While there are a great many genes that play roles in the morphological development of an animal, including other homeobox-containing genes, what makes *Hox* genes so powerful is that they serve as “master control genes” that can turn on or off large numbers of other genes. *Hox* genes do this by encoding transcription factors that control the expression of numerous other genes. *Hox* genes are homologous across the animal kingdom, that is, the genetic sequences of *Hox* genes and their positions on chromosomes are remarkably similar across most animals because of their presence in a common ancestor, from worms to flies, mice, and humans (**Figure 27.5**). In addition, the order of the genes reflects the anterior-posterior axis of the animal's body. One of the contributions to increased animal body complexity is that *Hox* genes have undergone at least two and perhaps as many as four duplication events during animal evolution, with the additional genes allowing for more complex body types to evolve. All vertebrates have four (or more) sets of *Hox* genes, while invertebrates have only one set.

visual CONNECTION

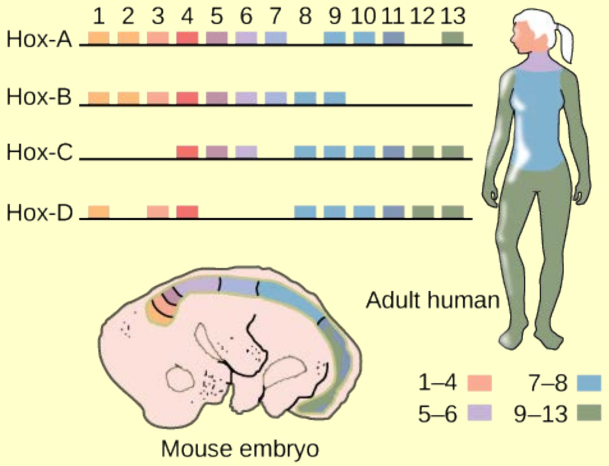

Figure 27.5 *Hox* genes. *Hox* genes are *highly conserved genes* encoding transcription factors that determine the course of embryonic development in animals. In vertebrates, the genes have been duplicated into four clusters on *different chromosomes*: *Hox-A*, *Hox-B*, *Hox-C*, and *Hox-D*. Genes within these clusters are expressed in certain body segments at certain stages of development. Shown here is the homology between *Hox* genes in mice and humans. Note how *Hox* gene expression, as indicated with orange, pink, blue, and green shading, occurs in the same body segments in both the mouse and the human. While at least one copy of each Hox gene is present in humans and other vertebrates, some *Hox* genes are missing in some chromosomal sets.

If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

Two of the five clades within the animal kingdom do *not* have *Hox* genes: the Ctenophora and the Porifera. In spite of the superficial similarities between the Cnidaria and the Ctenophora, the Cnidaria have a number of *Hox* genes, but the Ctenophora have none. The absence of *Hox* genes from the ctenophores has led to the suggestion that they might be “basal” animals, in spite of their tissue differentiation. Ironically, the Placozoa, which have only a few cell types, do have at least one *Hox* gene. The presence of a *Hox* gene in the Placozoa, in addition to similarities in the genomic organization of the Placozoa, Cnidaria and Bilateria, has led to the inclusion of the three groups in a “Parahoxozoa” clade. However, we should note that at this time the reclassification of the Animal Kingdom is still tentative and requires much more study.

27.2 | Features Used to Classify Animals

By the end of this section, you will be able to do the following:

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most "rules" governing animal classification (**Figure 27.6**). Animals have been traditionally classified according to two characteristics: body plan and developmental pathway. The major feature of the body plan is its symmetry: how the body parts are distributed along the major body axis. Symmetrical animals can be divided into roughly equivalent halves along at least one axis. Developmental characteristics include the number of germ tissue layers formed during development, the origin of the mouth and anus, the presence or absence of an internal body cavity, and other features of embryological development, such as larval types or whether or not periods of growth are interspersed with molting.

visual CONNECTION

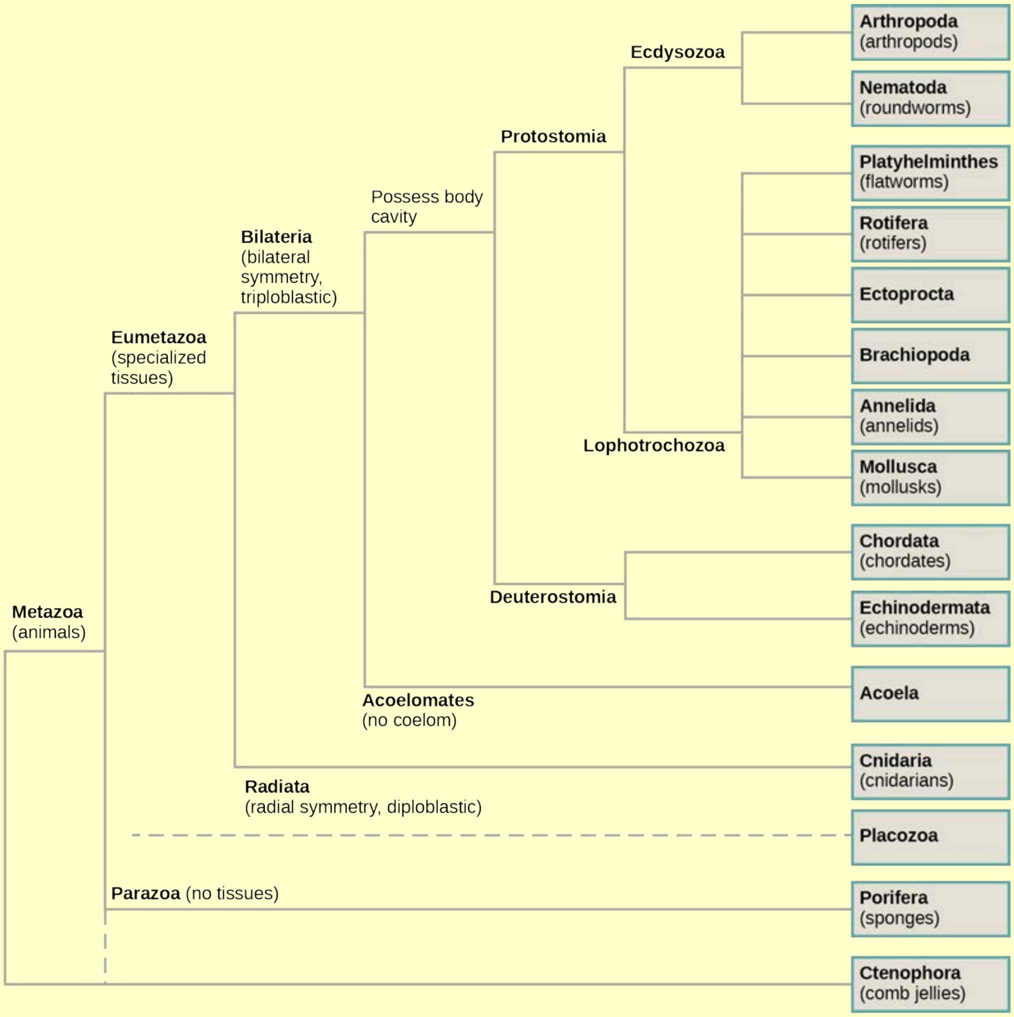

Figure 27.6 Animal phylogeny. The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence. The Ctenophora and Porifera are both considered to be basal because of the absence of Hox genes in this group, but how they are related to the "Parahoxozoa" (Placozoa + Eumetazoa) or to each other, continues to be a matter of debate.

Which of the following statements is false?

a. Eumetazoans have specialized tissues and parazoans don't.
b. Lophotrochozoa and Ecdysozoa are both Bilataria.
c. Acoela and Cnidaria both possess radial symmetry.
d. Arthropods are more closely related to nematodes than they are to annelids.

Animal Characterization Based on Body Symmetry

At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is seen in two modern clades, the Parazoa (Figure 27.7**a**) and Placozoa. (Although we should note that the ancestral fossils of the Parazoa apparently exhibited bilateral symmetry.) One clade, the Cnidaria (Figure 27.7**b,c**), exhibits radial or biradial symmetry: Ctenophores have rotational symmetry (Figure 27.7**e**). Bilateral symmetry is seen in the largest of the clades, the Bilateria (Figure 27.7**d**); however the Echinodermata are bilateral as larvae and metamorphose secondarily into radial adults. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a bicycle wheel or pie. It results in animals having top and bottom surfaces but no left and right sides, nor front or back. If a radially symmetrical animal is divided in any direction along the oral/aboral axis (the side with a mouth is "oral side," and the side without a mouth is the "aboral side"), the two halves will be mirror images. This form of symmetry marks the body plans of many animals in the phyla Cnidaria, including jellyfish and adult sea anemones (Figure 27.7**b, c**). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions. Bilaterally symmetrical animals, like butterflies (Figure 27.7**d**) have only a single plane along which the body can be divided into equivalent halves. The Ctenophora (Figure 27.7**e**), although they look similar to jellyfish, are considered to have rotational symmetry rather than radial or biradial symmetry because division of the body into two halves along the oral/aboral axis divides them into two copies of the same half, with one copy rotated 180^{o}, rather than two mirror images.

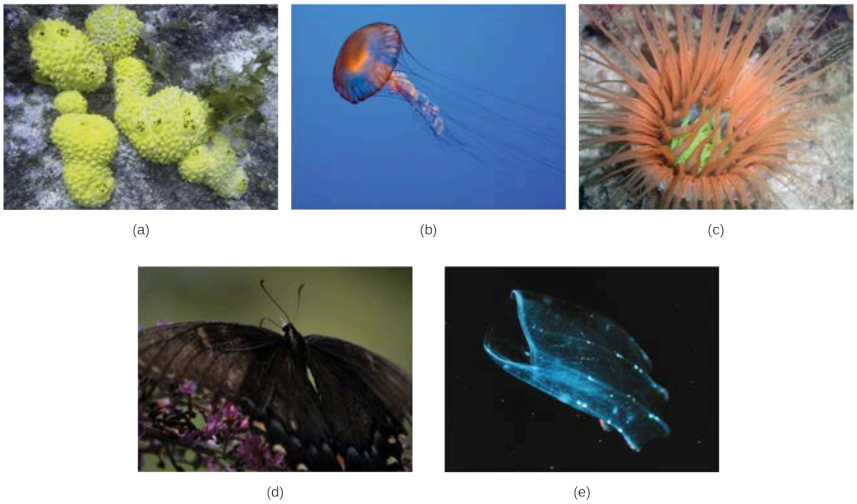

Figure 27.7 Symmetry in animals. The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, the (d) butterfly is bilaterally symmetrical. Rotational symmetry (e) is seen in the ctenophore *Beroe,* shown swimming open-mouthed. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker; credit e: modification of work by NOAA)

Bilateral symmetry involves the division of the animal through a midsagittal plane, resulting in two superficially mirror images, right and left halves, such as those of a butterfly (Figure 27.7**d**), crab, or human body. Animals with bilateral symmetry have a "head" and "tail" (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides (Figure 27.8). All Eumetazoa except those with secondary radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal's anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active and controlled directional mobility and increased sophistication of resource-seeking and predator-prey relationships.

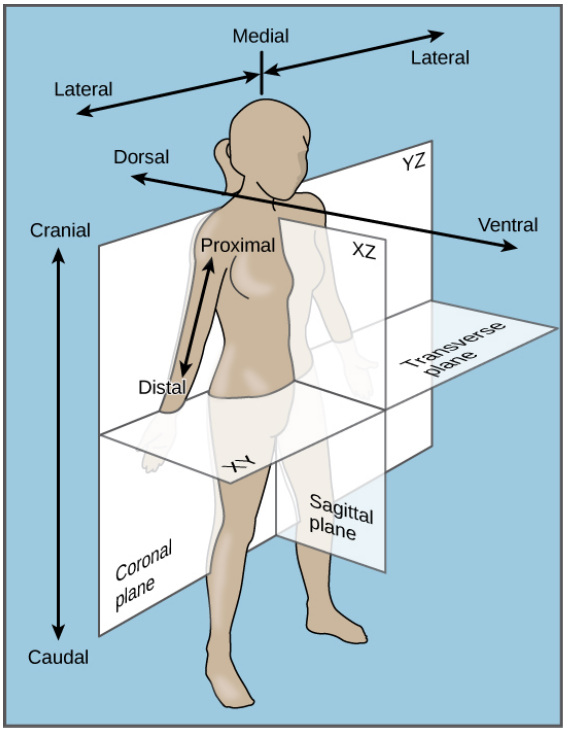

Figure 27.8 Bilateral symmetry. The bilaterally symmetrical human body can be divided by several planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display modified radial symmetry as adults, but as we have noted, their larval stages (such as the bipinnaria) initially exhibit bilateral symmetry until they metamorphose in animals with radial symmetry (this is termed secondary radial symmetry). Echinoderms evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

LINK TO LEARNING

Watch this video to see a quick sketch of the different types of body symmetry. **(This multimedia resource will open in a browser.) (http://cnx.org/content/m66578/1.3/#eip-id1165785284264)**

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during *gastrulation*, and that each germ layer typically gives rise to specific types of embryonic tissues and organs. Animals develop either two or three embryonic germ layers (Figure 27.9). The animals that display radial, biradial, or rotational symmetry develop two germ layers, an inner layer (*endoderm* or *mesendoderm*) and an outer layer (*ectoderm*). These animals are called **diploblasts**, and have a nonliving middle layer between the endoderm and ectoderm (although individual cells may be distributed through this middle layer, there is no *coherent* third layer of tissue). The four clades considered to be diploblastic have different levels of complexity and different developmental pathways, although there is little information about development in Placozoa. More complex animals (usually those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called **triploblasts**.

visual CONNECTION

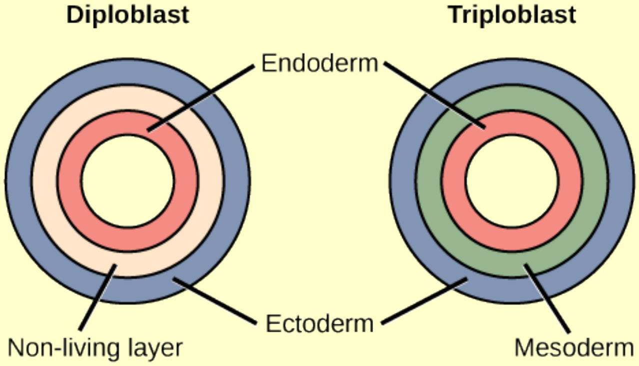

Figure 27.9 Diploblastic and triploblastic embryos. During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm or mesendoderm. Triploblasts develop a third layer—the mesoderm—which arises from mesendoderm and resides between the endoderm and ectoderm.

Which of the following statements about diploblasts and triploblasts is false?

a. Animals that display only radial symmetry during their lifespans are diploblasts.
b. Animals that display bilateral symmetry are triploblasts.
c. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
d. The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to specific body tissues and organs, although there are variations on these themes. Generally speaking, the endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the endoderm and ectoderm in triploblasts. This germ layer gives rise to all specialized muscle tissues (including the cardiac tissues and muscles of the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen. Diploblastic animals may have cell types that serve multiple functions, such as epitheliomuscular cells, which serve as a covering as well as contractile cells.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal *body cavity* derived from mesoderm, called a **coelom**, and those that do not. This epithelial cell-lined *coelomic cavity*, usually filled with fluid, lies between the visceral organs and the body wall. It houses many organs such as the digestive, urinary, and reproductive systems, the heart and lungs, and also contains the major arteries and veins of the circulatory system. In mammals, the body cavity is divided into the thoracic cavity, which houses the heart and lungs, and the abdominal cavity, which houses the digestive organs. In the thoracic cavity further subdivision produces the pleural cavity, which provides space for the lungs to expand during breathing, and the pericardial cavity, which provides room for movements of the heart. The evolution of the coelom is associated with many functional advantages. For example, the coelom provides cushioning and shock absorption for the major organ systems that it encloses. In addition, organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called **acoelomates**, and their mesoderm region is completely filled with tissue, although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called **eucoelomates** (or coelomates) (Figure 27.10). In such cases, a true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some freedom of movement. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom lined partly by mesoderm and partly by endoderm. Although still functionally a coelom, these are considered “false” coeloms, and so we call these animals **pseudocoelomates**. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on other features of their early embryological development.

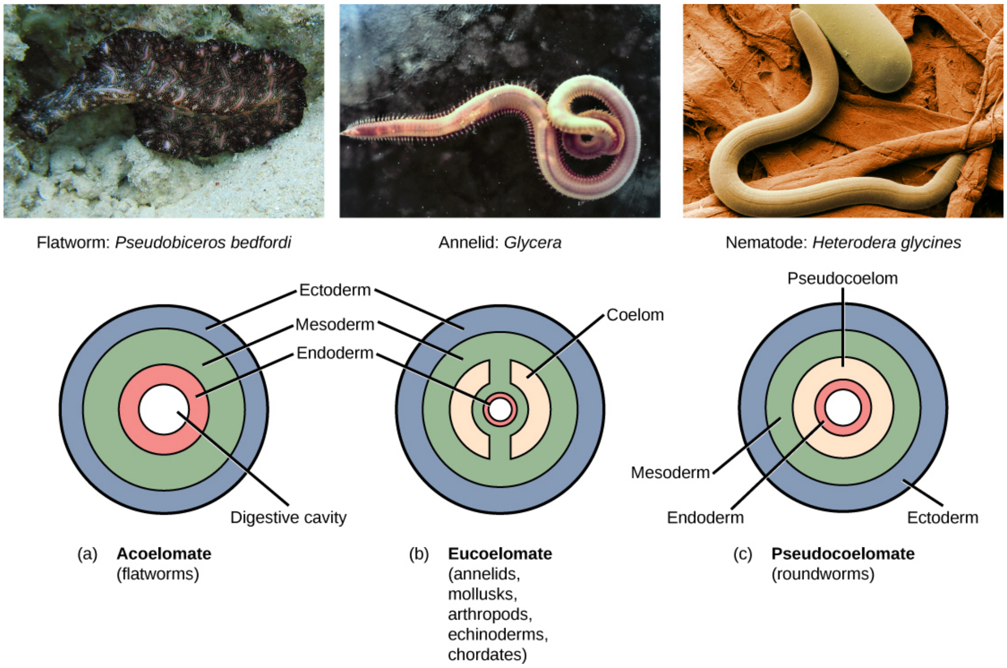

Figure 27.10 Body cavities. Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, in which both the gut and the body wall are lined with mesoderm. Pseudocoelomates also have a body cavity, but only the body wall is lined with mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, tribloblastic eucoelomates can be further divided into two groups based on differences in the origin of the mouth. When the primitive gut forms, the opening that first connects the gut cavity to the outside of the embryo is called the blastopore. Most animals have openings at both ends of the gut: mouth at one end and anus at the other. One of these openings will develop at or near the site of the **blastopore**. In **Protostomes** ("mouth first"), the mouth develops at the blastopore (Figure 27.11). In **Deuterostomes** ("mouth second"), the mouth develops at the other end of the gut (Figure 27.11) and the anus develops at the site of the blastopore. Protostomes include arthropods, mollusks, and annelids. Deuterostomes include more complex animals such as chordates but also some “simple” animals such as echinoderms. Recent evidence has challenged this simple view of the relationship between the location of the blastopore and the formation of the mouth, however, and the theory remains under debate. Nevertheless, these details of mouth and anus formation reflect *general* differences in the organization of protostome and deuterostome embryos, which are also expressed in other developmental features.

One of these differences between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. Since body cavity formation tends to accompany the formation of the mesoderm, the mesoderm of protostomes and deuterostomes forms differently. The coelom of most protostomes is formed through a process called **schizocoely**. The mesoderm in these organisms is usually the product of specific *blastomeres*, which migrate into the interior of the embryo and form two clumps of mesodermal tissue. Within each clump, cavities develop and merge to form the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called **enterocoely**. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse and expand to fill the space between the gut and the body wall, giving rise to the coelom.

Another difference in organization of protostome and deuterostome embryos is expressed during cleavage. Protostomes undergo **spiral cleavage**, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of cleavage relative to the two poles of the embryo. Deuterostomes undergo **radial cleavage**, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the parallel (up-and-down) alignment of the cells between the two poles.

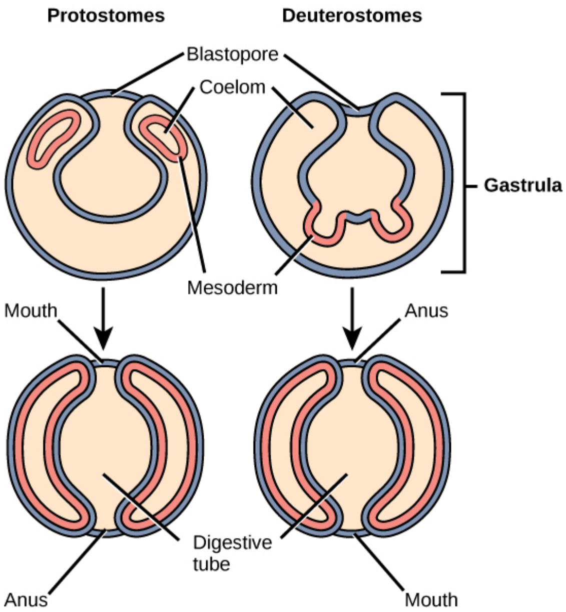

Figure 27.11 Protostomes and deuterostomes. Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, the mouth forms at or near the site of the blastopore and the body cavity forms by splitting the mesodermal mass during the process of schizocoely. In deuterostomes, the mouth forms at a site opposite the blastopore end of the embryo and the mesoderm pinches off to form the coelom during the process of enterocoely.

A second distinction between the types of cleavage in protostomes and deuterostomes relates to the fate of the resultant *blastomeres* (cells produced by cleavage). In addition to spiral cleavage, protostomes also undergo **determinate cleavage**. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A given cell does not have the ability to develop into any cell type other than its original destination. Removal of a blastomere from an embryo with determinate cleavage can result in missing structures, and embryos that fail to develop. In contrast, deuterostomes undergo **indeterminate cleavage**, in which cells are not yet fully committed at this early stage to develop into specific cell types. Removal of individual blastomeres from these embryos does not result in the loss of embryonic structures. In fact, twins (clones) can be produced as a result from blastomeres that have been separated from the original mass of blastomere cells. Unlike protostomes, however, if some blastomeres are damaged during embryogenesis, adjacent cells are able to compensate for the missing cells, and the embryo is not damaged. These cells are referred to as undetermined cells. This characteristic of deuterostomes is reflected in the existence of familiar *embryonic stem cells*, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

evolution CONNECTION

The Evolution of the Coelom

One of the first steps in the classification of animals is to examine the animal's body. One structure that is used in classification of animals is the body cavity or coelom. The body cavity develops *within* the mesoderm, so only triploblastic animals can have body cavities. Therefore body cavities are found only within the Bilateria. In other animal clades, the gut is either close to the body wall or separated from it by a jelly-like material. The body cavity is important for two reasons. Fluid within the body cavity protects the organs from shock and compression. In addition, since in triploblastic embryos, most muscle, connective tissue, and blood vessels develop from mesoderm, these tissues developing within the lining of the body cavity can reinforce the gut and body wall, aid in motility, and efficiently circulate nutrients.

To recap what we have discussed above, animals that do not have a coelom are called *acoelomates*. The major acoelomate group in the Bilateria is the flatworms, including both free-living and parasitic forms such as tapeworms. In these animals, mesenchyme fills the space between the gut and the body wall. Although two layers of muscle are found just under the epidermis, there is no muscle or other mesodermal tissue around the gut. Flatworms rely on passive diffusion for nutrient transport across their body.

In *pseudocoelomates*, there is a body cavity between the gut and the body wall, but only the body wall has mesodermal tissue. In these animals, the mesoderm forms, but does not develop cavities within it. Major pseudocoelomate phyla are the rotifers and nematodes. Animals that have a true coelom are called *eucoelomates*; all vertebrates, as well as molluscs, annelids, arthropods, and echinoderms, are eucoelomates. The coelom develops within the mesoderm during embryogenesis. Of the major bilaterian phyla, the molluscs, annelids, and arthropods are *schizocoels*, in which the mesoderm splits to form the body cavity, while the echinoderms and chordates are *enterocoels*, in which the mesoderm forms as two or more buds off of the gut. These buds separate from the gut and coalesce to form the body cavity. In the vertebrates, mammals have a subdivided body cavity, with the thoracic cavity separated from the abdominal cavity. The pseudocoelomates may have had eucoelomate ancestors and may have lost their ability to form a complete coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

27.3 | Animal Phylogeny

By the end of this section, you will be able to do the following:

- Interpret the metazoan phylogenetic tree
- Describe the types of data that scientists use to construct and revise animal phylogeny
- List some of the relationships within the modern phylogenetic tree that have been discovered as a result of modern molecular data

Biologists strive to understand the evolutionary history and relationships of members of the animal kingdom, and all of life, for that matter. The study of *phylogeny* (the branching sequence of evolution) aims to determine the evolutionary relationships between phyla. Currently, most biologists divide the animal kingdom into 35 to 40 phyla. Scientists develop phylogenetic trees, which serve as *hypotheses* about which species have evolved from which ancestors.

Recall that until recently, only morphological characteristics and the fossil record were used to determine phylogenetic relationships among animals. Scientific understanding of the distinctions and hierarchies between anatomical characteristics provided much of this knowledge. Used alone, however, this information can be misleading. Morphological characteristics (such as skin color, body shape, etc.) may evolve multiple times, and independently, through evolutionary history. Analogous characteristics may appear similar between animals, but their underlying evolution may be very different. With the advancement of *molecular technologies*, modern phylogenetics is now informed by genetic and molecular analyses, in addition to traditional morphological and fossil data. With a growing understanding of genetics, the animal evolutionary tree has changed substantially