Chapter 33

An Introduction to Invertebrates

Lecture Outline

Overview: Life Without a Backbone

- **Invertebrates**—animals without a backbone—account for 95% of known animal species and all but one of the roughly 35 animal phyla that have been described.
- Invertebrates live in nearly all habitats on Earth, from the scalding water of deep-sea hydrothermal vents to the rocky, frozen ground of Antarctica.
  - Adaptation to varied environments has produced a great diversity of invertebrate form.

Concept 33.1 Sponges are basal animals that lack true tissues

- Animals in the phylum Porifera are known informally as sponges.
  - Recent molecular studies indicate sponges are likely monophyletic; this remains a topic of active debate.
- Sponges are sedentary and were mistaken for plants by ancient Greeks.
- They range in size from a few millimeters to a few meters.
- Most are marine, although a few live in freshwater environments.
- Sponges are **suspension feeders**, capturing food particles suspended in water.
- The body of a simple sponge resembles a sac perforated with pores.
  - Water is drawn through the pores into a central cavity, the **spongocoel**, and flows out through a larger opening, the **osculum**.
  - More complex sponges have folded body walls, and many contain branched water canals and several oscula.
- Sponges are basal animals, representing a lineage that originates near the root of the phylogenetic tree of animals.

Sponges lack true tissues but have several different cell types.

- Unlike nearly all other animals, sponges lack true tissues, groups of similar cells that form a functional unit and are isolated from other tissues by membranous layers.
  - The sponge body does contain different cell types. Lining the interior of the spongocoel are flagellated **choanocytes** or collar cells that engulf bacteria by phagocytosis.
- Based on both molecular evidence and the morphology of their choanocytes, sponges evolved from a colonial choanoflagellate ancestor.
- The body of a sponge consists of two cell layers separated by a gelatinous region, the **mesohyl**.

- Both cell layers are in contact with water. As a result, gas exchange and waste removal can occur by diffusion across the membranes of these cells.

- **Amoebocytes**, named for their use of pseudopodia, wander though the mesohyl, taking up food from water and choanocytes, digesting it, and carrying nutrients to other cells.
- Amoebocytes also manufacture tough skeletal fibers within the mesohyl.
  - In some groups of sponges, these skeletal fibers are sharp spicules of calcium carbonate or silica.
  - Other sponges produce more flexible fibers from a collagen protein called spongin.
- Amoebocytes are capable of differentiating into other types of sponge cells.
  - This enables the sponge body to adjust its shape in response to changes in its physical environment (such as the direction of water currents).
- Most sponges are sequential **hermaphrodites**, producing both sperm *and* eggs in sequence.
- Gametes arise from choanocytes or amoebocytes.
  - Eggs are retained within the mesohyl, but sperm are carried out of the sponge by the water current.
  - Sperm are drawn into neighboring individuals and fertilize eggs in the mesohyl, where the zygotes develop into flagellated, swimming larvae that disperse from the parent.
  - After settling on a suitable substratum, the larva develops into a sessile adult.
- Sponges produce a variety of antibiotics and other defensive compounds.
  - Some of these compounds hold promise in fighting human disease.
  - A compound called cribrostatin isolated from marine sponges can kill penicillin-resistant strains of the bacterium *Streptococcus.*
  - Other sponge-derived compounds are being tested as possible anti-cancer agents.

Concept 33.2 Cnidarians are an ancient phylum of eumetazoans

- All animals except sponges (and a few other groups) belong to the clade Eumetazoa, animals with true tissues.
- One of the oldest lineages in the clade is the phylum Cnidaria.
- Cnidarians have diversified into a wide range of motile and sessile forms, including jellyfish, corals, and hydras.
- They exhibit a simple, diploblastic, radial body plan that arose 560 million years ago.
- The basic cnidarian body plan is a sac with a central digestive compartment, the **gastrovascular cavity**.
  - A single opening to this cavity functions as both mouth and anus.
- This basic body plan has two variations: the sessile polyp and the motile medusa.
- Cylindrical **polyps**, such as hydras and sea anemones, adhere to the substratum by the aboral end and extend their tentacles, waiting for prey.
- **Medusae,** including free-swimming jellies, resemble flattened, mouth-down versions of polyps that move by drifting passively and by contracting their bell-shaped bodies.
  - The tentacles of a jelly dangle from the oral surface, which points downward.

- Some cnidarians exist only as polyps or only as medusae. Others have both a medusa stage and a polyp stage in their life cycle.
- Cnidarians are carnivores that use tentacles arranged in a ring around the mouth to capture prey and push the food into the gastrovascular cavity for digestion.
  - Enzymes are secreted into the cavity, where digestion begins.
  - Cells lining the cavity absorb the nutrients and complete digeston.
  - Undigested remains are expelled through the mouth/anus.
- Batteries of **cnidocytes** on the tentacles defend the animal and capture prey.
  - Cnidocytes contain cnidae, capsule-like organelles that explode outward.
  - Specialized cnidae called **nematocysts** are capsules that contain a stinging thread that can inject poison into the prey and stick to or entangle the target.
- Contractile tissues and nerves exist in their simplest forms in cnidarians.
  - Cells of the epidermis and gastrodermis have bundles of microfilaments arranged into contractile fibers.
- The gastrovascular cavity acts as a hydrostatic skeleton against which the contractile cells can work.
  - When a cnidarian closes its mouth, the volume of the cavity is fixed, and contraction of selected cells causes the animal to change shape.
- Movements are controlled by a noncentralized nerve net.
  - The nerve net is associated with simple sensory receptors that are distributed radially around the body, allowing the animal to detect and respond to stimuli from all directions.
- The phylum Cnidaria is divided into four major clades: Hydrozoa, Scyphozoa, Cubozoa, and Anthozoa.
- Most hydrozoans alternate polyp and medusa forms, as in the life cycle of *Obelia*.
  - The polyp stage, a colony of interconnected polyps, is more conspicuous than the medusa.
- Hydras, among the few freshwater cnidarians, exist only in the polyp form.
  - When environmental conditions are favorable, a hydra reproduces asexually by budding.
  - When environmental conditions deteriorate, hydras reproduce sexually to form resistant zygotes that remain dormant until conditions improve.
- The medusa generally is the predominant stage in the life cycle of the clade Scyphozoa.
  - The medusae of most species live among the plankton as jellies.
- Most coastal scyphozoans go through small polyp stages during their life cycle, while jellies that live in the open ocean generally lack the sessile polyp stage.
- Cubozoans have a dominant box-shaped medusa stage.
- Cubozoans can be distinguished from scyphozoans in other significant ways, such as having complex eyes in the fringe of the medusae.
- Cubozoans, which generally live in tropical oceans, are comparatively strong swimmers and often equipped with highly toxic cnidocytes.
  - The sea wasp *(Chironex fleckeri)*, a cubozoan that lives off the coast of northern Australia, is one of the deadliest organisms on Earth: Its sting causes intense pain and can lead to respiratory failure, cardiac arrest, and death within minutes.

- Sea anemones and corals, which occur only as polyps, belong to the clade Anthozoa.
- Coral animals live as solitary or colonial forms, often forming symbiosis with algae.
- Many species secrete a hard external skeleton of calcium carbonate.
  - Each polyp generation builds on the skeletal remains of earlier generations to form skeletons that we call corals.
- In tropical seas, coral reefs provide habitat for a great diversity of invertebrates and fishes.
- Coral reefs in many parts of the world are currently being destroyed.
  - Pollution and overfishing are major threats.
  - Global warming is contributing to the demise of coral reefs by raising seawater temperatures above the narrow ranges in which corals thrive.

Concept 33.3 Lophotrochozoans, a clade identified by molecular data, have the widest range of animal body forms

- The vast majority of animal species belong to the clade Bilateria, which consists of animals with bilateral symmetry and triploblastic development.
- Most bilaterians are have a coelom and a digestive tract with a mouth and anus.
- The most recent common ancestor of living bilaterians probably lived in the late Proterozoic (about 575 million years ago).
  - Many of the major groups of bilaterians first appeared in the fossil record during the Cambrian explosion.
- Molecular evidence suggests that there are three major clades of bilaterally symmetrical animals: Lophotrochozoa, Ecdysozoa, and Deuterostomia.
- Althought the clade Lophotrochozoa was identified by molecular data, its name comes from two features found in some of its members.
  - Some lophotrochozoans develop a structure called a *lophophore*, a crown of ciliated tentacles that function in feeding, while others go through a distinctive larval stage called the *trochophore larva*.
  - Other members of the group have neither of these features.
- Few other unique morphological features are shared by most members of the group, and the lophotrochozoans are the most diverse animal clade in terms of body plans.
  - Lophotrochozoa includes about 18 animal phyla, more than twice the number found in any other clade of animals.
  - Lophotrochozoan phyla include the flatworms, rotifers, ectoprocts, brachiopods, molluscs, and annelids.

Phylum Platyhelminthes: Flatworms are acoelomates with gastrovascular cavities.

- Flatworms live in marine, freshwater, and damp terrestrial habitats.
- Flatworms also include many parasitic species, such as the flukes and tapeworms.
- Members of the group have thin, dorsoventrally flattened bodies, and range in size from nearly microscopic free-living species to tapeworms more than 20 m long.
- Flatworms undergo triploblastic development but are acoelomate and lack a body cavity.

- The flat shape of a flatworm places all cells close to the surrounding water, enabling gas exchange and the elimination of nitrogenous wastes (ammonia) by diffusion across the body surface.
- Flatworms have no specialized organs for gas exchange and circulation, and their relatively simple excretory apparatus functions mainly to maintain osmotic balance.
    - This excretory apparatus consists of **protonephridia**, a network of tubules with ciliated cells called *flame bulbs* that pull fluid through branched ducts that open to the outside.
- Most flatworms have a gastrovascular cavity with only one opening, with branches that distribute food directly to the flatworm's cells.
- Early in their evolutionary history, flatworms separated into two lineages, Catenulida and Rhabditophora.
- Catenulida is a small clade of about 100 flatworm species, most living in freshwater habitats.
    - Catenulids reproduce asexually by budding at their posterior end.
    - The offspring often produce their own buds before detaching from the parent, thereby forming a chain of two to four genetically identical individuals.
- The other flatworm lineage, Rhabditophora, is a diverse clade of about 20,000 freshwater and marine species.
    - Free-living rhabditophorans feed as predators and scavengers in a wide range of freshwater and marine habitats.
- The best-known members of this group are freshwater species in the genus *Dugesia*, commonly called **planarians**.
- Planarians prey on smaller animals or feed on dead animals.
- They move by using cilia on their ventral surface, gliding along a film of mucus they secrete.
    - Some rhabditophorans use muscles to swim through water with an undulating motion.
- A planarian has a head with a pair of eyespots to detect light and lateral flaps that function mainly for smell.
- The planarian nervous system is more complex and centralized than the nerve net of cnidarians, and planarians can learn to modify their responses to stimuli.
- Some planarians reproduce asexually through regeneration.
    - The parent constricts in the middle, and each half regenerates the missing end.
- Planarians can also reproduce sexually, as hermaphrodites cross-fertilize each other.
- Over half the known species of rhabditophorans live as parasites in or on other animals.
    - Many have suckers for attaching to the inner organs or outer surfaces of their hosts.
    - In most species, a tough covering protects the parasites.
    - Reproductive organs nearly fill the interior of these worms.
- Trematodes parasitize a wide range of hosts, and most species have complex life cycles with alternating sexual and asexual stages.
- Many trematodes require an intermediate host in which the larvae develop before infecting the final hosts (usually a vertebrate) where the adult worm lives.
    - The blood fluke *Schistosoma* causes schistosomiasis, a disease that infects 200 million people, leading to pain, anemia, and dysentery.

- The intermediate host for *Schistosoma* is a snail, and living within different hosts puts demands on trematodes that free-living animals do not face.
    - A blood fluke must evade the immune systems of two very different hosts.
    - By mimicking their host's surface proteins, blood flukes create a partial immunological camouflage.
    - Blood flukes also release molecules that manipulate the host's immune system.
    - These defenses are so effective that individual flukes can survive in a human host for more than 40 years.
- Tapeworms are a large and diverse group of parasitic rhabditophorans, with adults that live mostly in vertebrates, including humans.
- Suckers and hooks on the anterior end, or scolex, anchor the tapeworm in the digestive tract of the host.
- Tapeworms lack a mouth and gastrovascular cavity, and absorb food from their hosts across their body surface.
- A long series of proglottids, sacs of sex organs, lie posterior to the scolex.
    - Mature proglottids, loaded with thousands of fertilized eggs, are released from the posterior end of the tapeworm and leave with the host's feces.
- In one type of cycle, tapeworm eggs in contaminated food or water are ingested by intermediary hosts, such as pigs or cattle.
    - The eggs develop into larvae that encyst in the muscles of their host.
    - Humans acquire the larvae by eating undercooked meat contaminated with cysts, and the larvae develop into mature adults within the human.
- Large tapeworms can block the intestines and rob enough nutrients from the human host to cause nutritional deficiencies.
    - An orally administered drug named niclosamide kills the adult tapeworms.

Phylum Rotifera: Rotifers are pseudocoelomates with jaws, crowns of cilia, and complete digestive tracts.

- Rotifers are tiny animals (50 µm to 2 mm) found fresh water, marine, and damp soil habitats.
- Rotifers are smaller than many protists but are multicellular, with specialized organ systems.
- Rotifers have an **alimentary canal**, a digestive tract with a separate mouth and anus.
- Their internal organs lie in the pseudocoelom, a body cavity not fully lined with mesoderm.
- The fluid in the pseudocoelom serves as a hydrostatic skeleton.
- Movements of a rotifer's body distribute the fluid throughout the body, circulating nutrients and wastes.
- The word *rotifer,* "wheel-bearer," refers to the crown of cilia that draws a vortex of water into the mouth.
    - Microorganisms drawn in by the cilia are captured by the jaws (trophi) in the pharynx and ground up. Digestion is completed further along the alimentary canal.
- Some rotifers exist only as females that produce more females from unfertilized eggs, a form of reproduction called **parthenogenesis**.

- Other rotifer species reproduce sexually under certain conditions, such as high levels of crowding. They do this by producing two types of eggs, one of which forms females, and the other of which develops into males.
    - In some species, the males do not feed and survive only long enough to fertilize eggs.
    - The fertilized eggs develop into resistant embryos that remain dormant for years.
    - Once the embryos break dormancy, they develop into a new female generation that reproduces by parthenogenesis until conditions again favor sexual reproduction.
- It is puzzling that many rotifers survive without males because the vast majority of animals and plants reproduce sexually at least some of the time, and sexual reproduction has certain advantages over asexual reproduction.
    - Species that reproduce asexually tend to accumulate harmful mutations in their genomes faster than sexually reproducing species.
    - As a result, asexual species experience higher rates of extinction and lower rates of speciation.
- Researchers are studying a clade of asexual rotifers called Bdelloidea, consisting of 360 species that all reproduce by parthenogenesis without males.
    - The morphology of thirty-five-million-year-old bdelloid rotifers preserved in amber resembles the female form, with no evidence of males.
    - DNA comparisons of bdelloids with their closest sexually reproducing rotifer relatives suggest that bdelloids have been asexual for much longer than 35 million years.
    - Bdelloid rotifers raise interesting questions about the evolution of sex.

Bilaterians in the phyla Ectoprocta and Brachiopoda are known as lophophorates because they have a lophophore.

- Bilaterians in the phyla Ectoprocta and Brachiopoda are called lophophorate animals because they have a *lophophore*, a crown of ciliated tentacles that surround the mouth.
    - As the cilia draw water toward the mouth, the tentacles trap suspended food particles.
- In addition to the lophophore, these phyla share a U-shaped digestive tract and the absence of a distinct head. These may be adaptations to a sessile existence.
- In contrast to flatworms, which lack a body cavity, and rotifers, which have a pseudocoelom, lophophorates have true coeloms completely lined with mesoderm.
- **Ectoprocts** are colonial animals that superficially resemble clumps of moss.
- In most species of ectoprocts, the colony is encased in a hard **exoskeleton**, and the lophophores extend through pores in the exoskeleton.
- Most ectoprocts live in the ocean, where they are widespread and numerous sessile animals, with several species that are important reef builders. Others live in lakes and rivers.
- **Brachiopods**, or lampshells, superficially resemble clams and other bivalve molluscs.
    - The halves of the brachiopod are dorsal and ventral, rather than lateral as in clams.
- All brachiopods are marine.
- Most live attached to the substratum by a stalk, opening their shell slightly to allow water to flow over the lophophore.
- The living brachiopods are remnants of a richer past; thirty thousand species of brachiopod fossils have been described from the Paleozoic and Mesozoic eras.

- Some living brachiopods, such as those in the genus *Lingula*, are nearly identical to fossils of species that lived 400 million years ago.

The phylum Mollusca includes many diverse forms.

- The phylum Mollusca includes snails and slugs, oysters and clams, and octopuses and squids.
- There are 93,000 known species, making them the second most diverse phylum of animals after arthopods.
- Most molluscs are marine, but 8,000 species inhabit fresh water, and 28,000 species of snails and slugs live on land.
- Molluscs are soft-bodied, and most secrete a hard shell of calcium carbonate.
  - Slugs, squids, and octopuses have a reduced internal shell or have lost their shells completely during their evolution.
- Despite their apparent differences, all molluscs have a similar body plan.
  - Molluscs are coelomate.
  - Their bodies have three main parts: a muscular **foot** used for movement; a **visceral mass** contains most of the internal organs; and a **mantle**, a fold of tissue that drapes over the visceral mass and secretes the shell.
- In many molluscs, the mantle creates a water-filled chamber, the **mantle cavity**, which holds the gills, anus, and excretory pores.
- Many molluscs feed by using a straplike rasping organ, a **radula**, to scrape up food.
- Most molluscs have separate sexes, with gonads located in the visceral mass.
  - However, many snails are hermaphrodites.
- The life cycle of many marine molluscs includes a ciliated larva, the trochophore, which is also found in marine annelids (segmented worms) and some other lophotrochozoans.
- The basic molluscan body plan has evolved in various ways in the phylum's seven or eight clades.
- The four most prominent clades are the Polyplacophora (chitons), Gastropoda (snails and slugs), Bivalvia (clams, oysters, and other bivalves), and Cephalopoda (squids, octopuses, cuttlefish, and chambered nautiluses).
- Chitons are oval-shaped marine animals with and shells composed eight dorsal plates.
  - The chiton body is unsegmented.
  - Chitons use their muscular foot to grip the rocky substrate and creep over the rock surface.
  - Chitons are grazers that use their radula to scrape and ingest algae.
- Almost three-quarters of all living species of molluscs are gastropods.
- Most gastropods are marine, but there are freshwater species and many snails and slugs have adapted to land.
- During embryonic development, gastropods undergo **torsion**, in which the visceral mass rotates up to 180°, so that the anus and mantle cavity are above the head in adults.
  - After torsion, some organs that were bilateral are reduced or lost on one side of the body.
- Most gastropods are protected by single, spiraled shells into which the animals can retreat if threatened.

- Torsion and formation of the coiled shell are independent developmental processes.

- Although most gastropod shells are conical, the shells of abalones and limpets are flattened.
- Many gastropods have distinct heads with eyes at the tips of tentacles.
- Gastropods move by a rippling motion of their foot or by means of cilia, often leaving a trail of slime in their wake.
- Most gastropods use their radulas to graze on algae or plants, but some gastropod species are predators.
    - In predatory species, the radula is modified to bore holes into the shells of other organisms or to tear apart prey.
    - In tropical marine cone snails, the teeth on the radula form poison darts, which are used to subdue prey.
- In place of the gills found in most aquatic gastropods, the lining of the mantle cavity of terrestrial snails functions as a lung.
- The clade Bivalvia includes clams, oysters, mussels, and scallops.
- Bivalves have shells divided in half. The two parts are hinged at the middorsal line, and powerful adductor muscles close the shell tightly to protect the animal.
- Bivalves have no distinct head, and the radula has been lost.
- Some bivalves have eyes and sensory tentacles along the outer edge of the mantle.
- The mantle cavity of a bivalve contains gills that are used for feeding and gas exchange.
- Most bivalves are suspension feeders, trapping fine particles in mucus that coats the gills.
    - Cilia convey the particles to the mouth.
    - Water flows into the mantle cavity via the incurrent siphon, passes over the gills, and exits via the excurrent siphon.
- Most bivalves live sedentary lives, a characteristic suited to suspension feeding.
    - Mussels secrete strong threads that tether them to rocks, docks, boats, and the shells of other animals.
    - Clams can pull themselves into the sand or mud, using their muscular foot as an anchor.
    - Scallops can swim in short bursts by flapping their shells.
- Cephalopods are active marine predators that use their tentacles to grasp prey, which they bite with beak-like jaws and immobilize with a poison found in their saliva.
- The foot of a cephalopod has been modified into a muscular excurrent siphon and parts of the tentacles.
- Squids dart about by drawing water into their mantle cavity and then firing a jet of water through the excurrent siphon.
    - By pointing the siphon in different directions, the squid can steer in different directions.
    - Octopuses use a similar mechanism to escape predators.
- A mantle covers the visceral mass, but the shell is reduced and internal in squids and cuttlefish, and is missing in some cuttlefishes and octopuses.
    - One small group of shelled cephalopods, the chambered nautiluses, survives today.
- Cephalopods are the only molluscs with a closed circulatory system.
- They also have well-developed sense organs and a complex brain.

- The ability to learn and demonstrate complex behaviors is more important to fast-moving predators than to sedentary animals such as clams.
- The ancestors of octopuses and squid were probably shelled molluscs that took up a predatory lifestyle.
  - Shelled cephalopods called **ammonites** were the dominant invertebrate predators of the seas for hundreds of millions of years until their disappearance in the mass extinctions at the end of the Cretaceous period.
- Most squids are less than 75 cm long, but some are much longer.
  - The giant squid *(Architeuthis dux)* was the largest squid known, with a mantle up to 2.25 m long and a total length of 18 m.
  - In 2003, a squid of the rare species *Mesonychoteuthis hamiltoni* with a mantle 2.5 m long was captured near Antarctica. It was likely a juvenile, perhaps half the size of an adult.
- Unlike *A. dux*, which has large suckers and small teeth on its tentacles, *M. hamiltoni* has rotating rows of hooks at the ends of its tentacles that can deliver deadly lacerations.
  - It is likely that *A. dux* and *M. hamiltoni* spend most of their time in the deep ocean, where they may feed on large fishes.
- Remains of both giant squid species have been found in the stomachs of sperm whales, which are probably their only natural predator.
- In 2005, scientists reported the first observations of *A. dux* in the wild, photographed while attacking baited hooks at a depth of 900 m.
  - *M. hamiltoni* has never been observed in nature.

Molluscs are the animal group with the largest number of documented extinctions.

- Threats to molluscs are especially severe in two groups, freshwater bivalves and terrestrial gastropods.
  - Pearl mussels, a group of freshwater bivalves that make pearls, are among the world’s most endangered animals.
  - 10% of the 300 pearl mussel species that once lived in North America have become extinct in the last 100 years. Two thirds of those that remain are threatened by extinction.
  - Over 50% of Pacific island land snails are extinct or under imminent threat of extinction.
- Threats faced by freshwater and terrestrial molluscs include habitat loss, pollution, and competition or predation by non-native species introduced by humans.
- Is it too late to protect these molluscs?
  - Some mollusc populations have rebounded after remedial actions: As a result of reduced water pollution and changes in the release of water through dams, pearl mussel populations have increased dramatically in some locations.

Annelids are segmented worms.

- All annelids (“little rings”) have segmented bodies.
- Annelids are coleomates that range in length from less than 1 mm to 3 m for the giant Australian earthworm.
- The phylum Annelida can be divided into two main groups: Polychaeta (polychaetes) and Oligochaeta (earthworms and their relatives; leeches).
- Recent phylogenetic analyses suggest that oligochaetes are actually a subgroup of polychaetes.

- Each segment of a polychaete has a pair of paddle-like structures called parapodia that function in locomotion.
    - Each parapodium has numerous chaetae.
    - In many polychaetes, the parapodia are richly supplied with blood vessels and also function as gills.
- Polychaetes make up a large and diverse group, most of whose members are marine.
- Some species live as plankton, others crawl on or burrow in the seafloor, and many others live in tubes built from a variety of substances.
- Oligochaetes have relatively sparse chaetae, or bristles made of chitin.
- Molecular data indicate that these segmented worms form a diverse clade including the earthworms and their aquatic relatives, along with the leeches.
- Earthworms eat their way through soil, extracting nutrients as the soil passes through the alimentary canal.
    - Undigested material mixed with mucus is eliminated as fecal castings.
    - Earthworms till and aerate soil, enriching it with their castings.
- Earthworms are cross-fertilizing hermaphrodites.
    - Two earthworms exchange sperm and then separate.
    - The sperm are stored while a special organ, the clitellum, secretes a mucous cocoon.
    - The cocoon slides along the body, picking up the eggs and stored sperm and sliding off the body into the soil.
    - The embryos develop within the cocoon.
- Some earthworms can also reproduce asexually by fragmentation followed by regeneration.
- The majority of leeches inhabit fresh water, but there are also marine leeches and land leeches, which move through moist vegetation.
- Leeches range from about 1 to 30 cm long.
- Many leeches feed on other invertebrates, but some blood-sucking parasites feed by attaching temporarily to other animals, including humans.
    - Some parasitic species use blade-like jaws to slit the host's skin, while others secrete enzymes that digest a hole through the skin.
    - The host is usually unaware of the attack because the leech secretes an anesthetic.
    - The leech also secretes hirudin, an anticoagulant, into the wound, which allows the leech to suck as much blood as it can hold, often more than ten times its own weight.
    - After gorging, a leech can live for months without another meal.
- Until this century, leeches were frequently used by physicians for bloodletting.
    - Leeches are still used to drain blood that accumulates in tissues following injury or surgery.
- Researchers are investigating the potential use of hirudin to dissolve unwanted blood clots caused by surgery or heart disease.
    - Recombinant forms of hirudin have been developed and are approved for clinical use.

Concept 33.4 Ecdysozoans are the most species-rich animal group

- Although the clade Ecdysozoa is defined primarily by molecular evidence, it includes animals that shed a tough external coat (cuticle) as they grow.
    - The group derives its name from *ecdysis,* or **molting**.
- The ecdysozoan clade consists of eight animal phyla and contains more known species than all other protist, fungus, plant, and animal groups combined.
- The two largest ecdysozoan phyla, nematodes and arthropods, are among the most successful and abundant of all animal groups.

Nematodes are among the most widespread of all animals.

- Nematodes, or roundworms, are found in most aquatic habitats, wet soil, moist tissues of plants, and the body fluids and tissues of animals.
- The bodies of nematodes are not segmented.
- Nematodes range in length from less than 1 mm to more than a meter.
- The cylindrical bodies of roundworms are covered with a tough exoskeleton, the **cuticle**.
- As the worm grows, it periodically sheds its old cuticle and secretes a new, larger one.
- Nematodes have an alimentary tract and use the fluid in their pseudocoelom to transport nutrients, since they lack a circulatory system.
- The thrashing motion of nematodes is due to contraction of longitudinal muscles.
- Nematodes usually reproduce sexually.
    - The sexes are separate in most species, and fertilization is internal.
    - Females may lay 100,000 or more fertilized eggs per day.
    - The zygotes of most nematodes are resistant cells that can survive harsh conditions.
- Abundant, free-living nematodes live in moist soil and in decomposing organic matter on the bottoms of lakes and oceans.
- There are 25,000 described species of nematodes, and perhaps 20 times that number exist.
    - If nothing but nematodes remained, it has been said, they would still preserve Earth’s outline and many of its features.
- Free-living nematodes play a major role in decomposition and nutrient recycling, but little is known about most species.
    - The soil nematode, *Caenorhabditis elegans,* is a well-studied model organism in biology.
- Phylum Nematoda includes many species that are important agricultural pests that attack plant roots.
- Other species of nematodes parasitize animals, including some species that benefit humans by attacking crop pests.
    - Over 50 nematode species, including pinworms and hookworms, parasitize humans.
- *Trichinella spiralis* causes trichinosis when the nematode worms encyst in a variety of human organs, including skeletal muscle.
    - Humans acquire this nematode by eating undercooked meat that has juvenile worms encysted in the muscle tissue.
- Parasitic nematodes hijack cellular functions of their hosts to evade their immune systems.
    - Some species inject molecules that induce the development of root cells that provide nutrients to the parasites.

- *Trichenella* in human muscle cells controls the expression of muscle cell genes that code for proteins that make the cell elastic enough to house the nematode.
- The muscle cell releases signals to attract blood vessels that supply the nematode with nutrients.

Arthropods are the most diverse and abundant animals on Earth.

- The world arthropod population has been estimated at a billion billion (10^{18}) individuals.
- Over a million arthropod species have been described, most of them insects.
  - Two of every three known species of life on Earth are arthropods.
  - Arthropods are found in nearly all habitats in the biosphere.
- By the criteria of species diversity, distribution, and sheer numbers, arthropods must be regarded as the most successful animal phylum.
- The diversity and success of **arthropods** are largely due to three features: body segmentation, hard exoskeleton, and jointed appendages.
- The earliest fossils that show the arthropod body plan are from the Cambrian explosion.
- The fossil record of the Cambrian explosion also contains many species of *lobopods*, an extinct group from which arthropods may have evolved.
  - Lobopods, such as *Hallucigenia,* had segmented bodies made up of identical segments.
  - Early arthropods, such as trilobites, also showed little variation from segment to segment.
- As arthropods continued to evolve, groups of segments fused and appendages became specialized for a variety of functions, permitting efficient division of labor among regions.
  - These evolutionary changes resulted not only in great diversification but also in an efficient body plan that permitted division of labor among different regions.
- What genetic changes led to the increasing complexity of the arthropod body plan?
- Living arthropods have two unusual *Hox* genes, both of which influence body segmentation.
- To test whether the origin of these genes could have driven the evolution of increased body-segment diversity in arthropods, Sean Carroll of the University of Wisconsin and his colleagues studied *Hox* genes in onychophorans, close relatives of arthropods.
  - Their results indicate that arthropod body-plan diversity did *not* arise from the acquisition of new *Hox* genes.
  - The evolution of body-segment diversity in arthropods may have been driven by changes in the sequence or regulation of existing *Hox* genes.
- The appendages of some arthropods have become modified to specialize in functions such as walking, feeding, sensory reception, copulation, and defense.
- The body of an arthropod is completely covered by the **cuticle**, an **exoskeleton** constructed from layers of protein and chitin.
  - The exoskeleton is thick and inflexible in some regions, such as crab claws, and thin and flexible in others, such as joints.
  - The exoskeleton protects the animal and provides points of attachment for the muscles that move appendages.
- In order to grow, an arthropod must shed its old exoskeleton and secrete a larger one, an energetically expensive molting process that leaves the animal vulnerable to predators.

- The exoskeleton's relative impermeability to water prevented desiccation and provided support on land.
- Arthropods moved to land after the colonization of land by plants and fungi during the early Paleozoic.
  - In 2004, an amateur fossil hunter found a 428-million-year-old fossil of a millipede.
  - Fossilized arthropod tracks date from 450 million years ago.
- Arthropods have well-developed sense organs, including eyes for vision, olfactory receptors for smell, and antennae for touch and smell.
  - Most, though not all, sense organs are located at the anterior end of the animal.
- Arthropods have an **open circulatory system** in which *hemolymph* fluid is propelled by a heart through short arteries into sinuses surrounding tissues and organs.
- Hemolymph returns to the heart through valved pores.
  - The *hemocoel* is not a coelom, although it is the main body cavity in adults.
  - The true coelom becomes much reduced as development proceeds.
  - Open circulatory systems evolved convergently in arthropods and molluscs.
- Arthropods have evolved a variety of specialized organs for gas exchange.
  - Most aquatic species have gills with thin, feathery extensions that have an extensive surface area in contact with water.
  - Terrestrial arthropods generally have internal surfaces specialized for gas exchange.
  - Insects have tracheal systems, branched air ducts leading into the interior from pores in the cuticle.
- Morphological and molecular evidence suggests that living arthropods consist of four major lineages that diverged early in the evolution of the phylum: **chelicerates** (sea spiders, horseshoe crabs, scorpions, ticks, mites, and spiders), **myriapods** (centipedes and millipedes), **hexapods** (insects and their wingless, six-legged relatives), and **crustaceans** (crabs, lobsters, shrimps, barnacles, and many others).
- Chelicerates are named for clawlike feeding appendages, chelicerae, serving as pincers or fangs.
- Chelicerates have an anterior cephalothorax and a posterior abdomen.
- They lack sensory antennae, and most have simple eyes (with a single lens).
- The earliest Chelicerates were **eurypterids**, or water scorpions, marine and freshwater predators that grew up to 3 m long.
- Modern marine Chelicerates include the sea spiders (pycnogonids) and the horseshoe crabs.
- Most living Chelicerates are arachnids, a group including scorpions, spiders, ticks, and mites.
- Nearly all ticks are blood-sucking parasites on the body surfaces of reptiles or mammals.
- Parasitic mites live on or in a wide variety of vertebrates, invertebrates, and plants.
- The arachnid cephalothorax has six pairs of appendages, including the chelicerae, four pairs of walking legs, and a pair of *pedipalps* that function in sensing, feeding, or reproducing.
- Spiders inject poison from glands on their fang-like chelicerae to immobilize their prey.
- As the chelicerae pierce the prey, the spider secretes digestive juices into the prey's tissues and sucks up the liquid meal.

- In most spiders, gas exchange is carried out by **book lungs**, stacked plates in an internal chamber.
    - The plates present an extensive surface area, enhancing the exchange of gases between the hemolymph and air.
- A unique adaptation of many spiders is the ability to catch insects in webs of silk.
    - The silk protein is produced as a liquid by abdominal glands and spun by spinnerets into fibers that solidify.
- Web designs are characteristic of each species.
    - Silk fibers also function as egg covers, droplines for rapid escape, and "gift wrapping" for nuptial gifts.
    - Many small spiders extrude silk into the air and are transported by wind, a behavior known as "ballooning."
- Millipedes and centipedes belong to the subphylum Myriapoda, the myriapods.
- All living myriapods are terrestrial.
- The myriapod head has a pair of antennae and three pairs of appendages modified as mouthparts, including jaw-like **mandibles**.
- Millipedes have two pairs of walking legs on each of their many trunk segments, each formed by two fused segments.
    - Millipedes eat decaying leaves and plant matter.
    - They were among the earliest land animals, living on mosses and early vascular plants.
- Centipedes are terrestrial carnivores.
    - Each segment in a centipede's trunk region has one pair of walking legs.
    - Centipedes have poison claws on their foremost trunk segment that paralyze prey and aid in defense.
- Insects and their relatives (subphylum Hexapoda) are more species-rich than all other forms of life combined.
    - Insects live in almost every terrestrial habitat and in fresh water; flying insects fill the air.
    - Insects are rare, but not absent, from the sea, where crustaceans dominate.
- The oldest insect fossils date back to the Devonian period, about 416 million years ago.
    - When insect flight evolved in the Carboniferous and Permian periods, it sparked an explosion in insect diversity.
    - Diversification of mouthparts for feeding on gymnosperms and other Carboniferous plants also contributed to the early adaptive radiations of insects.
    - A major increase in insect diversity was stimulated by the evolutionary expansion of flowering plants during the mid-Cretaceous period, about 90 million years ago.
    - Although insect and plant diversity decreased during the Cretaceous mass extinctions, both groups have rebounded over the past 65 million years.
- Flight is one key to the great success of insects.
    - Flying animals can escape many predators, find food and mates, and disperse to new habitats faster than organisms that crawl on the ground.
- Many insects have one or two pairs of wings that emerge from the dorsal side of the thorax.
    - Because wings are extensions of the cuticle and not true appendages, insects can fly without sacrificing the use of walking legs.

- Various hypotheses have been proposed for the evolution of insect wings.
  1. Wings first evolved as extensions of the cuticle that helped the insect absorb heat and were later modified for flight.
  2. Wings enabled animals to glide from vegetation to the ground.
  3. Wings served as gills in aquatic insects.
  4. Wings functioned for swimming before they functioned for flight.
- Morphological and molecular data suggest that wings evolved only once in insects.
- Dragonflies, among the first insects to fly, have two similar pairs of wings.
- Several insect orders that evolved later have modified flight equipment.
  - The wings of bees and wasps are hooked together and move as a single pair.
  - Butterfly wings operate similarly because the anterior wings overlap the posterior wings.
  - In beetles, the posterior wings function in flight, whereas the anterior wings act as covers that protect the flight wings when the beetle is on the ground or burrowing.
- Many insects undergo metamorphosis during their development.
- In **incomplete metamorphosis** (seen in grasshoppers and some other orders), the young (nymphs) resemble adults but are smaller, have different body proportions, and lack wings.
  - Through a series of molts, the young look more like adults until they reach full size.
  - With the final molt, the insect reaches full size, acquires wings, and becomes sexually mature.
- In **complete metamorphosis**, larval stages specialized for eating and growing change morphology completely during the pupal stage and emerge as an adult stage specialized for dispersal and reproduction.
- Reproduction in insects is usually sexual, with separate male and female individuals.
  - Coloration, sound, and odor bring together opposite sexes at the appropriate time.
- Fertilization is generally internal. In most species, sperm cells are deposited directly into the female’s vagina at the time of copulation.
  - In a few species, females pick up a sperm packet deposited by a male.
- The females store sperm in the spermatheca, usually enough to fertilize more than one batch of eggs.
  - Many insects mate only once in a lifetime.
- After mating, females lay their eggs on a food source that is appropriate for the next generation.
- Insects are classified in more than 30 orders.
- Insects affect the lives of most other terrestrial organisms.
  - They consume enormous quantities of plant matter, play key roles as predators, parasites, and decomposers, and are an essential source of food for larger animals such as lizards, rodents, and birds.
  - Insects are important natural and agricultural pollinators and an important source of protein for many human populations.
  - Insects are carriers for many diseases, including malaria and African sleeping sickness.
  - Insects compete with humans for food, consuming up to 75% of African crops.
  - Farmers spend billions of dollars each year on pesticides to minimize losses to insects.

- Although arachnids and insects thrive on land, most crustaceans remain in marine and freshwater environments.
- Crustaceans typically have highly specialized appendages.
  - Lobsters and crayfish have 19 pairs of appendages, adapted to a variety of tasks.
  - In addition to two pairs of antennae, crustaceans have three or more pairs of mouthparts, including hard mandibles.
  - Walking legs are on the thorax, and other appendages for swimming or reproduction are on the abdomen.
  - Crustaceans can regenerate lost appendages during molting.
- Small crustaceans exchange gases across thin areas of the cuticle; larger species have gills.
- Nitrogenous wastes are excreted by diffusion through thin areas of the cuticle, but glands regulate the salt balance of the hemolymph.
- Most crustaceans have separate sexes.
  - In lobsters and crayfish, males use a specialized pair of appendages to transfer sperm to the female's reproductive pore during copulation.
- Most aquatic crustaceans go through several swimming larval stages.
- The **isopods**, with over 11,000 species, are one of the largest groups of crustaceans.
  - Isopods include terrestrial, freshwater, and marine species.
  - Isopods also include land-dwelling pill bugs which live underneath moist logs and leaves.
- **Decapods**, including lobsters, crayfish, crabs, and shrimp, are among the largest crustaceans.
  - The cuticle of a decapod is hardened with calcium carbonate.
  - The exoskeleton over the cephalothorax forms a shield called the carapace.
  - Although most decapods are marine, crayfish live in fresh water, and some tropical crabs are terrestrial as adults.
- Many small crustaceans are important members of marine and freshwater plankton communities.
  - Planktonic crustaceans include many species of **copepods**, which are among the most numerous of all animals. Some copepods feed on algae, while others are predatory.
  - Krill are shrimplike planktonic organisms that grow to 5 cm long.
- A major food source for baleen whales and other ocean predators, krill are now harvested extensively by humans for food and agricultural fertilizer.
  - The larvae of many larger-bodied crustaceans are planktonic.
- Barnacles are primarily sessile crustaceans whose cuticle is hardened into a shell containing calcium carbonate.
  - Barnacles anchor themselves to rocks, boat hulls, and pilings and strain food from the water by extending their appendages.
  - Their adhesive is as strong as any synthetic glue.
- Barnacles were not recognized as crustaceans until the 1800s, when naturalists discovered that barnacle larvae resemble the larvae of other crustaceans.

Concept 33.5 Echinoderms and chordates are deuterostomes

- At first glance, sea stars and other echinoderms (phylum Echinodermata) seem to have little in common with vertebrates and other members of the phylum Chordata.
    - DNA evidence indicates that echinoderms and chordates are closely related, with both phyla belonging to the Deuterostomia clade of bilaterian animals.
    - Echinoderms and chordates also share features characteristic of a deuterostome mode of development, such as radial cleavage and formation of the anus from the blastopore.
- Some animal phyla with members that have deuterostome developmental features, including ectoprocts and brachiopods, are not in the deuterostome clade.
    - Despite its name, the clade Deuterostomia is defined primarily by DNA similarities—not by developmental similarities.

Phylum Echinodermata: Echinoderms have a water vascular system and secondary radial symmetry.

- Sea stars and most other **echinoderms** are sessile or slow-moving marine animals.
- A thin skin covers an endoskeleton of hard calcareous plates, and most echinoderms are prickly from skeletal bumps and spines.
- Unique to echinoderms is the **water vascular system**, a network of hydraulic canals branching into extensions called **tube feet** that function in locomotion and feeding.
- Sexual reproduction in echinoderms usually involves the release of gametes into seawater by separate males and females.
- The internal and external parts of the animal radiate from the center, often as five spokes.
    - The radial anatomy of adult echinoderms is a secondary adaptation, because echinoderm larvae have bilateral symmetry.
- The symmetry of adult echinoderms is not truly radial.
    - For example, the opening (madreporite) of a sea star's water vascular system is not central but shifted to one side.
- Living echinoderms are divided into five clades: Asteroidea (sea stars and sea daisies), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies and feather stars), and Holothuroidea (sea cucumbers).
- Sea stars have multiple arms radiating from a central disk, the undersurfaces of which bear tube feet.
    - By a combination of muscular and chemical actions, tube feet can be attached to or detached from a substrate.
    - Although the base of the tube foot has a flattened disk that resembles a suction cup, the gripping action results from adhesive chemicals, not suction.
- Sea stars use their tube feet to grasp the substrate, to creep slowly over the surface, or to capture prey.
- When feeding on closed bivalves, the sea star grasps the bivalve tightly and everts its stomach through its mouth and into the narrow opening between the shells of the bivalve.
    - Enzymes from the sea star's digestive organs then begin to digest the soft body of the bivalve inside its own shell.
    - The stomach is brought back inside the seastar's body, where digestion of the mollusc's body is completed.

- Sea stars and some other echinoderms can regenerate lost arms and, in a few cases, even regrow an entire body from a single arm if part of the central disk remains attached.
- The clade Asteroidea also includes a small group of armless *sea daisies*.
    - Discovered in 1986, only three species of sea daisies are known.
    - All live on submerged wood.
- A sea daisy's body is typically disk-shaped.
    - It has a five-sided organization and is less than a centimeter in diameter.
    - The edge of the body is ringed with small spines.
- Sea daisies absorb nutrients through a membrane that surrounds their body.
- Brittle stars have a distinct central disk and long, flexible arms.
- The tube feet of brittle stars lack the flattened disks found in sea stars but do secrete adhesive chemicals.
    - Like sea stars and other echinoderms, brittle stars can use their tube feet to grip substrates.
- Brittle stars move by a serpentine lashing of their arms.
- Some brittle stars are suspension feeders, and others are scavengers or predators.
- Sea urchins and sand dollars have no arms, but use five rows of tube feet for locomotion.
    - Sea urchins can also move by pivoting their long spines, which also function in protection.
- The mouth of a sea urchin is ringed by complex jaw-like structures adapted for eating seaweed.
- Sea urchins are roughly spherical, whereas sand dollars are flattened and disk-shaped.
- Sea lilies are attached to the substratum by stalks, and feather stars crawl using their long, flexible arms.
- Both sea lilies and feather stars use their arms for suspension feeding.
    - The arms circle the mouth, which is directed upward away from the substrate.
- Crinoids are an ancient group whose morphology has changed little for 500 million years.
- Sea cucumbers do not look much like other echinoderms: They lack spines, the endoskeleton is much reduced, and the oral-aboral axis is elongated.
- Sea cucumbers have five rows of tube feet like other echinoderms, as well as other shared features.
    - Some tube feet around the mouth function as feeding tentacles for suspension feeding or deposit feeding.

Phylum Chordata: The chordates include two invertebrate subphyla and all vertebrates.

- The phylum to which humans belong consists of two subphyla of invertebrate animals plus the hagfishes and vertebrates.
- Both groups of deuterostomes, echinoderms and chordates, have existed as distinct phyla for over half a billion years.