

Chapter 32

Overview of Animal Diversity

Chapter Outline

- 32.1 Some General Features of Animals
- 32.2 Evolution of the Animal Body Plan
- 32.3 The Classification of Animals
- 32.4 The Roots of the Animal Tree of Life



Introduction

We now explore the great diversity of modern animals, the result of a long evolutionary history. Animals are among the most abundant living organisms. Found in almost every habitat, they bewilder us with their diversity in form, habitat, behavior, and lifestyle. About a million and a half species have been described, and several million more are thought to await discovery. Despite their great diversity, animals have much in common. For example, locomotion is a distinctive characteristic, although not all animals can move about. Early naturalists thought that sponges and corals were plants because the adults are attached to the surface on which they live.

32.1 Some General Features of Animals

Learning Outcome

1. Identify three features that characterize all animals and three that characterize only some types of animals.

Animals are so diverse that few criteria fit them all. But some, such as animals being eaters, or consumers, apply to all. Others, such as their being mobile (they can move about) have excep-

tions. Taken together, the universal characteristics and other features of major importance that have exceptions are convincing evidence that animals are monophyletic—that they descended from a common ancestor. Table 32.1 describes the general features of animals.

Learning Outcome Review 32.1

All animals are multicellular and heterotrophic, and their cells lack cell walls. Most animals can move from place to place, can reproduce sexually, and possess unique tissues. Animals can be found in almost all habitats.

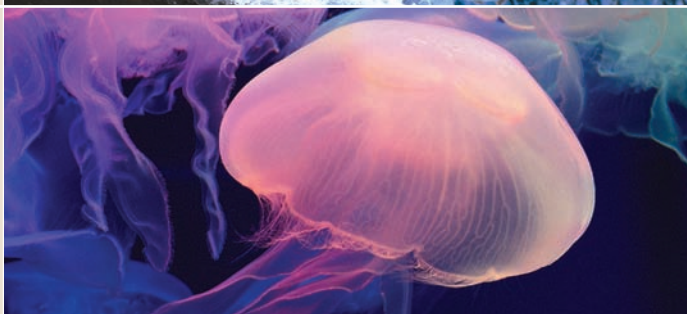
- What evidence is there that animals could not have been the first type of life to have evolved?

TABLE 32.1 General Features of Animals

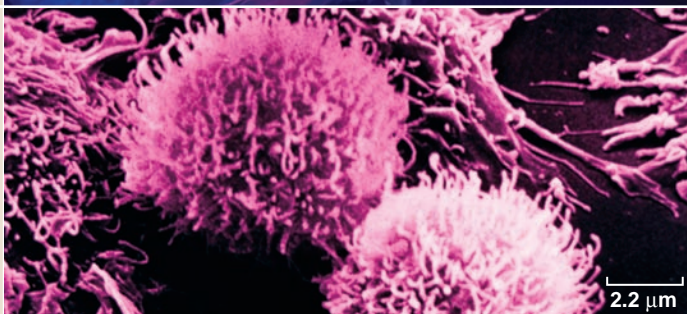
Heterotrophy. All animals are heterotrophs—that is, they obtain energy and organic molecules by ingesting other organisms. Unlike autotrophic plants and algae, animals cannot construct organic molecules from inorganic chemicals. Some animals (herbivores) consume autotrophs; other animals (carnivores) consume heterotrophs; some animals (omnivores) consume both autotrophs and heterotrophs; and still others (detritivores) consume decomposing organisms.



Multicellularity. All animals are multicellular; many have complex bodies like that of this jellyfish (phylum Cnidaria). The unicellular heterotrophic organisms called Protozoa, which were at one time regarded as simple animals, are now considered members of the large and diverse kingdom Protista, discussed in chapter 29.



No Cell Walls. Animal cells differ from those of other multicellular organisms: they lack rigid cell walls and are usually quite flexible. The many cells of animal bodies are held together by extracellular frames of structural proteins such as collagen. Other proteins form unique intercellular junctions between animal cells.



Active Movement. Animals move more rapidly and in more complex ways than members of other kingdoms—this ability is perhaps their most striking characteristic, one directly related to the flexibility of their cells and the evolution of nerve and muscle tissues. A remarkable form of movement unique to animals is flying, a capability that is well developed among vertebrates and insects such as this butterfly (phylum Arthropoda). Many animals cannot move from place to place (they are sessile) or do so rarely or slowly (they are sedentary) although they have muscles or muscle fibers that allow parts of their bodies to move. Sponges, however, have little capacity for movement.



TABLE 32.1 General Features of Animals, *continued*

Diversity in Form. Animals vary greatly in form, ranging in size from organisms too small to see with the unaided eye to enormous whales and giant squids. Almost all animals, like this millipede (phylum Arthropoda), lack a backbone—they are therefore called invertebrates. Of the million known living animal species, only 42,500 have a backbone—they are therefore referred to as **vertebrates**. Probably most of the many millions of animal species awaiting discovery are invertebrates.



Diversity in Habitat. The animal kingdom is divided into 35–40 phyla, most of which have members that occur only in the sea like this brittlestar (phylum Echinodermata). Members of fewer phyla occur in fresh water, and members of fewer still occur on land. Members of three phyla that are successful in the marine environment—Arthropoda, Mollusca, and Chordata—also dominate animal life on land. Only one animal phylum, Onychophora (velvet worms) is entirely terrestrial.



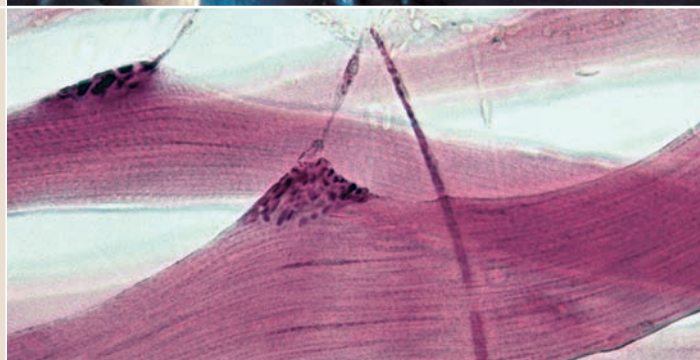
Sexual Reproduction. Most animals reproduce sexually; these tortoises (phylum Chordata) are engaging in the first step of that process. Animal eggs, which are nonmobile, are much larger than the small, usually flagellated sperm. In animals, cells formed in meiosis function as gametes. These haploid cells do not divide by mitosis first, as they do in plants and fungi, but rather fuse directly with each other to form the zygote. Consequently, there is no counterpart among animals to the alternation of haploid (gametophyte) and diploid (sporophyte) generations characteristic of plants. Some individuals of some species and all individuals of a very few animal species are incapable of sexual reproduction.



Embryonic Development. An animal zygote first undergoes a series of mitotic divisions, called *cleavage*, and like this dividing frog's egg, that produces a ball of cells, the **blastula**. In most animals, the blastula folds inward at one point to form a hollow sac with an opening at one end called the **blastopore**. An embryo at this stage is called a **gastrula**. The subsequent growth and movement of the cells of the gastrula differ from one group of animals to another, reflecting the evolutionary history of the group. Embryos of most kinds of animals develop into a larva, which looks unlike the adult of the species, lives in a different habitat, and eats different sorts of food; in most groups, it is very small. A larva undergoes metamorphosis, a radical reorganization, to transform into the adult body form.



Tissues. The cells of all animals except sponges are organized into structural and functional units called **tissues**, collections of cells that together are specialized to perform specific tasks. Animals are unique in having two tissues associated with movement: (1) muscle tissue, which contracts, and (2) nervous tissue, which conducts signals among cells. Neuromuscular junctions, where nerves connect with muscle tissue, are shown here.



32.2 Evolution of the Animal Body Plan

Learning Outcomes

1. Differentiate between a pseudocoelom and a coelom.
2. Explain the difference between protostomes and deuterostomes.
3. Describe the advantages of segmentation.

The features described in the preceding section evolved over the course of millions of years. We can understand how the history of life has proceeded by examining the types of animal bodies and body plans present in fossils and in existence today.

Five key innovations can be noted in animal evolution:

1. The evolution of symmetry
2. The evolution of tissues, allowing specialized structures and functions
3. The evolution of a body cavity
4. The evolution of various patterns of embryonic development
5. The evolution of segmentation, or repeated body units

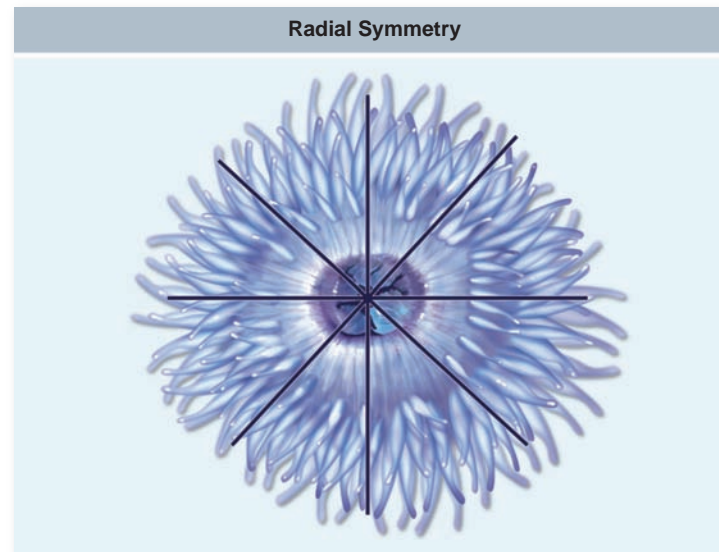
These innovations are explained in the sections that follow. Some innovations appear to have evolved only once, some twice or more. Scientists use an innovation that evolved once as evidence that all the animals possessing it are more closely related to one another than they are to any animal lacking the innovation. The animals with the innovation and their ancestor in which the innovation arose are said to constitute a clade—an evolutionarily coherent group (see chapter 23). On the other hand, some innovations evolve more than once in different clades. This is the phenomenon of convergent evolution (see chapter 23). Although not indicative of close evolutionary relationship, convergently evolved innovations may be important to how species have adapted to their environments.

Most animals exhibit radial or bilateral symmetry

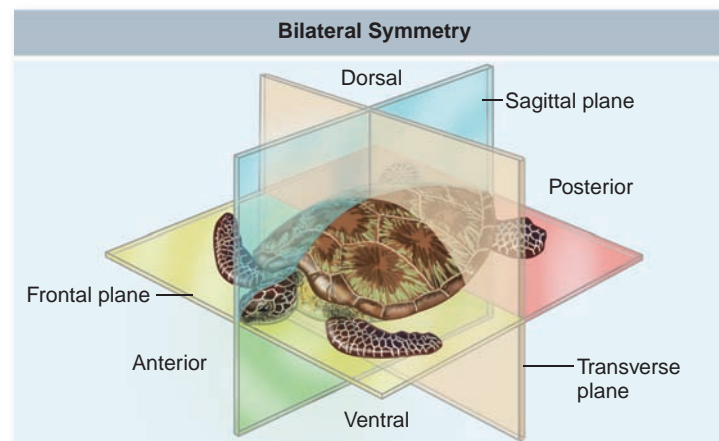
A typical sponge lacks definite symmetry, growing as an irregular mass. Virtually all other animals have a definite shape and symmetry that can be defined along an imaginary axis drawn through the animal's body. The two main types of symmetry are radial and bilateral.

Radial symmetry

The body of a member of phylum Cnidaria (jellyfish, sea anemones, and corals: the C of Cnidaria is silent; see chapter 34) exhibits **radial symmetry**. Its parts are arranged in such a way that any longitudinal plane passing through the central axis divides the organism into halves that are approximate mirror images (figure 32.1*a*). A pie, for example, is radially symmetrical. In cnidarians such as corals and sea anemones, the mouth is not circular, but oval, because it opens into a sort of throat that is like a flattened sleeve. Thus there are two planes that divide the body into mirror-



a.



b.

Figure 32.1 A comparison of radial and bilateral symmetry. *a.* Radially symmetrical animals, such as this sea anemone (phylum Cnidaria), can be bisected into equal halves by any longitudinal plane that passes through the central axis. *b.* Bilaterally symmetrical animals, such as this turtle (phylum Chordata), can only be bisected into equal halves in one plane (the sagittal plane).

image halves, one along the mouth and one perpendicular to it; these animals are actually biradially symmetrical (figure 32.1*b*).

Bilateral symmetry

The bodies of most animals other than sponges and cnidarians exhibit **bilateral symmetry**, in which the body has right and left halves that are mirror images of each other. Animals with this body plan are collectively termed the Bilateria. The sagittal plane defines these halves. A bilaterally symmetrical body has, in addition to left and right halves, dorsal and ventral portions, which are divided by the frontal plane, and anterior (front) and posterior (rear) ends, which are divided by the transverse plane (in an animal that walks on all fours, dorsal is the top side). In echinoderms (sea stars and their relatives), adults are radially symmetrical (actually pentaradially symmetrical, because the body has five clear sections), but the larvae are bilaterally symmetrical.

Bilateral symmetry constitutes a major evolutionary advance in the animal body plan. Bilaterally symmetrical animals have the ability to move through the environment in a consistent direction (typically with the anterior end leading)—a feat that is difficult for radially symmetrical animals. Associated with directional movement is the grouping of nerve cells into a brain, and sensory structures, such as eyes and ears, at the anterior end of the body. This concentration of nervous tissue at the anterior end, which appears to have occurred early in evolution, is called **cephalization**. Much of the layout of the nervous system in bilaterally symmetrical animals is centered on one or more major longitudinal nerve cords that transmit information from the anterior sense organs and brain to the rest of the body. Cephalization is often considered a consequence of the development of bilateral symmetry.

The evolution of tissues allowed for specialized structures and functions

The zygote (a fertilized egg), has the capability to give rise to all the kinds of cells in an animal's body. That is, it is totipotent (all powerful). During embryonic development, cells specialize to carry out particular functions. In all animals except sponges, the process is irreversible: once a cell differentiates to serve a function, it and its descendants can never serve any other.

A sponge cell that had specialized to serve one function (such as lining the cavity where feeding occurs) can lose the special attributes that serve that function and change to serve another function (such as being a gamete). Thus a sponge cell can dedifferentiate and redifferentiate. Cells of all other animals are organized into tissues, each of which is characterized by cells of particular morphology and capability. But their competence to dedifferentiate prevents sponge cells from forming clearly defined tissues (and therefore, of course, organs, which are composed of tissues).

Because cells differentiate irreversibly in all animals except sponges, scientists infer that bodies containing cells specialized to serve particular functions have an advantage compared to those with cells that potentially have multiple functions. Judging by the relative diversity of animals with specialized tissues and those lacking them, tissues are a favorable adaptation. Presumably the advantage to the animal is embodied in the old adage “Jack of all trades, master of none.”

A body cavity made possible the development of advanced organ systems

In the process of embryonic development, the cells of animals of most groups organize into three layers (called germ layers): an outer **ectoderm**, an inner **endoderm**, and an intermediate **mesoderm**. Animals with three embryonic cell layers are said to be triploblastic. Part of the maturation from the embryo is that certain organs and organ systems develop from each germ layer. The ectoderm gives rise to the outer covering of the body and the nervous system; the endoderm gives rise to the digestive system, including the intestine; and the skeleton and muscles develop from the mesoderm. Cnidarians have only two layers (thus they are diploblastic), the endoderm and the ectoderm, and lack organs. Sponges lack germ layers altogether; they, of course, have no tissues or organs. All triploblastic animals are members of the Bilateria.

A key innovation in the body plan of some bilaterians was a body cavity isolated from the exterior of the animal. This is different from the digestive cavity, which is open to the exterior at least through the mouth, and in most animals at the opposite end as well, via the anus. The evolution of efficient organ systems within the animal body was not possible until a body cavity evolved for accommodating and supporting organs (such as our heart and lungs), distributing materials, and fostering complex developmental interactions. The cavity is filled with fluid: in most animals, the fluid is liquid, but in vertebrates, it is gas—the body cavity of humans filling with liquid is a life-threatening condition. A very few types of bilaterians have no body cavity, the space between tissues that develop from the mesoderm and those that develop from the endoderm being filled with cells and connective tissue. These are the so-called acoelomate animals (figure 32.2).

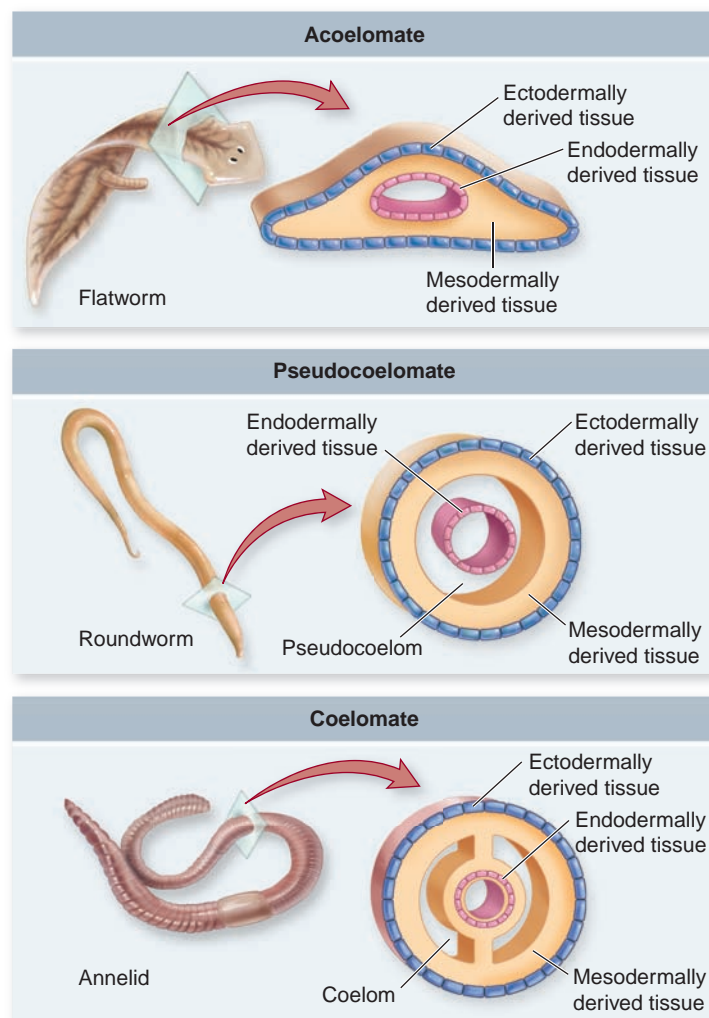


Figure 32.2 Three body plans for bilaterally symmetrical animals. Acoelomates, such as flatworms, have no body cavity between the digestive tract (derived from the endoderm) and the musculature layer (derived from the mesoderm). Pseudocoelomates have a body cavity, the pseudocoelom, between tissues derived from the endoderm and those derived from the mesoderm. Coelomates have a body cavity, the coelom, that develops entirely within tissues derived from the mesoderm, and so is lined on both sides by tissue derived from the mesoderm.

Body cavities

Body cavities appear to have evolved multiple times in the Bilateria (see figure 32.2). A body cavity called the **pseudocoelom** develops embryologically between mesoderm and endoderm, so occurs in the adult between tissues derived from the mesoderm and those derived from endoderm; animals with this type of body cavity are termed pseudocoelomates. Although the word *pseudocoelom* means “false coelom,” this is a true body space and characterizes many successful groups of animals. A **coelom** is a cavity that develops entirely within the mesoderm. The coelom is surrounded by a layer of epithelial cells derived from the mesoderm and termed the peritoneum.

Zoologists previously inferred that the first animals were acoelomate, that some of their descendants evolved a pseudocoelom, and that some pseudocoelomate descendants evolved the coelom. However, as you saw in chapter 21, evolution rarely occurs in such a linear and directional way. Rather, pseudocoeloms seem to have evolved several times, and some animals have lost the body space, becoming acoelomate secondarily. However, a coelom appears to have evolved just once. Thus, species possessing a coelom form a clade, but those with a pseudocoelom do not.

The circulatory system

In many small animals, nutrients and oxygen are distributed and wastes are removed by fluid in the body cavity. Most larger animals, in contrast, have a **circulatory system**, a network of vessels that carry fluids to and from the parts of the body distant from the sites of digestion (gut) and gas exchange (gills or lungs). The circulating fluid carries nutrients and oxygen to the tissues and removes wastes, including carbon dioxide, by diffusion between the circulatory fluid and the other cells of the body.

In an **open circulatory system**, the blood passes from vessels into sinuses, mixes with body fluid that bathes the cells of tissues, then reenters vessels in another location. In a **closed circulatory system**, the blood is entirely confined to blood vessels, so is physically separated from other body fluids. Blood moves through a closed circulatory system faster and more efficiently than it does through an open system; open systems are typical of animals that are relatively inactive and so do not have a high demand for oxygen. In small animals, blood can be pushed through a closed circulatory system by movement of the animal. In larger animals, the body musculature does not provide enough force, so the blood must be propelled by contraction of one or more hearts, which are specialized, muscular parts of the blood vessels.

Bilaterians have two main types of development

The processes of embryonic development in animals is discussed fully in chapter 54. Briefly, development of a bilaterally symmetrical animal begins with mitotic cell divisions (called cleavages) of the egg that lead to the formation of a hollow ball of cells, which subsequently indents to form a two-layered ball. The internal space that is created through such indentation (figure 54.11) is the **archenteron** (literally

the “primitive gut”); it communicates with the outside by a **blastopore**.

In a protostome, the mouth of the adult animal develops from the blastopore or from an opening near the blastopore (protostome means “first mouth”—the first opening becomes the mouth). **Protostomes** include most bilaterians, including flatworms, nematodes, mollusks, annelids, and arthropods. In some protostomes, both mouth and anus form from the embryonic blastopore; in other protostomes, the anus forms later in another region of the embryo. Two outwardly dissimilar groups, the echinoderms and the chordates, together with a few other small phyla, constitute the **deuterostomes**, in which the mouth of the adult animal does not develop from the blastopore. The deuterostome blastopore gives rise to the organism’s anus, and the mouth develops from a second pore that arises later in development (deuterostome means “second mouth”). Protostomes and deuterostomes differ in several other aspects of embryology too, as discussed later.

Cleavage patterns

The cleavage pattern relative to the embryo’s polar axis determines how the resulting cells lie with respect to one another. In some protostomes, each new cell cleaves off at an angle oblique to the polar axis. As a result, a new cell nestles into the space between the older ones in a closely packed array. This pattern is called **spiral cleavage** because a line drawn through a sequence of dividing cells spirals outward from the polar axis (figure 32.3 top). Spiral cleavage is characteristic of annelids, mollusks, nemertean, and related phyla; the clade of animals with this cleavage pattern is therefore known as the Spiralia.

In all deuterostomes, by contrast, the cells divide parallel to and at right angles to the polar axis. As a result, the pairs of cells from each division are positioned directly above and below one another, a process that gives rise to a loosely packed ball. This pattern is called **radial cleavage** because a line drawn through a sequence of dividing cells describes a radius outward from the polar axis (figure 32.3 bottom).

Determinate versus indeterminate development

Many protostomes exhibit **determinate development**, in which the type of tissue each embryonic cell will form in the adult is determined early, in many lineages even before cleavage begins, when the molecules that act as developmental signals are localized in different regions of the egg. Consequently, the cell divisions that occur after fertilization segregate molecular signals into different daughter cells, specifying the fate of even the very earliest embryonic cells. Each embryonic cell is destined to occur only in particular parts of the adult body, so if the cells are separated, development cannot proceed.

Deuterostomes, on the other hand, display **indeterminate development**. The first few cell divisions of the zygote produce identical daughter cells. If the cells are separated, any one can develop into a complete organism because the molecules that signal the embryonic cells to develop differently are not segregated in different cells until later in the embryo’s development. (This is how identical twins are formed.) Thus, each cell remains totipotent and its fate is not determined for several cleavages.

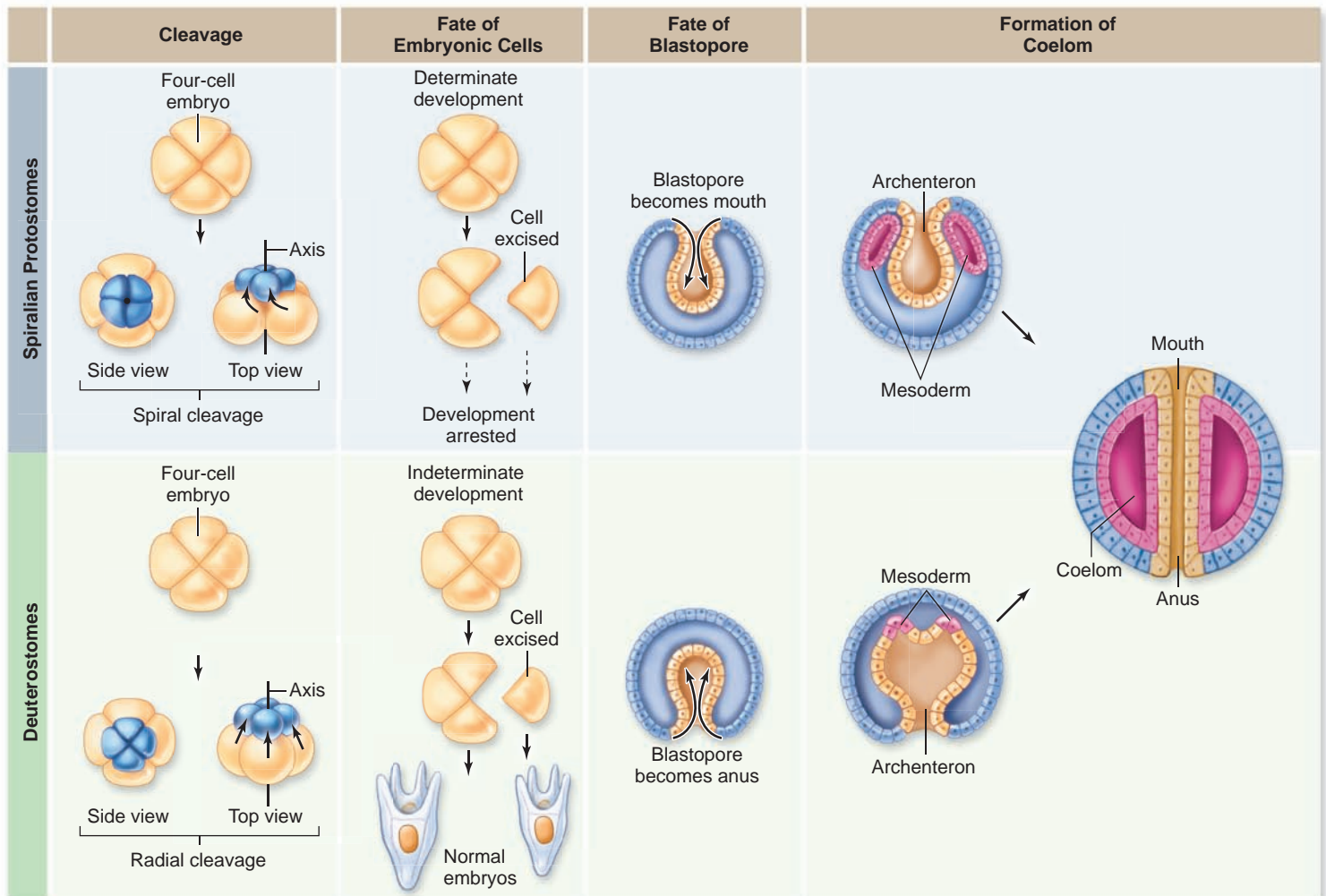


Figure 32.3 Embryonic development in protostomes and deuterostomes. In spiralian protostomes, embryonic cells cleave in a spiral pattern and exhibit determinate development; the blastopore becomes the animal’s mouth, and the coelom originates from a split among endodermal cells. In deuterostomes, embryonic cells cleave radially and exhibit indeterminate development; the blastopore becomes the animal’s anus, and the coelom originates from an invagination of the archenteron.

Formation of the coelom

The coelom arises within the mesoderm. In protostomes, cells simply move apart from one another to create an expanding coelomic cavity within the mass of mesodermal cells. In deuterostomes, groups of cells pouch off the end of the archenteron, which you will recall is the primitive gut—the hollow in the center of the developing embryo that is lined with endoderm.

The consistency of deuterostome development and its distinctiveness from that of the protostomes suggest that it evolved once, in the ancestor of the deuterostome phyla. The mode of development in protostomes is more diverse, but because of the distinctiveness of spiral development, scientists infer it also evolved once, in the common ancestor to all spiralian phyla.

Segmentation allowed for redundant systems and improved locomotion

Segmented animals consist of a series of linearly arrayed compartments that typically look alike (see figure 34.14), at least

early in development, but that may have specialized functions. Development of segmentation is mediated at the molecular level by *Hox* genes (see chapters 19 and 25, and in section 32.4). During early development, segments first are obvious in the mesoderm but later are reflected in the ectoderm and endoderm. Two advantages result from early embryonic segmentation:

1. In highly segmental animals, such as earthworms (phylum Annelida), each segment may develop a more or less complete set of adult organ systems. Because these are redundant systems, damage to any one segment need not be fatal because other segments duplicate the damaged segment’s functions.
2. Locomotion is more efficient when individual segments can move semi-independently. Because partitions isolate the segments, each can contract or expand autonomously. Therefore, a long body can move in ways that are often quite complex.

Segmentation underlies the organization of body plans of the most morphologically complex animals. In some adult

arthropods, the segments are fused, but segmentation is usually apparent in embryological development. In vertebrates, the backbone and muscle blocks are segmented, although segmentation is often disguised in the adult form.

Previously, zoologists considered that true segmentation was found only in annelids, arthropods, and chordates, but segmentation is now recognized to be more widespread. Animals such as onychophorans (velvet worms), tardigrades (water bears), and kinorhynchans (mud dragons) are also segmented.

Learning Outcomes Review 32.2

Animals are distinguished on the basis of symmetry, tissues, type of body cavity, sequence of embryonic development, and segmentation. A pseudocoelom is a space that develops between the mesoderm and endoderm; a coelom develops entirely within mesoderm. In bilaterians, protostomes develop the mouth prior to the anus; deuterostomes develop the mouth after the anus has formed. Segmentation allows redundant systems and more efficient locomotion.

- How is cephalization related to body symmetry?

32.3 The Classification of Animals

Learning Outcomes

1. List the major criteria scientists have used to distinguish animal phyla.
2. Distinguish between spiralian and ecdysozoan organisms.
3. Identify the placement of humans among the animal phyla.

Multicellular animals, or metazoans, are traditionally divided into 35 to 40 phyla (singular, *phylum*). There is little disagreement among biologists about the placement of most animals in phyla, although zoologists disagree on the status of some, particularly those with few members or recently discovered ones. The diversity of animals is obvious in tables 32.2 and 32.3, which describe key characteristics of 20 of the phyla.

Traditionally, the phylogeny of animals has been inferred using features of anatomy and aspects of embryological development, as discussed earlier, from which a broad consensus emerged over the last century concerning the main branches of the animal tree of life. In the past 30 years, data derived from molecular features have been added, leading to some rethinking of classification schemes. Depending on the features compared, biologists may draw quite different family trees—although, of course, there is only one way that evolution actually occurred, and the goal of phylogeny is to detect that history.

Whether morphological or molecular characters (or both) are used, the underlying principle is the same: systematists use features they assume to have evolved only once, so the animals sharing such a feature are inferred to be more closely

related to one another than they are to animals not sharing the feature. The shared derived characters unique to a group and its ancestors define a monophyletic assemblage termed a clade (see chapter 23). The animal phylogenetic tree viewed in these terms is a hierarchy of clades nested within larger clades, and containing smaller clades.

Tissues and symmetry separate the Parazoa and Eumetazoa

Systematists traditionally divided the kingdom Animalia (also termed Metazoa) into two main branches. Parazoa (“near animals”) comprises animals that, for the most part, lack definite symmetry, and that do not possess tissues. These are the sponges, phylum Porifera. Because they are so different in so many ways from other animals, some scientists inferred that sponges were not closely related to other animals, which would mean that what we consider animals had two separate origins. Eumetazoa (“true animals”) are animals that have a definite shape and symmetry. All have tissues, and most have organs and organ systems. Now most systematists agree that Parazoa and Eumetazoa are descended from a common ancestor, so animal life had a single origin. And although most trees constructed including molecular data consider Parazoa to be at the base of the animal tree of life, some do not.

Further divisions are based on other key features, as discussed previously. Bilaterally symmetrical animals (which are also triploblastic) are divided into the groups Protostomia and Deuterostomia depending on whether the embryonic blastopore (see figure 32.3) becomes the mouth or the anus (or both), respectively, in the adult animal.

Animals are traditionally classified into 35 to 40 phyla. The evolutionary relationships among the animal phyla are based on the inference that phyla sharing certain fundamental morphological and molecular characters are more closely related to one another than they are to phyla not sharing those characters. Phylogenetically informative characters are inferred to have arisen only once.

Molecular data help reveal evolutionary relationships











Gene sequence data are accumulating at an accelerating pace for all animal groups. Phylogenies developed from different molecules sometimes suggest quite different evolutionary relationships among the same groups of animals. However, combining data from multiple genes has resolved the relationships of most phyla. Current studies are using sequences from hundreds of genes to try to fully resolve the animal tree of life.

Molecular data are helping to resolve some problems with the traditional phylogeny, such as puzzling groups that did not fit well into the widely accepted phylogeny. These data may be especially helpful in clarifying relationships that conventional data cannot, as, for example, in animals such as parasites. Through dependence on their host, the anatomy, physiology, and behavior of parasites tends to be greatly altered, so features that may reveal the phylogenetic affinities of free-living animals can be highly modified or lost.

TABLE 32.2 Animal Phyla with the Most Species

Phylum	Typical Examples		Key Characteristics	Approximate Number of Named Species
Arthropoda (arthropods)	Beetles, other insects, crabs, spiders, krill, scorpions, centipedes, millipedes		Chitinous exoskeleton covers segmented, coelomate body. With paired, jointed appendages; many types of insects have wings. Occupy marine, terrestrial, and freshwater habitats. Most arthropods are insects (as are most animals!).	1,000,000
Mollusca (mollusks)	Snails, oysters, clams, octopuses, slugs		Coelomate body of many mollusks is covered by one or more shells secreted by a part of the body termed the mantle. Many kinds possess a unique rasping tongue, a radula. Members occupy marine, terrestrial, and freshwater habitats (35,000 species are terrestrial).	110,000
Chordata (chordates)	Mammals, fish, reptiles, amphibians		Each coelomate individual possesses a notochord, a dorsal nerve cord, pharyngeal slits, and a postanal tail at some stage of life. In vertebrates, the notochord is replaced during development by the spinal column. Members occupy marine, terrestrial, and freshwater habitats (20,000 species are terrestrial).	56,000
Platyhelminthes (flatworms)	Planarians, tapeworms, liver and blood flukes		Unsegmented, acoelomate, bilaterally symmetrical worms. Digestive cavity has only one opening; tapeworms lack a gut. Many species are parasites of medical and veterinary importance. Members occupy marine, terrestrial, and freshwater habitats (as well as the bodies of other animals)	20,000
Nematoda (roundworms)	<i>Ascaris</i> , pinworms, hookworms, filarial worms		Pseudocoelomate, unsegmented, bilaterally symmetrical worms; tubular digestive tract has mouth and anus. Members occupy marine, terrestrial, and freshwater habitats; some are important parasites of plants and animals, including humans.	25,000 (but it is thought by some that the number of nematode species may be much greater)
Annelida (segmented worms)	Earthworms, polychaetes, tube worms, leeches		Segmented, bilaterally symmetrical, coelomate worms with a complete digestive tract; most have bristles (chaetae) on each segment that anchor them in tubes or aid in crawling. Occupy marine, terrestrial, and freshwater habitats.	16,000
Cnidaria (cnidarians)	Jellyfish, <i>Hydra</i> , corals, sea anemones, sea fans		Radially symmetrical, acoelomate body has tissues but no organs. Mouth opens into a simple digestive sac and is surrounded by tentacles armed with stinging capsules (nematocysts). In some groups, individuals are joined into colonies; some can secrete a hard exoskeleton. The very few nonmarine species live in fresh water.	10,000
Echinodermata (echinoderms)	Sea stars, sea urchins, sand dollars, sea cucumbers		Adult body pentaradial (fivefold) in symmetry. Water-vascular system is a coelomic space; endoskeleton of calcium carbonate plates. Many can regenerate lost body parts. Fossils are more diverse in body plan than extant species. Exclusively marine.	7000
Porifera (sponges)	Barrel sponges, boring sponges, basket sponges, bath sponges		Bodies of most asymmetrical: defining “an individual” is difficult. Body lacks tissues or organs, being a meshwork of cells surrounding channels that open to the outside through pores, and that expand into internal cavities lined with food-filtering flagellated cells (choanocytes). Most species are marine (150 species live in fresh water).	7000
Bryozoa (moss animals) (also called Polyzoa and Ectoprocta)	Sea mats, sea moss		The only exclusively colonial phylum; each colony comprises small, coelomate individuals (zooids) connected by an exoskeleton (calcareous in marine species, organic in most freshwater ones). A ring of ciliated tentacles (lophophore) surrounds the mouth of each zooid; the anus lies beyond the lophophore.	4500

TABLE 32.3
Some Important Animal Phyla with Fewer Species—and Three Recently Discovered Ones

Phylum	Typical Examples		Key Characteristics	Approximate Number of Named Species
Rotifera (wheel animals)	Rotifers		Small pseudocoelomates with a complete digestive tract including a set of complex jaws. Cilia at the anterior end beat so they resemble a revolving wheel. Some are very important in marine and freshwater habitats as food for predators such as fishes.	2000
Nemertea (ribbon worms) (also called Rhynchocoela)	<i>Lineus</i>		Protostome worms notable for their fragility—when disturbed, they fragment in pieces. Long, extensible proboscis occupies a coelomic space; that of some tipped by a spearlike stylet. Most marine, but some live in fresh water, and a few are terrestrial.	900
Tardigrada (water bears)	<i>Hypsibius</i>		Microscopic protostomes with five body segments and four pairs of clawed legs. An individual lives a week or less but can enter a state of suspended animation (“cryptobiosis”) in which it can survive for many decades. Occupy marine, freshwater, and terrestrial habitats.	800
Brachiopoda (lamp shells)	<i>Lingula</i>		Protostomous animals encased in two shells that are oriented with respect to the body differently than in bivalved mollusks. A ring of ciliated tentacles (lophophore) surrounds the mouth. More than 30,000 fossil species are known.	300
Onychophora (velvet worms)	<i>Peripatus</i>		Segmented protostomous worms resembling tardigrades; with a chitinous soft exoskeleton and unsegmented appendages. Related to arthropods. The only exclusively terrestrial phylum, but what are interpreted as their Cambrian ancestors were marine.	110
Ctenophora (sea walnuts)	Comb jellies, sea walnuts		Gelatinous, almost transparent, often bioluminescent marine animals; eight bands of cilia; largest animals that use cilia for locomotion; complete digestive tract with anal pore.	100
Chaetognatha (arrow worms)	<i>Sagitta</i>		Small, bilaterally symmetrical, transparent marine worms with a fin along each side, powerful bristly jaws, and lateral nerve cords. Some inject toxin into prey and some have large eyes. It is uncertain if they are coelomates, and, if so, whether protostomes or deuterostomes.	100
Loricifera (loriciferans)	<i>Nanaloricus mysticus</i>		Tiny marine pseudocoelomates that live in spaces between grains of sand. The mouth is borne on the tip of a flexible tube. Discovered in 1983.	10
Cycliophora (cycliophorans)	<i>Symbion</i>		Microscopic animals that live on mouthparts of claw lobsters. Discovered in 1995.	3
Micrognathozoa (micrognathozoans)	<i>Limnognathia</i>		Microscopic animals with complicated jaws. Discovered in 2000 in Greenland.	1

Morphology- and molecule-based phylogenies agree on many major groupings

Although they differ from one another in some respects, phylogenies incorporating molecular data or based entirely on them share some deep structure with the traditional animal tree of life. Figure 32.4 is a summary of animal phylogeny developed from morphological, molecular, life-history, and other types of relevant data. Some aspects of this view have been contradicted by studies based on particular characters or using particular analytical methods. It is an exciting time to be a systematist, but shifts in understanding of relationships among groups of animals can be frustrating to some! Like any scientific idea, a phylogeny is a hypothesis, open to challenge and to being revised in light of additional data.

One consistent result is that Porifera (sponges) constitutes a monophyletic group that shares a common ancestor with other animals. Some systematists had considered sponges to comprise two (or three) groups that are not particularly closely related, but molecular data support what had been the majority view, that phylum Porifera is monophyletic. And, as mentioned earlier, all animals are found to be monophyletic.

Among eumetazoans, molecular data are in accord with the traditional view that cnidarians (hydras, sea jellies, and corals) branch off the tree before the origin of animals with bilateral symmetry. Our understanding of the phylogeny of the deuterostome branch of Bilateria (discussed in chapter 34) has not changed much, but our understanding of the phylogeny of protostomes has been altered by molecular data.

Most revolutionary is that annelids and arthropods, which had been considered closely related based on the occurrence of segmentation in both, belong to separate clades. Now arthropods are grouped with protostomes that molt their cuticles at least once during their life. These are termed ecdysozoans, which means “molting animals” (see chapter 34). Molecular sequence data can help test our ideas of which morphological features reveal evolutionary relationships best; in this case, molecular data allowed us to see that, contrary to our hypothesis, segmentation seems to have evolved convergently, but molting did not.

But not all features are easy to diagnose, and molecular data do not resolve all uncertainties. The enigmatic phylum Ctenophora (comb jellies)—pronounced with a silent C—has been considered both diploblastic and triploblastic and has been thought to have both a complete gut and a blind gut. Likewise the enigmatic phylum Chaetognatha (arrow worms) has been considered both coelomate and pseudocoelomate, and if coelomate, both protostome and deuterostome (as reflected in figure 32.4). Their placement in phylogenies varies, seeming to depend on the features and methods used to construct the tree. Further research is needed to resolve these uncertainties.

Molecular data are contributing to our understanding of relationships among animal phyla. Animals are monophyletic, as are sponges—relationships that were uncertain using only morphological data. Molecular data confirm that cnidarians branched off from the rest of animals before bilateral symmetry evolved. Although the position of ctenophores has not been

resolved, molecular data have significantly altered some ideas of protostome evolution.

Morphology-based phylogeny focused on the state of the coelom

In the morphology-based animal family tree, bilaterally symmetrical animals comprised three major branches. If the body has no cavity (other than the gut), the animal is said to be acoelomate; members of phylum Platyhelminthes are acoelomates.

A body cavity not lined with tissue derived from mesoderm is a pseudocoelom; members of the phylum Nematoda are pseudocoelomate. A body cavity lined with tissue derived from mesoderm is a coelom; we and members of the phylum Annelida are coelomate. All acoelomates and pseudocoelomates are protostomes; some coelomates are protostomes and some are deuterostomes.

Protostomes consist of spiralian and ecdysozoans

Two major clades of protostomes are recognized as having evolved independently since ancient times: the spiralian and the ecdysozoans (see figure 32.4).

Spiralia

Spiralian animals grow by gradual addition of mass to the body. Most live in water, and propel themselves through it using cilia or contractions of the body musculature. Spiralian undergo spiral cleavage (see figure 32.3).

There are two main groups of spiralian: Lophotrochozoa and Platyzoa. Lophotrochozoa includes most coelomate protostome phyla; those animals move by muscular contractions. Most platyzoans are acoelomates; these animals are tiny or flat, and move by ciliary action. Some platyzoans (such as rotifers, gnathostomulids, and the recently discovered phylum Micrognathozoa have a set of complicated jaws. The most prominent group is phylum Platyhelminthes; a flatworm has a simple body with no circulatory or respiratory system but a complex reproductive system. This group includes marine and freshwater planarians as well as the parasitic flukes and tapeworms.

Lophotrochozoa consists of two major phyla and several smaller ones. Many of the animals have a type of free-living larva known as a **trochophore**, and some have a feeding structure termed a **lophophore**, a horseshoe-shaped crown of ciliated tentacles around the mouth used in filter-feeding. The phyla characterized by a lophophore are Bryozoa and Brachiopoda. Lophophorate animals are sessile (anchored in place).

Among the lophotrochozoans with a trochophore are phyla Mollusca and Annelida. Mollusks are unsegmented, and their coelom is reduced to a hemocoel (open circulatory space) and some other small body spaces. This phylum includes animals as diverse as octopuses, snails, and clams. Annelids are segmented coelomate worms, the most familiar of which is the earthworm, but also includes leeches and the largely marine polychaetes.

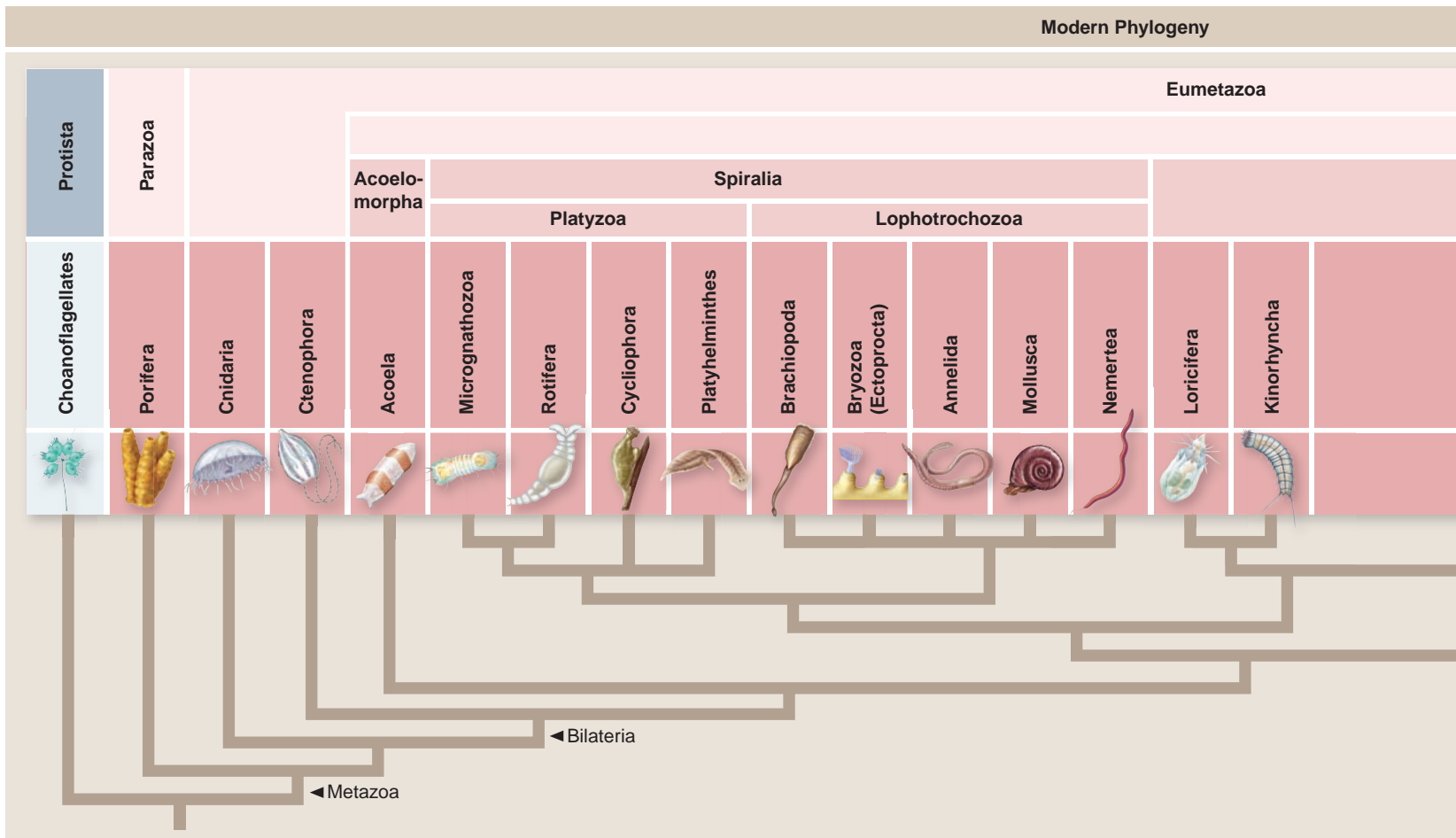


Figure 32.4 Proposed revision of the animal tree of life. A phylogeny of many of the 35–40 phyla reflects the consensus as of 2005 based on interpretation of anatomical and developmental data as well as results derived from molecular phylogenetic studies. Whether Chaetognatha is a protostome or a deuterostome is unclear.

Ecdysozoa

The other major clade of protosomes is the Ecdysozoa. Ecdysozoans are animals that molt, a phenomenon that seems to have evolved only once in the animal kingdom. When an animal grows large enough that it completely fills its hard external skeleton, it must lose that skeleton (by molting, a process also called ecdysis). While the animal grows, it forms a new exoskeleton underneath the existing one. The first step in molting is for the body to swell until the existing exoskeleton cracks open and is shed (figure 32.5). Upon molting that skeleton, the animal inflates the soft, new one, expanding it using body fluids (and, in many insects and spiders, air as well). When the new one hardens, it is larger than the molted one had been and has room for growth. Thus, rather than being continuous, as in other animals, the growth of ecdysozoans is step-wise.

Of the numerous phyla of protosomes assigned to the Ecdysozoa, Arthropoda contains the largest number of described species of any phylum. Each phylum contains one of the model organisms used in laboratory studies that have informed much of our current understanding of genetics and development: the fruit fly *Drosophila melanogaster* and the roundworm *Caenorhabditis elegans*.

Arthropods are coelomate animals with jointed appendages and segmented external skeletons composed of chitin. Ar-

thropods include insects, spiders, crustaceans, and centipedes, among many others. Arthropods have colonized almost all habitats, being found from the ocean floor to the air and in all terrestrial and freshwater environments.

Roundworms are pseudocoelomate worms that lack circulatory or gas exchange structures, and their bodies have only longitudinal muscles. Nematodes inhabit marine, freshwater, and terrestrial environments, and many species are parasitic in

Figure 32.5 Blue crab undergoing ecdysis (molting).

Members of Ecdysozoa grow step-wise because their external skeleton is rigid.



32.4 The Roots of the Animal Tree of Life

Learning Outcomes

1. Explain the colonial flagellate hypothesis of metazoan origin and why it is now favored.
2. Describe the possible role of Hox genes in the Cambrian explosion.

Some of the most exciting contributions of molecular systematics are being made to our understanding of the base of the animal family tree—the origins of the major clades of animals.

Metazoans appear to have evolved from colonial protists

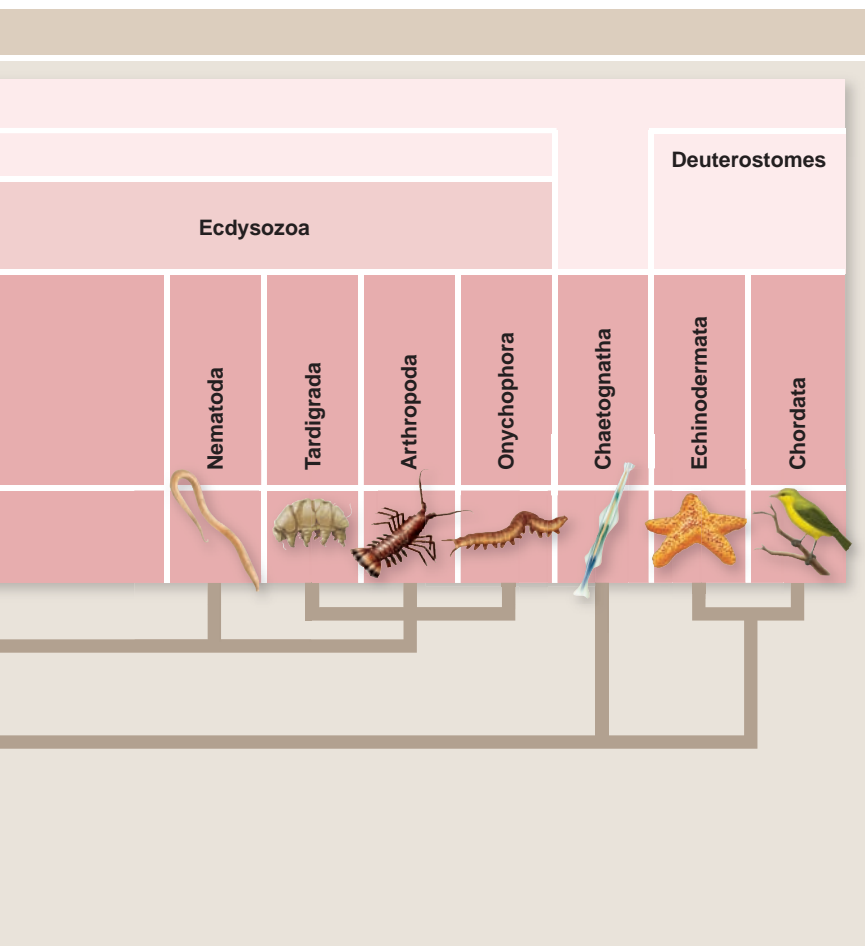
The ancestor to all animals was presumably a protist (see chapter 29), but it is not clear from which line of protists animals evolved. Evidence is available to support two major hypotheses.

- The multinucleate hypothesis is that metazoans arose from a multinuclear protist similar to today's ciliates. Each nucleus became compartmentalized into a cell, resulting in the multicellular condition.
- The **colonial flagellate hypothesis**, first proposed by Ernst Haeckel in 1874, is that metazoans descended from colonial protists. Each colony is a hollow sphere composed of flagellated cells. Some of the cells of sponges are strikingly like those of choanoflagellate protists.

Molecular data based on ribosomal RNA sequences favor the colonial flagellate hypothesis, and reject the multinucleate ciliate hypothesis based on evidence that metazoans are more closely related to eukaryotic algae than to ciliates.

Molecular analysis may explain the Cambrian explosion

Most major animal body plans can be seen in fossils of Cambrian age, dating from 543 to 525 MYA. Although fossil cnidarians are found in rocks from the Ediacaran period, as old as 565 million years, along with what appear to be fossil mollusks and the burrows of worms, the great diversity of animals evolved quite rapidly in geological terms around the beginning of the Cambrian period—an event known as the **Cambrian explosion**. Biologists have long debated what caused this enormous expansion of animal diversity (figure 32.6). Many have argued that the emergence of new body plans was biological—the consequence of the evolution of predation, which encouraged an arms race between defenses, such as armor, and innovations that improved mobility and hunting success. Others have attributed the rapid diversification in body plans to physical factors—such as the build-up of dissolved oxygen and minerals in the oceans.



plants or animals. It is said that if everything in the world except nematodes were to disappear, an outline of what had been there would be visible in the remaining nematodes!

Deuterostomes include chordates and echinoderms

Deuterostomes consist of fewer phyla and species than protostomes, and are more uniform in many ways, despite great differences in appearance. Echinoderms such as sea stars, and chordates such as humans, share a mode of development that is evidence of their evolution from a common ancestor, and separates them clearly from other animals.

Learning Outcomes Review 32.3

Scientists have defined phyla based on tissues, symmetry, characteristics such as presence or absence of a coelom or pseudocoelom, protostome versus deuterostome development, growth pattern and larval stages, and molecular data. Among protostomes, spiralian organisms have a growth pattern in which their body size simply increases; ecdysozoans must molt in order to grow larger. Among the deuterostome phyla are Echinodermata and Chordata, which includes humans.

- *Why do systematists attempt to characterize each group of animals by one or more features that have evolved only once?*



Figure 32.6 Diversity of animals that evolved during the Cambrian explosion. The Cambrian saw an astonishing variety of body plans, many of which gave rise to the animals we find today. The natural history of these species is open to speculation.

Whether these causes or others are at the heart of the Cambrian explosion, molecular studies in the field of evolutionary developmental biology may provide a mechanism for the emergence of so many body plans. Much of the variation in animal body plans is associated with changes in the location or time of expression of *homeobox* genes (*Hox* genes) in embryos (see chapters 19 and 25). *Hox* genes specify the identity of developing body parts, such as the legs, thorax, and antennae. Perhaps the Cambrian explosion reflects the evolution of the *Hox* developmental gene complex, which provides a mechanism for producing rapid changes in body plan.

Learning Outcomes Review 32.4

The hypothesis of evolution of metazoans from colonial flagellates is favored because of the similarity between flagellate colonies and metazoan sponges, and because of molecular data based on ribosomal RNA sequences. Animal fossils become highly abundant in the Cambrian period in what is known as the Cambrian explosion. *Hox* genes, which control development of body shape and parts, may be responsible for the diversity found in this period.

- *What alternative interpretations are there for the fossils that have led to the idea of the Cambrian explosion?*



Chapter Review

32.1 Some General Features of Animals

Features common to all animals are multicellularity, heterotrophic lifestyle, and lack of a cell wall. Other features include specialized tissues, ability to move, and sexual reproduction.

32.2 Evolution of the Animal Body Plan

Most animals exhibit radial or bilateral symmetry.

Most sponges are asymmetrical, but other animals are bilaterally or radially symmetrical at some time during their life. The body parts of radially symmetrical animals are arranged around a central axis. The body of a bilaterally symmetrical animal has left and right halves. Most bilaterally symmetrical organisms are cephalized and can move directionally.

The evolution of tissues allowed for specialized structures and functions.

Each tissue consists of differentiated cells that have characteristic forms and functions.

A body cavity made possible the development of advanced organ systems.

Most bilaterian animals possess a body cavity other than the gut. A coelom is a cavity that lies within tissues derived from mesoderm. A pseudocoelom lies between tissues derived from mesoderm and the gut (which develops from endoderm). The acoelomate condition and the pseudocoelom appear to have evolved more than once, but the coelom evolved only once.

A circulatory system is an example of a specialized organ system that assists with distribution of nutrients and removal of wastes.

Bilaterians have two main types of development.

In a protostome, the mouth develops from or near the blastopore. A protostome has determinate development, and many have spiral cleavage.

In a deuterostome, the anus develops from the blastopore. A deuterostome has indeterminate development and radial cleavage.

Segmentation allowed for redundant systems and improved locomotion.

Segmentation, which evolved multiple times, allows for efficient and flexible movement because each segment can move somewhat independently. Another advantage to segmentation is redundant organ systems.

32.3 The Classification of Animals

Animals are classified into 35 to 40 phyla based on shared characteristics. Systematists attempt to use features assumed to have evolved only once.

Tissues and symmetry separate the Parazoa and Eumetazoa.

With the exception of sponges, animals exhibit embryonic germ layers and differentiated cells that form tissues. These characteristics lead to most animals being termed collectively the Eumetazoa; other animals, including the sponges, are Parazoa.

Molecular data help reveal evolutionary relationships.

By incorporating molecular data into phylogenetic analyses, major alterations have been made to the traditional view of how members of these phyla are related.

Morphology- and molecule-based phylogenies agree on many major groupings.

Porifera (sponges) constitutes a monophyletic group that shares a common ancestor with other animals. Cnidarians (hydras, sea jellies, and corals) evolved before the origin of bilaterally symmetrical animals.

Annelids and arthropods had been considered closely related based on segmentation, but now arthropods are grouped with protostomes that molt their cuticles at least once during their life.

Morphology-based phylogeny focused on the state of the coelom.

The two groups of bilaterally symmetrical animals (the Bilateria)—protostomes and deuterostomes—differ in embryology. All acoelomates and pseudocoelomates are protostomes; some coelomates are protostomes and some are deuterostomes.

Protostomes consist of spiralian and ecdysozoans.

Spiralia comprises the clades Lophotrochozoa and Platyzoa. Spiralian animals grow by gradual addition of mass to the body

and undergo spiral cleavage. Examples of Lophotrochozoa include annelids and mollusks. Examples of Platyzoa are rotifers and platyhelminthine worms.

Ecdysozoans grow by molting the external skeleton; Ecdysozoa includes many varied species, ranging from the pseudocoelomate, unsegmented Nematoda to the coelomate, segmented Arthropoda.

Deuterostomes include chordates and echinoderms.

The major groups of deuterostomes are the echinoderms, which include animals such as sea stars and sea urchins, and the chordates, which include vertebrates.

Deuterostome development indicates that echinoderms and chordates evolved from a common ancestor, distinguishing them clearly from other animals.

32.4 The Roots of the Animal Tree of Life

Metazoans appear to have evolved from colonial protists.

Systematics based on ribosomal RNA supports the hypothesis that the Eumetazoa are monophyletic and arose from colonial flagellates.

Molecular analysis may explain the Cambrian explosion.

Molecular analysis suggests that the rapid diversification during the Cambrian explosion may have been due to evolution of the *Hox* genes.



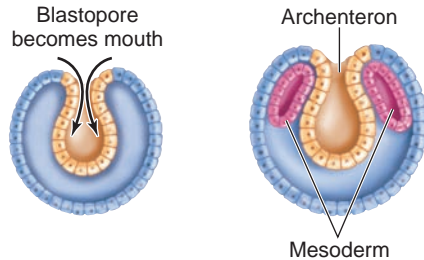
Review Questions

UNDERSTAND

- Which of the following characteristics is unique to all members of the animal kingdom?
 - Sexual reproduction
 - Multicellularity
 - Lack of cell walls
 - Heterotrophy
- Animals are unique in the fact that they possess _____ for movement and _____ for conducting signals between cells.
 - brains; muscles
 - muscle tissue; nervous tissue
 - limbs; spinal cords
 - flagella; nerves
- In animal sexual reproduction the gametes are formed by the process of
 - meiosis.
 - mitosis.
 - fusion.
 - binary fission.
- The evolution of bilateral symmetry was a necessary precursor for the evolution of
 - tissues.
 - segmentation.
 - a body cavity.
 - cephalization.
- A fluid-filled cavity that develops completely within mesodermal tissue is a characteristic of a
 - coelomate.
 - pseudocoelomate.
 - acoelomate.
 - all of the above
- Which of the following statements is not true regarding segmentation?
 - Segmentation allows the evolution of redundant systems.
 - Segmentation is a requirement for a closed circulatory system.
 - Segmentation enhances locomotion.
 - Segmentation represents an example of convergent evolution.
- Which of the following characteristics is used to distinguish between a parazoan and a eumetazoan?
 - Presence of a true coelom
 - Segmentation
 - Cephalization
 - Tissues
- With regard to classification in the animals, the study of which of the following is changing our understanding of the organization of the kingdom?
 - Molecular systematics
 - Origin of tissues
 - Patterns of segmentation
 - Evolution of morphological characteristics
- The _____ contain the greatest number of known species.
 - Chordata
 - Arthropoda
 - Porifera
 - Mollusca
- The evolution of which of the following occurred after the Cambrian explosion?
 - Cephalization
 - Coelom
 - Segmentation
 - None of the above
- A coelomate organism may have which of the following characteristics?
 - Circulatory system
 - Internal skeleton
 - Larger size than a pseudocoelomate
 - All of the above

APPLY

- The following diagram is of the blastopore stage of embryonic development. Based on the information in the diagram, which of the following statements is correct?
 - It is a diagram of a protostome.
 - It would have formed by radial cleavage.
 - It would exhibit determinate development.
 - All of the above are correct.



- Which of the following characteristics would not apply to a species in the Ecdysozoa?
 - Bilateral
 - Indeterminate cleavage
 - Molt at least once in their life cycle
 - Metazoan
- In the rain forest you discover a new species that is terrestrial, has determinate development, molts during its lifetime, and

possesses jointed appendages. To which phylum of animals should it be assigned?

SYNTHESIZE

- Worm evolution represents an excellent means of understanding the evolution of a body cavity. Using the phyla of worms Nematoda, Annelida, Platyhelminthes, and Nemetera, construct a phylogenetic tree based only on the form of body cavity (refer to figure 32.2 and table 32.2 for assistance). How does this relate to the material in figure 32.4? Should body cavity be used as the sole characteristic for classifying a worm?
- Most students find it hard to believe that Echinodermata and Chordata are closely related phyla. If it were not for how their members form a body cavity, where would you place Echinodermata in the animal kingdom? Defend your answer.

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