapulids than they are to the nematodes and nematomorphs. Synapomorphic characters for Panarthropoda are presented in chapter 15. This phylogeny is based on Dunn et al. 2008. Broad phylogenomic sampling improves resolution of the animal tree of life. Nature 452 (7188): 745–749.
The phylogenetic relationships within the Panarthropoda will be discussed at the end of chapter 15.

The five phyla described in this chapter are often designated as the clade Cycloneuralia. They all possess a collar-shaped neural ring ("brain") around the pharynx. Within this clade the Nematoda and Nematomorpha are sister groups. Kinorhyncha and Priapulida also share common ancestry. These relationships are supported by morphological evidence. The Nematoda and Nematomorpha possess a collagenous cuticular structure and the Kinorhyncha and Priapulida share a chitinous cuticular structure and an introvert with scalids. The relationship of the Loricifera to these other four phyla is less certain. Because loriciferans also possess a chitinous cuticle and an introvert with scalids, they are considered by some authorities to be a sister group to the kinorhynch/priapulid clade. The molecular data that could support this conclusion are scanty, and some of these data that do exist suggest that loriciferans are more closely related to the nematode/nematomorph clade. More studies are needed to resolve this uncertainty.

The largest and most important phylum covered in this chapter is Nematoda. Phylogenetic relationships within the phylum are even more contentious than the relationships within the Ecdysozoa as a whole. The traditional classes (Secernentea and Adenophorea) clearly do not reflect nematode phylogeny. Molecular studies reveal three major clades. Nematodes are usually assumed to have arisen in marine habitats, and members of some groups within the basal clade, Chromadorea, are predominantly marine. This clade diverged into multiple orders including many terrestrial and freshwater groups. The important nematode parasites described earlier are all members of a single chromadorean group, Spirurina. Two other major nematode clades are Enoplia and Dorylaimia. Dorylaimians are absent from marine habitats. Both clades are composed of a variety of predators, decomposers, and plant and animal parasites.

**Section Review 13.4**

Phylogenetic relationships within the Ecdysozoa are controversial. Two major clades include the Panarthropoda and Cycloneuralia. Within the Cycloneuralia, the nematodes and nematomorphs are sister groups. The kinorhynchs and priapulids are also closely related. The relationship of the loriciferans to these phyla is less certain. Two traditional nematode classes do not reflect phylogeny of this phylum. Molecular evidence suggests that there are three major clades within the Nematoda.

*What uncertainties exist in our understanding of phylogenetic relationships within the Ecdysozoa, and what type of evidence is required in order to resolve these uncertainties?*

**Summary**

**13.1 Evolutionary Perspective**

Ecdysozoans are united by molecular characteristics and in the presence of a cuticle that is molted during growth (ecdysis).

The cuticle of the ecdysozoans discussed in chapter 13 functions with the pseudocoelom in hydrostatic skeletal functions.

**13.2 Phylum Nematoda (Roundworms)**

Members of the phylum Nematoda are the roundworms. They are elongate, slender, and circular in cross section. They have a complete digestive tract, longitudinal body wall muscles, and renette cells that function in excretion. Sexes are separate.

Nematodes include many important human parasites.

**13.3 Other Ecdysozoan Phyla**

Adult Nematomorpha are threadlike and free living in freshwater. They lack a digestive system. Immature nematomorphs are parasites of arthropods.

Members of the phylum Kinorhyncha live in marine sediments. Their bodies are divided into zonites, and they possess a retractable introvert.

The phylum Priapulida contains only 16 known species of cucumber-shaped, worm-like animals that live buried in the bottom sand and mud in marine habitats.

The phylum Loricifera was described in 1983. These microscopic animals have a spiny head and thorax, and they live in gravel in marine environments.

**13.4 Further Phylogenetic Considerations**

Ecdysozoa is divided into two clades: Cycloneuralia and Panarthropoda. Cycloneuralia is characterized by a neural ring that encircles the pharynx. The Nematoda and Nematomorpha are sister groups within Cycloneuralia. Kinorhyncha and Priapulida are closely related. Relationships of these phyla to Loricifera are less certain. Nematoda is composed of three clades. Taxonomy within Nematoda is controversial.

**Concept Review Questions**

1. Which of the following is the most important synapomorphy for Ecdysozoa?
   a. They possess a fluid-filled body cavity.
   b. The following germ layers are present: ectoderm, endoderm, and mesoderm.
   c. They all have a complete digestive system.
   d. All members molt in order to grow.
   e. All members are microscopic in size.

2. All of the phyla discussed in this chapter are united by the presence of
   a. an introvert.
   b. a collagenous cuticle.
   c. a chitinous cuticle.
   d. a neural ring that encircles the pharynx.
   e. scalids.
3. Members of this phylum are freeliving in freshwater as adults, but they are parasites of arthropods in their larval stage.
   a. Nematoda
   b. Nematomorpha
   c. Loricifera
   d. Kinorhyncha
   e. Priapulida

4. The most likely route for an infection by *Trichinella spiralis* is
   a. wading in infested streams.
   b. fecal contamination of drinking water.
   c. eating poorly cooked pork.
   d. a mosquito bite.

5. Which of the following is FALSE with respect to members of the phylum Nematoda?
   a. They are vermiform in shape.
   b. They have a complete digestive tract.
   c. The body wall has both circular and longitudinal muscles.
   d. They contain renette cells and collecting tubules.
   e. They are pseudocoelomate.

**Analysis and Application Questions**

1. Discuss how the structure of the body wall places limitations on shape changes in nematodes.

2. What characteristics set the Nematomorpha apart from the Nematoda? What characteristics do the Nematomorpha share with the Nematoda?

3. How would you assess the state of taxonomy within the Ecdysozoa? What information would you request if you were to resolve phylogenetic questions pertaining to this clade?

4. Compare effective control strategies for infestations of *Necator americanus* and *Wuchereria*.

*connect* Enhance your study of this chapter with study tools and practice tests. Also ask your instructor about the resources available through Connect, including a media-rich eBook, interactive learning tools, and animations.