CHAPTER 18

The Evolution of Animal Diversity

Objectives

Introduction Describe the difficulties of classifying the duck-billed platypus and other Australian mammals.

Animal Evolution and Diversity

18.1 Define animals and distinguish them from other forms of life.
18.1 Describe the general animal life cycle and the basic body plan.
18.2 Describe the five-stage hypothesis for the evolution of animals from protists.
18.2 Describe the Cambrian explosion and list three hypotheses to explain its occurrence.

Invertebrates

18.3–18.15 Describe the characteristics of and distinguish between the following phyla: Porifera, Cnidaria, Platyhelminthes, Nematoda, Mollusca, Annelida, Arthropoda, Echinodermata, Chordata.
18.3–18.15 Distinguish between radially and bilaterally symmetric animals. Note which body type is found in each of the phyla examined in this chapter.
18.7, 18.8 Distinguish between a pseudocoelom and a coelom. Describe the functions of each and note the animal phyla where they occur.
18.10 Define segmentation, explain its functions, and note the animal phyla where it occurs.
18.13 Describe the common characteristics of insects. Distinguish between the seven insect orders described in this chapter.

Vertebrates

18.16 Describe the defining characteristics of vertebrates.
18.17–18.22 Describe the characteristics of and distinguish between the following vertebrate groups: agnathans, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, Mammalia.

Phylogeny of the Animal Kingdom

18.23 Describe the two main classifications of the major animal groups. Explain why there are differences in these two systems.
18.24 Describe the consequences of introduced species in Australia.

Key Terms

kingdom Animalia
ingestion
blastula
gastrula
ectoderm
endoderm
mesoderm
larva
metamorphosis
invertebrate
sponge
Porifera
radial symmetry
choanocyte
amoebocyte
suspension feeder
choanoflagellate
Cnidaria

polyp
medusa
gastrovascular cavity
cnidocyte
bilateral symmetry
anterior
posterior
dorsal
ventral
lateral
flatworm
Platyhelminthes
free-living flatworm
fluke
tapeworm
body cavity
pseudocoelom
coelom
roundworm
Nematoda
mollusk
Mollusca
foot
visceral mass
mantle
radula
gastropod
bivalve
cephalopod
segmentation
Annelida
earthworm
polychaete
leech
Arthropoda
arthropod
exoskeleton
molting
horseshoe crab
arachnid
crustacean
millipede
centipede
entomology
incomplete metamorphosis
complete metamorphosis
echinoderm
Echinodermata
endoskeleton
water vascular system
Chordata
dorsal, hollow nerve cord
notochord
pharyngeal slit
post-anal tail
chordate
vertebrate
tunicate
lancelet
skull
backbone
vertebra
agnathan
Chondrichthyes
Osteichthyes
cartilaginous fish
lateral line system
bony fish
operculum
swim bladder
ray-finned fish
lobe-finned fish
lungfish
Amphibia
Reptilia
amniotic egg
ectothermic
endothermic
Aves
Mammalia
monotreme
placenta
marsupial
placental
eutherian
protostome
deuterostome

Word Roots

choano- = a funnel; **-cyte** = cell (*choanocyte:* flagellated collar cells of a sponge)

cnido- = a nettle (*cnidocytes:* unique cells that function in defense and prey capture in cnidarians)

cuti- = the skin (*cuticle:* the exoskeleton of an arthropod)

deutero- = second (*deuterostome:* one of two distinct evolutionary lines of coelomates characterized by radial, indeterminate cleavage, enterocoelous formation of the coelom, and development of the anus from the blastopore)

echino- = spiny; **-derm** = skin (*echinoderm:* sessile or slow-moving animals with a thin skin that covers an exoskeleton; the group includes sea stars, sea urchins, brittle stars, crinoids, and basket stars)

ecto- = outside; **-derm** = skin (*ectoderm:* the outermost of the three primary germ layers in animal embryos)

endo- = inner; **therm-** = heat (*endotherm:* an animal that uses metabolic energy to maintain a constant body temperature, such as a bird or mammal)

gastro- = stomach; **-vascula** = a little vessel (*gastrovascular cavity:* the central digestive compartment, usually with a single opening that functions as both mouth and anus)

in- = without (*invertebrate:* an animal without a backbone)

marsupi- = a bag, pouch (*marsupial:* a mammal, such as a koala, kangaroo, or opossum, whose young complete their embryonic development inside a maternal pouch called the marsupium)

meso- = middle (*mesoderm:* the middle primary germ layer of an early embryo)

meta- = boundary, turning point; **-morph** = form (*metamorphosis:* the resurgence of development in an animal larva that transforms it into a sexually mature adult)

mono- = one (*monotreme:* an egg-laying mammal, represented by the platypus and echidna)

noto- = the back; **-chord** = a string (*notochord:* a longitudinal, flexible rod formed from dorsal mesoderm and located between the gut and the nerve cord in all chordate embryos)

proto- = first; **-stoma** = mouth (*protostome:* a member of one of two distinct evolutionary lines of coelomates characterized by spiral, determinate cleavage, schizocoelous formation of the coelom, and development of the mouth from the blastopore)

Lecture Outline

Introduction *What Am I?*

A. Most known organisms are animals.
   1. Of the 1.5 million known species, two-thirds are animals. Animal diversity progressed through millions of years of evolution and natural selection.
   2. Humans have a tendency to appreciate and study animals, but what is an animal? Do we know one when we see one and how do we classify different animals?

B. What am I (Figure 18.0)?
   1. The duck-billed platypus was a taxonomic nightmare when initially found by the first Europeans who visited Australia. It lays eggs, has a duck bill and webbed feet . . . it's a bird—no, it has fur, a tail like a beaver, and mammary glands . . . it's a mammal—well . . . a special mammal called a monotreme (an egg-laying mammal)!
   2. Australia is full of special mammals called monotremes and marsupials. The niches that were being filled with placental mammals on other continents were left empty when Australia broke away from Pangaea. Without competition from other placental mammals, monotremes and marsupials filled in the empty niches and became the dominant mammals in Australia.
      Preview: Zoologists distinguish between animals with internal skeletons (vertebrates) and those without internal skeletons (invertebrates). All but one animal phylum (our own, phylum Chordata) are invertebrates (Module 18.15).

I. Animal Evolution and Diversity

Module 18.1 What is an animal?

A. Animals are eukaryotic, multicellular heterotrophs that lack cell walls and obtain nutrition by **ingestion** (Figure 18.1A). This distinguishes animals from fungi that digest their food first and then absorb it. Most animals have muscle cells for movement and nerve cells for sensory perception.

B. The life cycle of most animals includes a dominant, diploid adult that produces eggs or sperm by meiosis. These gametes fuse to form a zygote. The zygote develops into the adult animal, passing through a series of embryonic stages, many of which are shared by most members of the animal kingdom (Figure 18.1).
   Review: This is an example of homology (Module 15.11).

C. In all animals the embryonic stages include the **blastula** (hollow ball of cells) and, in most, a **gastrula** (a saclike embryo with one opening and two layers of cells). Most further develop an additional layer of cells.
Preview: Embryonic development (Modules 27.9–27.15).

D. In many animals, the gastrula develops into one or more immature stages, for example, **larvae** that develop into the sexually mature adults only after **metamorphosis.**
NOTE: Larvae are dispersive stages that help an animal's offspring find suitable habitats before continuing to grow. They are also extremely important sources of food for many other animals in aquatic habitats.

E. Animals have unique types of cell junctions (Module 4.19).

F. Animals are, with the exception of the gametes, composed of diploid cells.

G. Special regulatory genes called *Hox* genes control zygote development. These homeotic genes are present only in animals.

Module 18.2 The animal kingdom probably originated from colonial protists.

A. Fossils of the oldest known animals date from the late Precambrian era, ≈600 mya.

B. A hypothetical evolutionary scenario leading to the first animal proceeds as follows:
1. Colonial protists of a few, identical, flagellated cells
2. Larger, hollow, spherical colonies that ingested organic materials suspended in the water around the colony
3. Colonies with cells specialized for somatic (movement, digestion, etc.) and reproductive functions
4. Differentiated entities with an infolded, temporary digestive region
5. "Protoanimals," completely infolded, with two-layered body walls (Figure 18.2)

C. These protoanimals probably "crawled," feeding on the ocean bottom.

D. The modern animal phyla evolved during the Cambrian period, ≈545 mya, a ten-million-year period of explosive evolution.

E. Three hypotheses explain the rapid expansion of animal diversity during the early Cambrian era:
1. Ecological causes; increased dependency on the predator/prey relationship.
2. Geologic changes; atmospheric oxygen may have reached a critical threshold that was high enough to support the active lifestyle of animals.
3. Genetic causes; the development of the *Hox* genes supported the diversity associated with variations in the spatial and temporal arrangement of the genes during embryonic stages of development.

NOTE: Some mutualistic synthesis of the three hypotheses is likely the correct answer.

II. Invertebrates

Module 18.3 Sponges have relatively simple, porous bodies.

A. **Sponges** are classified in the phylum **Porifera.** Most are marine and live singly, attached to a substrate, and range in height from 1 cm to 2 m (Figure 18.3A).

B. Many sponges are built on a body plan having **radial symmetry,** that is, similar shapes as mirror images around a central axis (Figure 18.3B).

C. The body of a sponge consists of two layers of cells. An inner layer of flagellated cells, called **choanocytes,** surround an inner chamber and sweep the water toward the larger pore; **amoebocytes** produce the skeletal fibers or proteins called spongin (Figure 18.3C). More complex sponges have folded body walls and branched water channels (Figure 18.3D).

D. Sponges feed when the choanocyte flagella beat, creating a flow of water in through the pores, through the collars, trapping bacteria in mucus, and out through the large, upper opening. The choanocytes then phagocytize the food and package it in vacuoles. Amoebocytes pick up the food vacuoles, digest the food, and carry the nutrients to other cells.
Preview: Contrast this with the structure of the digestive system of other animals (Module 21.3).

E. In addition to digesting and distributing food, amoebocytes also transport oxygen, dispose of waste, and manufacture skeletal elements. Further, amoebocytes can change into other cell types.
NOTE: Sponges function as complex colonies of differentiated but interchangeable cells, the amoebocytes being the central cell type that forms most of the others. If a sponge is pressed through a sieve and all the cells and skeletal elements are separated, they will reorganize themselves back into the same layers and similar shape.

F. Sponges are likely to have been a very early offshoot from the multicellular organisms that gave rise to the animals (Figure 18.23). Sponges retain several protistan characteristics, including not having a digestive tract and having intracellular digestion. Developmentally, sponges do not go through a gastrula stage. Sponge cells do not make tissues as in other animals and sponges lack nerves and muscles although individual cells can sense and react to changes in their surroundings.

G. Sponges likely descended from **choanoflagellates** (Figure 18.3E) in the late Precambrian. Choanoflagellates are colonial protists composed entirely of collar cells (choanocytes) but, as protists, they do not show cellular differentiation.

Module 18.4 Cnidarians are radial animals with stinging threads.

A. **Cnidarians** exhibit radial symmetry.

B. These animals may be in the form of a **polyp** (relatively fixed in position) or a **medusa** (swimming), or they may alternate between polyp and medusa forms. Both body plans have a central tubular body (surrounding a **gastrovascular cavity**), one opening ("mouth") into this cavity, and tentacles arranged around the mouth (Figure 18.4A, B, C).

C. Along the tentacles are **cnidocytes** (stinger cells) that function in defense and the capturing of food. The coiled thread in each cell is discharged, stinging or entangling the prey or predator as it brushes against the cnidocyte (Figure 18.4D).

D. Cnidarians trap food with their tentacles, then maneuver it into a gastrovascular cavity where it is digested and distributed throughout the body. Undigested food is eliminated through the mouth.

E. Cnidarians are built at the tissue level of construction, with several different cell types arranged in layers and having common functions. Muscle cells are arranged in groups that allow the body to extend, move tentacles, and contract. Nerve tissue coordinates this movement. But unlike the rest of the animal phyla (except sponges), cnidarians only have two types of embryonic tissue, an outer epidermis and an inner gastrovascular cell layer, no mesoderm.

F. Development includes a gastrula stage, like all the remaining animal phyla.

Module 18.5 Most animals are bilaterally symmetrical.

A. **Bilateral symmetry** means that an animal can be divided into mirror images (left and right sides) by a single plane (Figure 18.5).

B. Associated with bilateral symmetry is the division of the animal into head **(anterior),** tail **(posterior),** back **(dorsal),** bottom **(ventral),** and side **(lateral)** surfaces.

C. The head houses sensory structures and the brain.

D. Bilateral animals are fundamentally different from radial animals. In contrast to radial animals that sit or drift passively, bilateral animals actively move through their environments headfirst. Bilateral symmetry, a head, and forward movement are important evolutionary developments.

Module 18.6 Flatworms are the simplest bilateral animals.

A. **Flatworms** are classified in the phylum **Platyhelminthes** that is composed of approximately 20,000 species. There are three major groups of flatworms: **free-living** planarians that live on rocks in marine and fresh water, parasitic **flukes,** and tapeworms.

B. Like cnidarians, planarians and most flukes have a gastrovascular cavity and no other body cavities. The body normally has a head end with a concentration of sensory nerves. The mouth opens from the ventral surface and the gastrovascular cavity branches through the entire length of the body (Figure 18.6A).
NOTE: Flatworms are not quite at the organ level of construction.

C. Most flukes have a complex life cycle, including reproduction in more than one host and one or more larval stages. *Schistosoma* (blood fluke) adults live and permanently mate inside blood vessels, where they feed on blood. As many as 1000 fertilized eggs a day are produced, and they leave through the host's intestine. The eggs grow into larvae that infect snails. Asexual reproduction in the snail produces different larvae that infect humans (Figure 18.6B).

D. **Tapeworms** are highly adapted parasites that inhabit the digestive tracts of their hosts. Unlike other flatworms, tapeworms are segmented and lack a gastrovascular cavity, absorbing their predigested food directly. The anterior end (the head) attaches to the host with hooks and suckers, and a region behind generates segments. Sexual reproduction occurs in each segment; the oldest segments break off and leave the host via the feces. Many tapeworms produce larvae that infect the prey animal, while the adult tapeworms infect that prey animal's predator (Figure 18.6C).

Module 18.7 Most animals have a body cavity.

A. *Review:* Animal development (Figure 18.1).

B. Depending on how tissue regions develop from the gastrula stage, three body plans exist among animal phyla:

   1. The body is solid, except for the gastrovascular cavity, as in flatworms and cnidaria (Figures 18.7A).
   2. The body contains a **pseudocoelom,** an internal space in direct contact with the inner layer of the digestive tract, as in roundworms (Figures 18.7B).
   3. The body contains a **coelom,** an internal space completely lined by tissue of the middle layer, as in all other animals. (Figures 18.7C).

C. For each body plan, the skin and other outer layers develop from the outside of the gastrula, the inner lining of the digestive tract or gastrovascular cavity (yellow) develops from the inside of the gastrula, and the middle layer (pink) develops from outgrowths of the inner layer.

D. *Preview:* Two different paths of development of the middle layer distinguish two lines of animal evolution (Figure 18.23).

E. Advantages of having a **body cavity** include having greater flexibility, cushioning of internal organs, and providing room for internal organ growth.

F. In some animals (like earthworms), body cavities under pressure function as a skeleton.

G. The fluid in the cavity circulates nutrients and oxygen and aids in waste collection and disposal.

Module 18.8 Roundworms have a pseudocoelom and a complete digestive tract.

A. **Roundworms,** classified in the phylum **Nematoda,** are numerous and diverse in most environments. Most are important decomposers or parasites of plants or animals.

B. The roundworm body is cylindrical, includes a complete intestinal tract, and is covered by a tough, nonliving **cuticle** (Figure 18.8A).

C. Food passes in one direction along a digestive tract that includes regions specialized for certain functions: food intake, breakup, digestion, and absorption, and waste elimination. *NOTE:* Roundworms are tending toward the organ level of construction.

D. One free-living species, *Caenorhabditis elegans,* is an important organism for genetic research and one of the best-understood organisms. Researchers have been able to trace the developmental lineage of each of an adult's 1000 cells.

E. Trichinosis is a disease caused by the roundworm *Trichinella spiralis.* Humans get this parasite by eating raw pork (Figure 18.8B).

Module 18.9 Diverse mollusks are variations on a common body plan.

A. **Mollusks** are classified in the phylum **Mollusca.**

B. The basic body plan of a mollusk includes bilateral symmetry, a complete digestive tract, a coelom, and many internal organs.

C. Two distinctive characteristics of the phylum are a muscular **"foot"** and a **mantle,** an outgrowth of the body surface that drapes over the animal, functions in sensory reception, often secretes a shell, and usually houses gills that function in gas exchange and waste removal.

D. Mollusks also have a true circulatory system (in contrast to the circulatory function of the gastrovascular cavity of cnidarians and flatworms, and the pseudocoelom of roundworms) and separate sex organs. The life cycle includes a ciliated larva called a trochophore, a trait used in taxonomy.

E. Most have a **radula,** an organ used to scrape food, such as algae, off surfaces in the environment (Figure 18.9A).

F. Evolution has modified the basic body plan in different groups of mollusks. **Gastropods** include snails and slugs. **Bivalves** include clams, scallops, and oysters. Cephalopods include octopuses and squids (Figure 18.9B–F).

G. **Cephalopods** are built for speed, and have large brains and sophisticated sense organs, especially their eyes, which can focus a clear image on the retina.

Module 18.10 Many animals have a segmented body.

A. **Segmentation** is the subdivision of the body into repeated parts

B. The segments in an earthworm are clearly visible from the outside, outlining the repeating pattern of organs inside. The nervous, circulatory, and excretory systems all have repeating, mostly identical, parts in each segment (Figure 18.10A).

C. In other animals, segmentation may involve fewer segments or be less obvious (Figure 18.10B, C).

D. Advantages of segmentation include greater body flexibility and mobility. For example, in the earthworm, rhythmic alternating contractions and elongations of segments propel the worm into or along the ground. In many animals, the segments are the sites of insertion of walking legs or muscles.
NOTE: There are two important evolutionary advantages. Genetically speaking, it is easier to build a large, complex animal by repeating a single developmental sequence in many smaller units than by following a longer sequence of developmental steps for the whole region. Also, during evolution, animal groups (polychaete annelids, the insects and other arthropods, and the chordates) have segments specialized into different functional regions, working from a basic pattern; segments are often fused. But how did segmentation evolve? This is a question that is currently being debated among evolutionists and the answer may be found in the field of evo-devo.

Module 18.11 Earthworms and other annelids are segmented worms.

A. These worms are classified in the phylum **Annelida.** They live in the sea, in most freshwater habitats, and in damp soil. Annelids usually have one or more anterior segments specially modified into a head region.

B. **Earthworms** are one group of **annelids** adapted to life in soil. They consume the soil, digest the organic parts, and eliminate undigested soil and other waste products in their feces, improving soil texture in the process.

C. **Polychaete** worms are mostly marine inhabitants. They are characterized by segmental appendages with broad, paddlelike appendages and bristles. Some polychaetes show modification of anterior segments (Figure 18.11A, B). The appendages also increase the surface-to-volume ratio and increase O_2 uptake and waste removal.

D. **Leeches** are free-living carnivores of aquatic animals or blood-sucking parasites on vertebrates (Figure 18.11C). A blood-sucking leech cuts the skin with razor-sharp jaws and secretes an anesthetic and an anticoagulant. Leeches are still used in medicine, and their anticoagulants are being produced by genetic engineering.

Module 18.12 Arthropods are the most numerous and widespread of all animals.

A. In terms of diversity, geographical distribution, and sheer numbers, the phylum **Arthropoda** is the most successful that has ever lived.

B. Based on the presence of Cambrian fossils that display characteristics of both annelids and **arthropods,** it has been thought that arthropods evolved from annelids or segmented ancestors of annelids.

C. However, molecular evidence indicates that annelids and arthropods independently evolved from bilaterally symmetrical and segmented animals.

D. Arthropods are segmented (often fused), have jointed appendages, and have an **exoskeleton** composed of chitin and proteins (Figure 18.12A).
Preview: To facilitate movement, muscle tissue is attached to the inside of the exoskeleton (Module 30.2).

E. To grow, arthropods **molt** their exoskeleton, swell in size, and secrete a new, developing exoskeleton.

F. **Horseshoe crabs** are "living fossil" life forms that have survived for hundreds of millions of years with little change (see Module 14.8: equilibrium). A very close relative of the modern genus was abundant 300 mya (Figure 18.12B).

G. **Arachnids** include scorpions, spiders, ticks, and mites. Their ancestors were among the first terrestrial carnivores. Except for mites, arachnids are carnivores (Figure 18.12C).

H. **Crustaceans** include crabs, shrimps, lobsters, crayfish, and barnacles; they are mostly aquatic (Figure 18.12D).

I. **Millipedes** have segments with two pairs of appendages each and feed on decaying plants. **Centipedes** have segments with one pair of appendages each and are carnivorous. Both groups are terrestrial (Figure 18.12E).

Module 18.13 Insects are the most diverse group of organisms.

A. About one million insect species are known to biologists (**entomologists** are biologists who study insects), representing perhaps half of those that exist. Insects have been important aspects of terrestrial life for 400 million years, less so in aquatic and, especially, marine habitats.

B. Insects are united as a group in having a three-part body plan: head, thorax, and abdomen. The head has sensory appendages and mouthparts specialized for a particular diet. The thorax contains three pairs of walking legs and, usually, one or two pairs of wings (Figure 18.13A). The abdomen houses digestive and reproductive organs.

C. Metamorphosis is common to many insects. **Incomplete metamorphosis** (Orthoptera, Odonata, and Hemiptera) results in an adult that resembles the young but is larger and has different body proportions. **Complete metamorphosis** (Coleoptera, Lepidoptera, Diptera, Hymenoptera) occurs when a larval form specialized for eating and growing develops into a very different adult form that is specialized for reproduction and dispersal.

D. Grasshoppers (order Orthoptera) have biting and chewing mouthparts. Most species are herbivorous (mantids are an exception). They have two pairs of wings. The forewing is thickened and the hind wing is membranous.

E. Damselflies and dragonflies (order Odonata) have biting mouthparts and are carnivorous. They have two identical pairs of wings (Figure 18.13B).

F. True bugs (order Hemiptera) have piercing, sucking mouthparts, and most species feed on plant sap (bedbugs feed on blood). They have two pairs of wings (Figure 18.13C).

G. Beetles make up the largest order (Coleoptera) in the animal kingdom, with some 500,000 species known worldwide from all types of habitats. They have biting and chewing mouthparts, and are carnivorous, omnivorous, or herbivorous. They have two pairs of wings, and the forewings serve as protective covering for the hindwings (Figure 18.13D).

H. Moths and butterflies (order Lepidoptera) are the second most numerous insects. They have drinking-tube mouthparts for sipping nectar or other liquids, and have two pairs of scale-covered wings (Figure 18.13E).

I. Flies, gnats, and mosquitoes (order Diptera) have lapping mouthparts and feed on nectar or other liquids (mosquitoes have piercing, sucking mouthparts and suck blood). They have a single pair of functional wings, with the hindwings reduced to halteres to maintain balance (Figure 18.13F).

J. Ants, bees, and wasps (order Hymenoptera) are the third most numerous insects. They have chewing and sucking mouthparts, and many are herbivorous. They have two pairs of wings. Many in this group display complex behavior and social organization (Figure 18.13G).
NOTE: These social groups function as "superorganisms." Some aspects of their social behavior are covered in Chapter 37.

Module 18.14 Echinoderms have spiny skin, an endoskeleton, and a water vascular system for movement.

A. The phylum **Echinodermata** includes sea stars, sand dollars, and sea urchins (all marine) and represents a second branch of evolution in the animal kingdom. Similarities in embryonic development suggest that this phylum is closely related to our own, the phylum Chordata.

B. **Echinoderms** lack segmentation and bilateral symmetry as adults, but larvae are bilaterally symmetrical. Members of this phylum are noted for their regenerative capacity. Most have tubular **endoskeletons** composed of fused plates lying just under the skin. Unique to this phylum is the presence of a **water vascular system.** This is a network of water-filled canals that branch into extensions called tube feet that function in movement, ingestion, and gas exchange (Figure 18.14A).

C. Sea stars have flexible "arms" that bear the tube feet. They wrap these arms around a bivalve prey, pull the valves apart, extrude their stomach out their mouth and into the opening, and digest the soft parts (Figure 18.14B).

D. Sea urchins are spherical, with five double rows of tube feet running radially, with which they pull themselves along. They eat algae (Figure 18.14C).

Module 18.15 Our own phylum, **Chordata,** is distinguished by four features.

A. A **dorsal, hollow nerve cord.**

B. A **notochord:** a flexible, longitudinal rod located between the digestive tract and the nerve cord.

C. **Pharyngeal slits,** which are gill structures (slits and supports) in the pharynx region behind the mouth.

D. A muscular **post-anal tail.**

E. The most diverse **chordates** are vertebrates. However, there are several invertebrate groups in this phylum.

F. **Lancelets** are small, bladelike chordates that live anchored by their tails in marine sands and expose their heads and mouths, filtering and trapping organic particles in mucus around the gill slits. These animals show the clearest presentation of the chordate body plan (Figure 18.15B). Molecular evidence indicates that lancelets are the closest living relatives of vertebrates.

H. **Tunicates** (sea squirts) are another group of marine chordates (Figure 18.15A). As adults, they do not exhibit the chordate pattern of notochord and nerve cord. As stationary filter feeders, they use gill slits much like lancelets do. Larval tunicates exhibit the complete chordate pattern and look very much like adult lancelets. It is likely that during the Cambrian (500 mya), by paedomorphosis (Module 15.7), vertebrates evolved from chordates similar to larval tunicates.

III. Vertebrates

Module 18.16 A skull and a backbone are hallmarks of vertebrates.

A. A **skull** forms a case for the brain (Figure 18.16).

B. A segmented **backbone** composed of vertebrae encloses the nerve cord.

C. Most **vertebrates** have skeletal support for paired appendages (fins, legs, arms, wings).

D. The vertebrate skeleton is an endoskeleton of cartilage or bone. These nonliving materials contain living cells and grow as the animal grows, unlike the exoskeletons of arthropods, which must be molted prior to growth.

Module 18.17 Most vertebrates have hinged jaws.

A. One group of vertebrates, the lampreys (class **Agnatha**), lack jaws but have skeletal supports between their gill slits, and they lack paired appendages. Otherwise, they are superficially similar to fishes. Most are parasites on fish, boring a hole in the host and sucking its blood (Figure 18.17A).

B. Jaws evolved by modification of the first two pairs of skeletal supports of the gill slits. Similar events occur during the embryonic development of all fishes today (Figure 18.17B).

C. The oldest fossils of jawed vertebrates appear in rocks that were formed 450 mya. Jaws enabled vertebrates (mostly fish) to catch and consume a wider variety of foods than were available to filter feeders, thus replacing them (the agnathans).

Module 18.18 Fishes are jawed vertebrates with gills and paired fins.

A. Fish extract oxygen from water with their gills. Their paired fins help stabilize their bodies (Figure 18.18C).

B. The **cartilaginous fishes** (class **Chondrichthyes**) include the sharks and rays and have skeletons of flexible cartilage. Sharks have a keen sense of smell and sharp vision, and can sense minute vibrations with a pressure-sensitive **lateral line system.** Because they cannot pump water through the gills, they must swim in order to move the water (Figure 18.18A).

C. **Bony fishes** (class **Osteichthyes**) are more common and diverse and have a stiff skeleton of bone reinforced by hard calcium salts. Like sharks, they have a keen sense of smell and a lateral line system. They also have a keen sense of sight, and a bony flap over the gills called an **operculum** that helps move water through the gills when the fish is stationary (Figure 18.18B).

D. Bony fish also have a **swim bladder** that can act as a buoyant counter-balance to their heavier bones. Sometimes this is connected to the digestive tract, enabling certain species to gulp air to increase oxygen intake.

E. Bony fish, the largest class of vertebrates, are divided into two groups, the **ray-finned fish** and the **lobe-finned fish.** Thin, flexible skeletal rays support the fins of ray-finned fishes. The fins of lobe-finned fishes are muscular and supported by bones.

Module 18.19 Amphibians were the first land vertebrates.

A. **Amphibians** include frogs, toads, and salamanders.

B. Most amphibians are tied to water because their eggs and larvae (tadpoles) develop in water.

C. Tadpoles are aquatic, legless scavengers with gills, a tail, and a lateral line system (Figure 18.19A).

D. They undergo a radical metamorphosis (Figure 18.19B) to change into an adult that is often a terrestrial hunter, with paired legs, external eardrums, air-breathing lungs, and no lateral line (Figure 18.19C).

E. The documented decline of the amphibian population worldwide over the last 25 years has zoologists concerned. The decline may be attributable to acid rains that harm the eggs and larvae of amphibians (review Module 2.16).

F. Amphibians were the first land vertebrates and evolved about 400 mya from either lobed-finned fishes or lungfishes. Structurally, ancestral lobe-finned fish had strong fins, which may have been used to paddle and wriggle over dense vegetation, and saclike lungs (and gills). Molecular evidence indicates that ancestral lungfishes, which also had saclike lungs, gave rise to the first land vertebrates. A good example of a transition animal (from fish to amphibian) is the fossil record of Acanthostega, a four-legged fish from the Devonian era (Figure 18.19D).

G. Early amphibians thrived on insects and other invertebrates in the coal-producing forests of the Carboniferous period (Module 17.7). This period is known as the Age of Amphibians.

Module 18.20 Reptiles have more terrestrial adaptations than amphibians.

A. **Reptiles** include snakes, lizards, turtles, alligators, and crocodilians. Lizards are the most numerous and diverse reptile group, crocodiles and alligators are the largest, snakes likely descended from lizards, and turtles have changed little since they evolved. *Review:* Reptiles are not a monophyletic group. Cladistic analysis groups birds with crocodiles and lizards with snakes, and places the turtles in another clade (Module 15.13).

B. Reptiles have skin protected with protein (keratin), eggs with coatings that retain water, an internal fluid-filled sac (amnion) that bathes the embryo, and a food supply (yolk) in the **amniotic egg.** The young hatch as juveniles, bypassing the need for free-living larvae (Figure 18.20A).

C. Most modern reptiles are **ectothermic.** They warm up by absorbing external heat, rather than generating much of their own metabolic heat as **endothermic** animals do (Figure 18.20B).

D. Following the decline of prehistoric amphibians, reptilian lineages expanded and dominated Earth during the Age of Reptiles (200–65 mya). These dinosaurs may have been endothermic (Figure 18.20C).

E. When the dinosaurs died off ≈65 mya (Module 15.5), one line survived and evolved into birds.

Module 18.21 Birds share many features with their reptilian ancestors.

A. Birds (class **Aves**) have amniotic eggs, scales on their legs, and a reptilian body form. They evolved from one line of dinosaurs 150–200 mya.

B. Feathers, the most distinctive characteristic of birds, are derived from scales. Feathers shape bird wings into airfoils that create lift and enable birds to maneuver in the air.

C. *Archaeopteryx* is an extinct bird, with feathers and characteristics of bipedal dinosaurs such as teeth, claws, and a tail with many vertebrae (Figure 18.21A). With its heavy body, *Archaeopteryx* is more likely to have been a glider than a flier. *Archaeopteryx* is not the ancestor of modern birds.

D. Many bird groups became extinct about 65 mya, along with the rest of the dinosaurs. Thus, the bird lineage appears to have gone through a bottleneck (Module 13.11) about 65 mya (the 65-mya mass extinction) and modern birds evolved from a very few surviving groups.

E. Modern birds have additional adaptations for flight, including an absence of teeth, no claws on their wings, very short tailbones, hollow bones, large breast muscles, efficient lungs, and an extremely high rate of metabolism to provide energy. Birds also have relatively large brains and possibly the best vision of all vertebrates (Figure 18.21B). Birds are fabulous fliers, though some birds are flightless (Figure 18.21C).

Module 18.22 Mammals also evolved from reptiles.

A. **Mammals** evolved from very early reptiles, about 225 mya, but occupied minor parts of habitats during the Age of Reptiles. Once the dinosaurs died off, the mammalian lineages underwent adaptive radiation.
Review: Adaptive radiation (Module 14.4).

B. Most mammals are terrestrial, with a number of winged and totally aquatic species. The largest animal that has ever existed is the blue whale, a species that can reach 30 m in length.

C. Mammals are endothermic, and they have hair and mammary glands.

D. The **monotremes,** such as the platypus, are egg-laying mammals that live in Australia and Tasmania (Figure 18.22A).

E. The **marsupials,** such as the American opossum and the kangaroo, give birth to embryonic young that complete development in their mother's pouch. Most marsupials live in Australia, on neighboring islands, and in Central and South America (Figure 18.22B).
NOTE: Both groups evolved in isolation from other mammals in areas that were part of the Pangaean supercontinent, Gondwana (see Module 15.3).

F. The **eutherians (placentals),** comprising nearly 95% of all mammalian species, include dogs, cats, cows, rodents, bats, and whales. Their embryos are nurtured inside the mother by a **placenta,** an organ that includes both maternal and embryonic vascular tissue (Figure 18.22C).

G. Humans are eutherian mammals belonging to the order Primates. The relationship of humans to other primates is discussed in Chapter 19.

H. *Preview:* Unit V will cover many other details of the lives of animals, emphasizing humans, mammals, and vertebrates, in that order.

IV. Phylogeny of the Animal Kingdom

Module 18.23 A phylogenetic tree gives animal diversity an evolutionary perspective.

A. Construction of a phylogenetic tree should be based on several lines of evidence such as molecular data, comparative anatomy, embryonic development, cladistic analysis, and, of course, fossil records.

B. Figure 18.23A conveniently illustrates the major evolutionary steps of the animal phyla in a phylogenetic tree using a traditional approach.

1. Like most phylogenetic trees, this one is hypothetical and serves mainly to stimulate research and focus discussion.
2. Colonial protists were the ancestors of the animal kingdom.
3. Sponges may be a separate line of evolution, or a very early side lineage.
4. Two lines of tissue-level animals evolved: radially symmetrical animals, represented by cnidarians, and bilaterally symmetrical animals, the most primitive of which are represented by the flatworms.
5. Among the bilateral animals, two lines evolved: those with pseudocoeloms, represented by the roundworms, and those with coeloms, the most primitive of which are represented by the mollusks.
6. Among the coelomate animals, two lines evolved: those whose coelom developed from hollow outgrowths of the digestive tube—the echinoderms and chordates (deuterostomes); and those whose coelom developed from solid masses of cells—the mollusks, annelids, and arthropods (protostomes).

C. There is a debate regarding the development of segmentation and how often it evolved in animal evolution.

1. Echinoderms, which are not segmented, and chordates may have diverged prior to segmentation; or segmentation may have been lost in the echinoderms as they evolved radial symmetry.
2. Likewise, segmentation may have evolved in annelids and arthropods after the mollusks diverged; or segmentation may have been lost during the evolution of the mollusk lineage.
3. Segmentation itself may have evolved independently in the **deuterostome** and **protostome** lineages.
4. Molecular evidence indicates that segmentation arose early in the history of animal evolution, possibly in the ancestor of all bilateral animals. In this case segmentation, or its lack, may be due to genes that affect early development.

D. The molecular phylogenetic tree is based on nucleotide sequence data from rRNA (Figure 18.23B).

1. There are several similarities between the traditional tree and the molecular-based tree. For example the earliest branching in both trees recognizes those that have true tissues and those that do not. Bilateral and radial symmetry is a branch point in both trees. Deuterostomes are recognized in both trees.
2. One major difference in the molecular tree is that the protostomes are divided into two separate branches: the Lophotrochozoa have similarities in molecular sequence data and are named for the feeding apparatus and larva. The other branch of the protostomes, the Ecdysozoa, share a common feature: They need to shed their exoskeleton.
   Review: Gene expression and embryonic development (Chapter 11).

Module 18.24 Connections: Humans threaten animal diversity by introducing non-native species.

A. The introduction of a nonnative species to a new environment can result in only two scenarios: The species will die, or it will survive and have devastating effects on the ecosystem into which it was introduced.

B. Rabbits, foxes, and cane toads have been introduced to Australia and all three have ended in the second scenario.

C. Millions of dollars are now being spent each year by the Australian government in an effort to combat the ecological disaster caused by human intervention.

Class Activities

1. Ask your students to consider the advantages (and disadvantages) of cephalization. While this seems like a simple question, I find that students often struggle with developing a scientifically sound response.
2. To have your class gain a real appreciation of insect diversity, have your students start an insect collection.

Transparency Acetates

Media

See the beginning of this book for a complete description of all media available for instructors and students. Animations and videos are available in the Campbell Image Presentation Library. Media Activities and Thinking as a Scientist investigations are available on the student CD-ROM and web site.

Animations and Videos	File Name
Hydra Releasing Sperm Video	18-04A-HydraSpermVideo-B.mov
Hydra Releasing Sperm Video	18-04A-HydraSpermVideo-S.mov
Jelly Swimming Video	18-04B-JellySwimmingVideo-B.mov
Jelly Swimming Video	18-04B-JellySwimmingVideo-S.mov
Thimble Jellies Video	18-04B-ThimbleJellyVideo-B.mov
Thimble Jellies Video	18-04B-ThimbleJellyVideo-S.mov
Hydra Eating Water Flea Time-Lapse Video	18-04D-HydraEatingVideo-B.mov
Hydra Eating Water Flea Time-Lapse Video	18-04D-HydraEatingVideo-S.mov
C. elegans Crawling Video	18-08A-CelegansCrawlVideo-B.mov
C. elegans Crawling Video	18-08A-CelegansCrawlVideo-S.mov
C. elegans Embryo Development Time-Lapse Video	18-08A-CelegansDevelVideo-S.mov
Sea Slugs Video	18-09C-SeaSlugsVideo-B.mov
Sea Slugs Video	18-09C-SeaSlugsVideo-S.mov
Lobster Mouth Parts Close Up Video	18-12A-LobsterMouthVideo-B.mov
Lobster Mouth Parts Close Up Video	18-12A-LobsterMouthVideo-S.mov
Butterfly Emerging Video	18-13E-ButterflyVideo-B.mov
Butterfly Emerging Video	18-13E-ButterflyVideo-S.mov
Echinoderm Tube Feet Video	18-14B-EchinTubeFeetVideo-B.mov
Echinoderm Tube Feet Video	18-14B-EchinTubeFeetVideo-S.mov
Manta Ray Video	18-18A-MantaRayVideo-B.mov
Manta Ray Video	18-18A-MantaRayVideo-S.mov
Bat Licking Nectar Video	18-22-BatLickingVideo-B.mov
Bat Licking Nectar Video	18-22-BatLickingVideo-S.mov

Activities and Thinking as a Scientist	Module Number
Web/CD Activity 18A: *Characteristics of Invertebrates*	18.14
Web/CD Activity 18B: *Characteristics of Chordates*	18.22
Web/CD Activity 18C: *Animal Phylogenetic Tree*	18.23
Web/CD Thinking as a Scientist: *How Are Insect Species Identified?*	18.13
Web/CD Thinking as a Scientist: *How Does Bone Structure Shed Light on the Origin of Birds?*	18.21
Web/CD Thinking as a Scientist: *How Do Molecular Data Fit Traditional Phylogenies?*	18.23