27 | INTRODUCTION TO ANIMAL DIVERSITY

Figure 27.1 The leaf chameleon (*Brookesia micra*) was discovered in northern Madagascar in 2012. At just over one inch long, it is the smallest known chameleon. (credit: modification of work by Frank Glaw, et al., PLOS)

Chapter Outline

Introduction

Animal evolution began in the ocean over 600 million years ago with tiny creatures that probably do not resemble any living organism today. Since then, animals have evolved into a highly diverse kingdom. Although over one million extant (currently living) species of animals have been identified, scientists are continually discovering more species as they explore ecosystems around the world. The number of extant species is estimated to be between 3 and 30 million.

But what is an animal? While we can easily identify dogs, birds, fish, spiders, and worms as animals, other organisms, such as corals and sponges, are not as easy to classify. Animals vary in complexity—from sea sponges to crickets to chimpanzees—and scientists are faced with the difficult task of classifying them within a unified system. They must identify traits that are common to all animals as well as traits that can be used to distinguish among related groups of animals. The animal classification system characterizes animals based on their anatomy, morphology, evolutionary history, features of embryological development, and genetic makeup. This classification scheme is constantly developing as new information about species arises. Understanding and classifying the great variety of living species help us better understand how to conserve the diversity of life on earth.

27.1 | Features of the Animal Kingdom

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

- List the features that distinguish the kingdom Animalia from other kingdoms
- Explain the processes of animal reproduction and embryonic development
- Describe the roles that Hox genes play in development

Even though members of the animal kingdom are incredibly diverse, most animals share certain features that distinguish them from organisms in other kingdoms. All animals are eukaryotic, multicellular organisms, and almost all animals have a complex tissue structure with differentiated and specialized tissues. Most animals are motile, at least during certain life stages. All animals require a source of food and are therefore heterotrophic, ingesting other living or dead organisms; this feature distinguishes them from autotrophic organisms, such as most plants, which synthesize their own nutrients through photosynthesis. As heterotrophs, animals may be carnivores, herbivores, omnivores, or parasites (**Figure 27.2ab**). Most animals reproduce sexually, and the offspring pass through a series of developmental stages that establish a determined and fixed body plan. The **body plan** refers to the morphology of an animal, determined by developmental cues.

(a) (b)

Figure 27.2 All animals are heterotrophs that derive energy from food. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm *Dirofilaria immitis* is a parasite that derives energy from its hosts. It spends its larval stage in mosquitoes and its adult stage infesting the heart of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

Complex Tissue Structure

As multicellular organisms, animals differ from plants and fungi because their cells don’t have cell walls, their cells may be embedded in an extracellular matrix (such as bone, skin, or connective tissue), and their cells have unique structures for intercellular communication (such as gap junctions). In addition, animals possess unique tissues, absent in fungi and plants, which allow coordination (nerve tissue) of motility (muscle tissue). Animals are also characterized by specialized connective tissues that provide structural support for cells and organs. This connective tissue constitutes the extracellular surroundings of cells and is made up of organic and inorganic materials. In vertebrates, bone tissue is a type of connective tissue that supports the entire body structure. The complex bodies and activities of vertebrates demand such supportive tissues. Epithelial tissues cover, line, protect, and secrete. Epithelial tissues include the epidermis of the integument, the lining of the digestive tract and trachea, and make up the ducts of the liver and glands of advanced animals.

The animal kingdom is divided into Parazoa (sponges) and Eumetazoa (all other animals). As very simple animals, the organisms in group Parazoa (“beside animal”) do not contain true specialized tissues; although they do possess specialized cells that perform different functions, those cells are not organized into tissues. These organisms are considered animals since they lack the ability to make their own food. Animals with true tissues are in the group Eumetazoa (“true animals”). When we think of animals, we usually think of Eumetazoans, since most animals fall into this category.

The different types of tissues in true animals are responsible for carrying out specific functions for the organism. This differentiation and specialization of tissues is part of what allows for such incredible animal diversity. For example, the evolution of nerve tissues and muscle tissues has resulted in animals’ unique ability to rapidly sense and respond to changes in their environment. This allows animals to survive in environments where they must compete with other species to meet their nutritional demands.

LINK TO LEARNING

Watch a **presentation (http://openstaxcollege.org/l/saving_life)** by biologist E.O. Wilson on the importance of diversity.

Animal Reproduction and Development

Most animals are diploid organisms, meaning that their body (somatic) cells are diploid and haploid reproductive (gamete) cells are produced through meiosis. Some exceptions exist: For example, in bees, wasps, and ants, the male is haploid because it develops from unfertilized eggs. Most animals undergo sexual reproduction: This fact distinguishes animals from fungi, protists, and bacteria, where asexual reproduction is common or exclusive. However, a few groups, such as cnidarians, flatworm, and roundworms, undergo asexual reproduction, although nearly all of those animals also have a sexual phase to their life cycle.

Processes of Animal Reproduction and Embryonic Development

During sexual reproduction, the haploid gametes of the male and female individuals of a species combine in a process called fertilization. Typically, the small, motile male sperm fertilizes the much larger, sessile female egg. This process produces a diploid fertilized egg called a zygote.

Some animal species—including sea stars and sea anemones, as well as some insects, reptiles, and fish—are capable of asexual reproduction. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation, where part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain insects and vertebrates is called parthenogenesis (or "virgin beginning"), where unfertilized eggs can develop into new male offspring. This type of parthenogenesis is called haplodiploidy. These types of asexual reproduction produce genetically identical offspring, which is disadvantageous from the perspective of evolutionary adaptability because of the potential buildup of deleterious mutations. However, for animals that are limited in their capacity to attract mates, asexual reproduction can ensure genetic propagation.

After fertilization, a series of developmental stages occur during which primary germ layers are established and reorganize to form an embryo. During this process, animal tissues begin to specialize and organize into organs and organ systems, determining their future morphology and physiology. Some animals, such as grasshoppers, undergo incomplete metamorphosis, in which the young resemble the adult. Other animals, such as some insects, undergo complete metamorphosis where individuals enter one or more larval stages that may in differ in structure and function from the adult (**Figure 27.3**). For the latter, the young and the adult may have different diets, limiting competition for food between them. Regardless of whether a species undergoes complete or incomplete metamorphosis, the series of developmental stages of the embryo remains largely the same for most members of the animal kingdom.

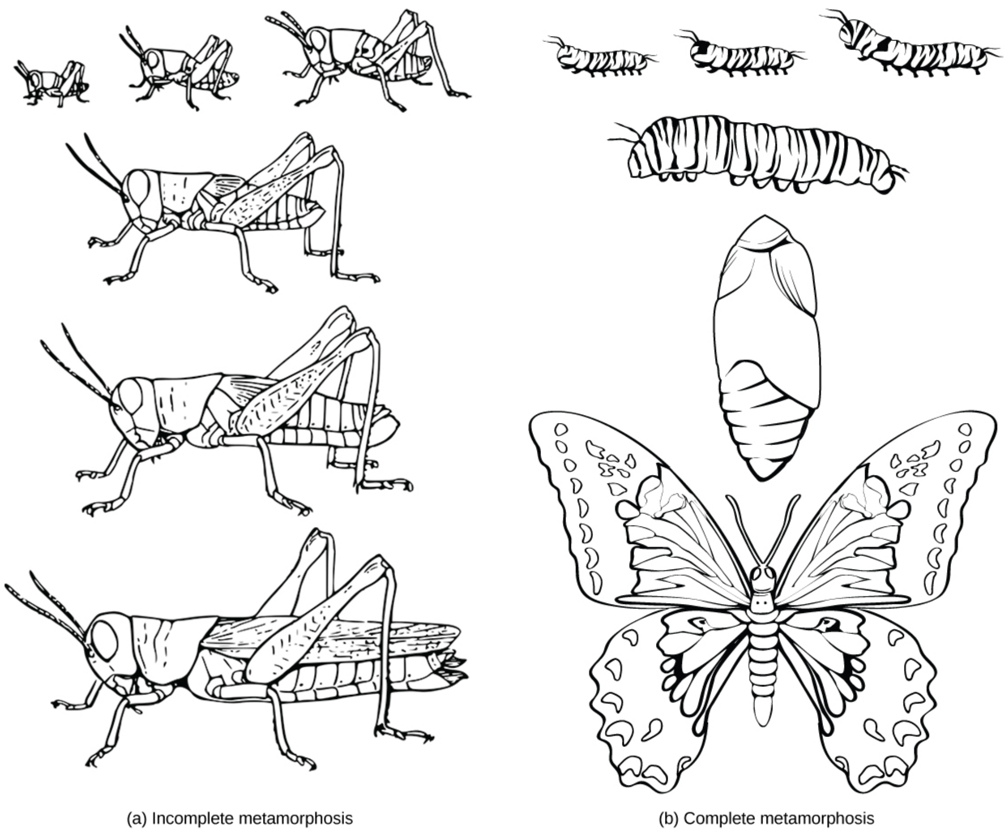

Figure 27.3 (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

The process of animal development begins with the **cleavage**, or series of mitotic cell divisions, of the zygote (**Figure 27.4**). Three cell divisions transform the single-celled zygote into an eight-celled structure. After further cell division and rearrangement of existing cells, a 6–32-celled hollow structure called a **blastula** is formed. Next, the blastula undergoes further cell division and cellular rearrangement during a process called gastrulation. This leads to the formation of the next developmental stage, the **gastrula**, in which the future digestive cavity is formed. Different cell layers (called **germ layers**) are formed during gastrulation. These germ layers are programmed to develop into certain tissue types, organs, and organ systems during a process called **organogenesis**.

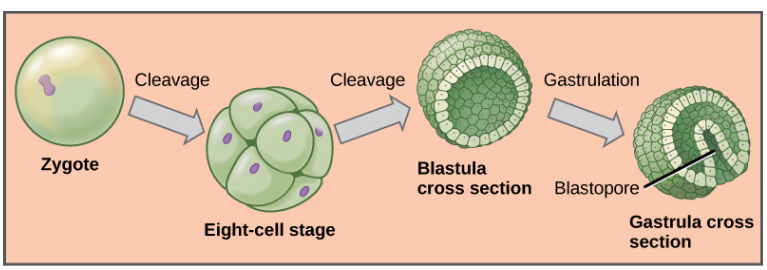

Figure 27.4 During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

LINK TO LEARNING

Watch the following **video (http://openstaxcollege.org/l/embryo_evol)** to see how human embryonic development (after the blastula and gastrula stages of development) reflects evolution.

The Role of Homeobox (Hox) Genes in Animal Development

Since the early 19^{th} century, scientists have observed that many animals, from the very simple to the complex, shared similar embryonic morphology and development. Surprisingly, a human embryo and a frog embryo, at a certain stage of embryonic development, look remarkably alike. For a long time, scientists did not understand why so many animal species looked similar during embryonic development but were very different as adults. They wondered what dictated the developmental direction that a fly, mouse, frog, or human embryo would take. Near the end of the 20^{th} century, a particular class of genes was discovered that had this very job. These genes that determine animal structure are called "homeotic genes," and they contain DNA sequences called homeoboxes. The animal genes containing homeobox sequences are specifically referred to as ***Hox* genes**. This family of genes is responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality. The first *Hox* genes to be sequenced were those from the fruit fly (*Drosophila melanogaster*). A single *Hox* mutation in the fruit fly can result in an extra pair of wings or even appendages growing from the "wrong" body part.

While there are a great many genes that play roles in the morphological development of an animal, 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 coding transcription factors that control the expression of numerous other genes. *Hox* genes are homologous in 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**). One of the contributions to increased animal body complexity is that *Hox* genes have undergone at least two duplication events during animal evolution, with the additional genes allowing for more complex body types to evolve.

art CONNECTION

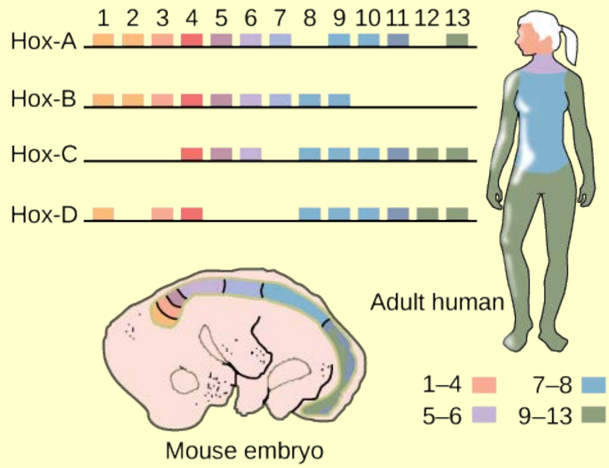

Figure 27.5 *Hox* genes are highly conserved genes encoding transcription factors that determine the course of embryonic development in animals. In vertebrates, the genes have been duplicated into four clusters: *Hox-A*, *Hox-B*, *Hox-C*, and *Hox-D*. Genes within these clusters are expressed in certain 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.

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

27.2 | Features Used to Classify Animals

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

- 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 are primarily classified according to morphological and developmental characteristics, such as a body plan. One of the most prominent features of the body plan of true animals is that they are morphologically symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development, such as the origin of the mouth and anus.

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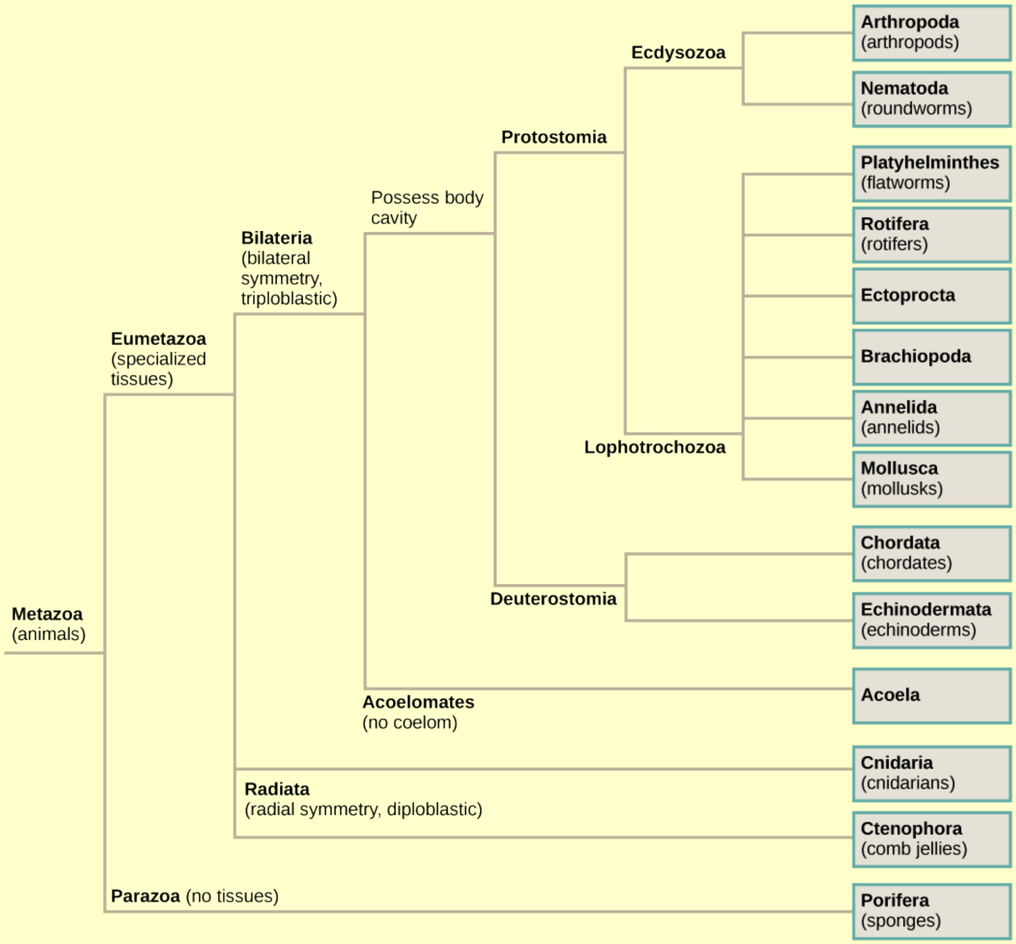


Figure 27.6 The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

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 a unique feature of Parazoa (**Figure 27.7a**). Only a few animal groups display radial symmetry. 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 drinking glass or pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or “oral side,” and the side without a mouth (the “aboral side”). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones (**Figure 27.7bc**). 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.

Figure 27.7 The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d) butterfly is bilaterally symmetrical. (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)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror image, right and left halves, such as those of a butterfly (**Figure 27.7d**), 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 true animals except those with 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 mobility and increased sophistication of resource-seeking and predator-prey relationships.

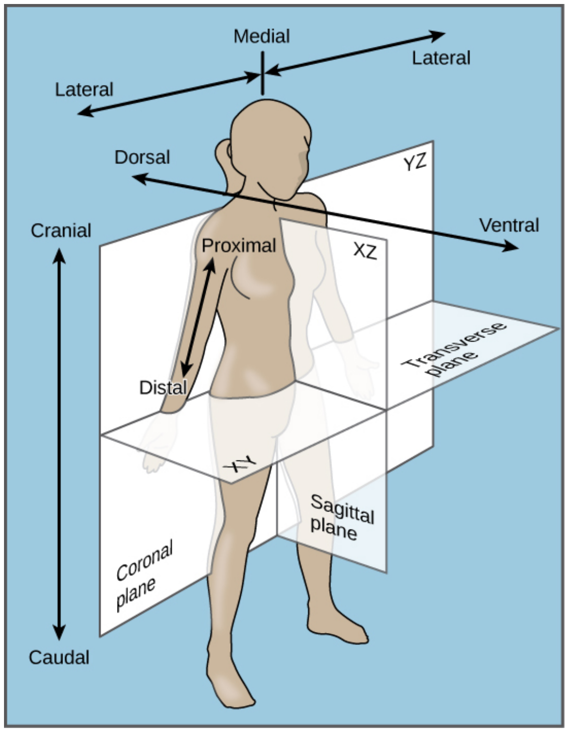


Figure 27.8 The bilaterally symmetrical human body can be divided into planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

LINK TO LEARNING

Watch this **video (http://openstaxcollege.org/l/symmetry)** to see a quick sketch of the different types of body symmetry.

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 they are predetermined to develop into the animal's specialized tissues and organs. Animals develop either two or three embryonic germs layers (**Figure 27.9**). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called **diploblasts**. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (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**.

art CONNECTION

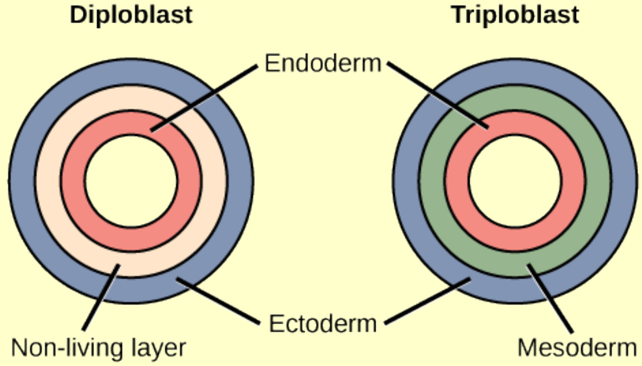


Figure 27.9 During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

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

a. Animals that display radial symmetry 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 particular body tissues and organs. 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 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.

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 represents a space, usually filled with fluid, which lies between the visceral organs and the body wall. It houses many organs such as the digestive system, kidneys, reproductive organs, and heart, and contains the circulatory system. In some animals, such as mammals, the part of the coelom called the pleural cavity provides space for the lungs to expand during breathing. The evolution of the coelom is associated with many functional advantages. Primarily, the coelom provides cushioning and shock absorption for the major organ systems. 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**). 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 free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is found between the two layers. Although still functional, these are considered false coeloms, and those animals are called **pseudocoelomates**. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.

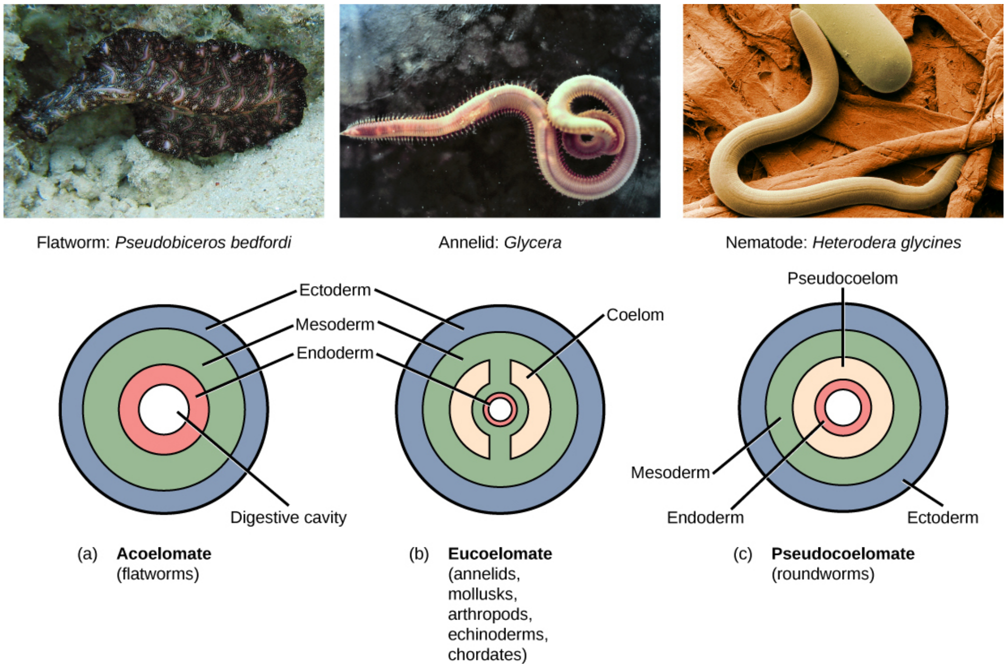


Figure 27.10 Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and 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 their early embryonic development. **Protostomes** include arthropods, mollusks, and annelids. **Deuterostomes** include more complex animals such as chordates but also some simple animals such as echinoderms. These two groups are separated based on which opening of the digestive cavity develops first: mouth or anus. The word protostome comes from the Greek word meaning “mouth first,” and deuterostome originates from the word meaning “mouth second” (in this case, the anus develops first). The mouth or anus develops from a structure called the blastopore (**Figure 27.11**). The **blastopore** is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus (**Figure 27.11**). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called **schizocoely**, meaning that during development, a solid mass of the mesoderm splits apart and forms 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 to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and deuterostomes is the type of cleavage undergone by the zygote. 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 the cleavage. Deuterostomes undergo **radial cleavage**, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.

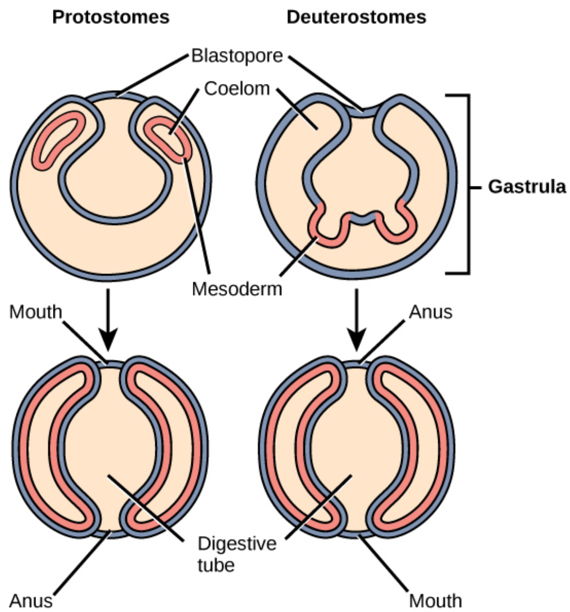


Figure 27.11 Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

There is a second distinction between the types of cleavage in protostomes and deuterostomes. 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 cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo **indeterminate cleavage**, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells are referred to as undifferentiated 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. Studying the body parts tells us not only the roles of the organs in question but also how the species may have evolved. One such structure that is used in classification of animals is the coelom. A coelom is a body cavity that forms during early embryonic development. The coelom allows for compartmentalization of the body parts, so that different organ systems can evolve and nutrient transport is possible. Additionally, because the coelom is a fluid-filled cavity, it protects the organs from shock and compression. Simple animals, such as worms and jellyfish, do not have a coelom. All vertebrates have a coelom that helped them evolve complex organ systems.

Animals that do not have a coelom are called acoelomates. Flatworms and tapeworms are examples of acoelomates. They rely on passive diffusion for nutrient transport across their body. Additionally, the internal organs of acoelomates are not protected from crushing.

Animals that have a true coelom are called eucoelomates; all vertebrates are eucoelomates. The coelom evolves from the mesoderm during embryogenesis. The abdominal cavity contains the stomach, liver, gall bladder, and other digestive organs. Another category of invertebrates animals based on body cavity is pseudocoelomates. These animals have a pseudo-cavity that is not completely lined by mesoderm. Examples include nematode parasites and small worms. These animals are thought to have evolved from coelomates and may have lost their ability to form a 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:

- 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 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 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 and continues to change as new DNA and RNA analyses are performed on additional animal species.

Constructing an Animal Phylogenetic Tree

The current understanding of evolutionary relationships between animal, or **Metazoa**, phyla begins with the distinction between "true" animals with true differentiated tissues, called **Eumetazoa**, and animal phyla that do not have true differentiated tissues (such as the sponges), called **Parazoa**. Both Parazoa and Eumetazoa evolved from a common ancestral organism that resembles the modern-day protists called choanoflagellates. These protist cells strongly resemble the sponge choanocyte cells today (Figure 27.12).

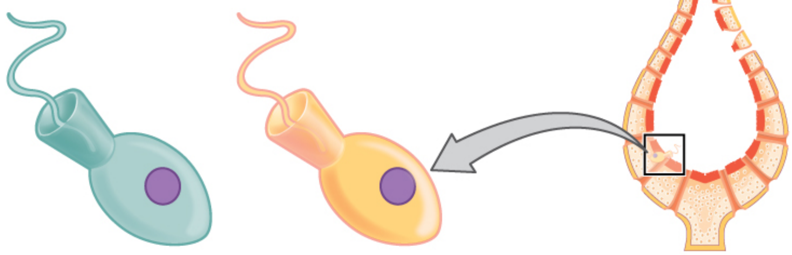


Figure 27.12 Cells of the protist choanoflagellate resemble sponge choanocyte cells. Beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and waste removed.

Eumetazoa are subdivided into radially symmetrical animals and bilaterally symmetrical animals, and are thus classified into clade Bilateria or Radiata, respectively. As mentioned earlier, the cnidarians and ctenophores are animal phyla with true radial symmetry. All other Eumetazoa are members of the Bilateria clade. The bilaterally symmetrical animals are further divided into deuterostomes (including chordates and echinoderms) and two distinct clades of protostomes (including ecdysozoans and lophotrochozoans) (Figure 27.13ab). **Ecdysozoa** includes nematodes and arthropods; they are so named for a commonly found characteristic among the group: exoskeletal molting (termed ecdysis). **Lophotrochozoa** is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called trochophore larvae, and other phyla are characterized by the presence of a feeding structure called a lophophore.

Figure 27.13 Animals that molt their exoskeletons, such as these (a) Madagascar hissing cockroaches, are in the clade Ecdysozoa. (b) Phoronids are in the clade Lophotrochozoa. The tentacles are part of a feeding structure called a lophophore. (credit a: modification of work by Whitney Cranshaw, Colorado State University, Bugwood.org; credit b: modification of work by NOAA)

LINK TO LEARNING

Explore an interactive tree (http://openstaxcollege.org/l/tree_of_life2) of life here. Zoom and click to learn more about the organisms and their evolutionary relationships.

Modern Advances in Phylogenetic Understanding Come from Molecular Analyses

The phylogenetic groupings are continually being debated and refined by evolutionary biologists. Each year, new evidence emerges that further alters the relationships described by a phylogenetic tree diagram.

LINK TO LEARNING

Watch the following **video (http://openstaxcollege.org/l/build_phylogeny)** to learn how biologists use genetic data to determine relationships among organisms.

Nucleic acid and protein analyses have greatly informed the modern phylogenetic animal tree. These data come from a variety of molecular sources, such as mitochondrial DNA, nuclear DNA, ribosomal RNA (rRNA), and certain cellular proteins. Many evolutionary relationships in the modern tree have only recently been determined due to molecular evidence. For example, a previously classified group of animals called lophophorates, which included brachiopods and bryozoans, were long-thought to be primitive deuterostomes. Extensive molecular analysis using rRNA data found these animals to be protostomes, more closely related to annelids and mollusks. This discovery allowed for the distinction of the protostome clade, the lophotrochozoans. Molecular data have also shed light on some differences within the lophotrochozoan group, and some scientists believe that the phyla Platyhelminthes and Rotifera within this group should actually belong to their own group of protostomes termed Platyzoa.

Molecular research similar to the discoveries that brought about the distinction of the lophotrochozoan clade has also revealed a dramatic rearrangement of the relationships between mollusks, annelids, arthropods, and nematodes, and a new ecdysozoan clade was formed. Due to morphological similarities in their segmented body types, annelids and arthropods were once thought to be closely related. However, molecular evidence has revealed that arthropods are actually more closely related to nematodes, now comprising the ecdysozoan clade, and annelids are more closely related to mollusks, brachiopods, and other phyla in the lophotrochozoan clade. These two clades now make up the protostomes.

Another change to former phylogenetic groupings because of molecular analyses includes the emergence of an entirely new phylum of worm called Acoelomorpha. These acoel flatworms were long thought to belong to the phylum Platyhelminthes because of their similar “flatworm” morphology. However, molecular analyses revealed this to be a false relationship and originally suggested that acoels represented living species of some of the earliest divergent bilaterians. More recent research into the acoelomorphs has called this hypothesis into question and suggested a closer relationship with deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

27.4 | The Evolutionary History of the Animal Kingdom

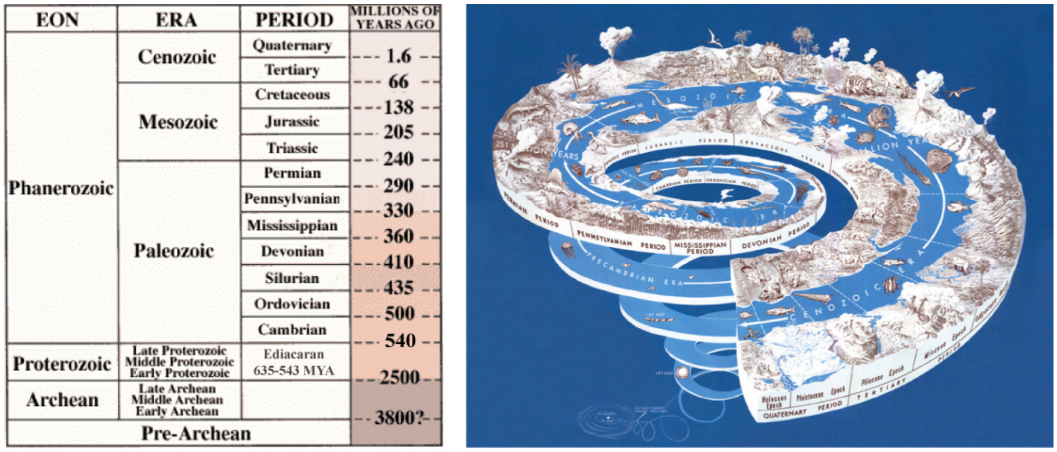
By the end of this section, you will be able to:

- Describe the features that characterized the earliest animals and when they appeared on earth
- Explain the significance of the Cambrian period for animal evolution and the changes in animal diversity that took place during that time
- Describe some of the unresolved questions surrounding the Cambrian explosion
- Discuss the implications of mass animal extinctions that have occurred in evolutionary history

Many questions regarding the origins and evolutionary history of the animal kingdom continue to be researched and debated, as new fossil and molecular evidence change prevailing theories. Some of these questions include the following: How long have animals existed on Earth? What were the earliest members of the animal kingdom, and what organism was their common ancestor? While animal diversity increased during the Cambrian period of the Paleozoic era, 530 million years ago, modern fossil evidence suggests that primitive animal species existed much earlier.

Pre-Cambrian Animal Life

The time before the Cambrian period is known as the **Ediacaran period** (from about 635 million years ago to 543 million years ago), the final period of the late Proterozoic Neoproterozoic Era (**Figure 27.14**). It is believed that early animal life, termed Ediacaran biota, evolved from protists at this time. Some protest species called choanoflagellates closely resemble the choanocyte cells in the simplest animals, sponges. In addition to their morphological similarity, molecular analyses have revealed similar sequence homologies in their DNA.



(a) (b)

Figure 27.14 (a) Earth's history is divided into eons, eras, and periods. Note that the Ediacaran period starts in the Proterozoic eon and ends in the Cambrian period of the Phanerozoic eon. (b) Stages on the geological time scale are represented as a spiral. (credit: modification of work by USGS)

The earliest life comprising Ediacaran biota was long believed to include only tiny, sessile, soft-bodied sea creatures. However, recently there has been increasing scientific evidence suggesting that more varied and complex animal species lived during this time, and possibly even before the Ediacaran period.

Fossils believed to represent the oldest animals with hard body parts were recently discovered in South Australia. These sponge-like fossils, named *Coronacollina acula*, date back as far as 560 million years, and are believed to show the existence of hard body parts and spicules that extended 20–40 cm from the main body (estimated about 5 cm long). Other fossils from the Ediacaran period are shown in **Figure 27.15ab**.

(a) (b)

Figure 27.15 Fossils of (a) *Cyclomedusa* and (b) *Dickinsonia* date to 650 million years ago, during the Ediacaran period. (credit: modification of work by "Smith609"/Wikimedia Commons)

Another recent fossil discovery may represent the earliest animal species ever found. While the validity of this claim is still under investigation, these primitive fossils appear to be small, one-centimeter long, sponge-like creatures. These fossils from South Australia date back 650 million years, actually placing the putative animal before the great ice age extinction event that marked the transition between the **Cryogenian period** and the Ediacaran period. Until this discovery, most scientists believed that there was no animal life prior to the Ediacaran period. Many scientists now believe that animals may in fact have evolved during the Cryogenian period.

The Cambrian Explosion of Animal Life

The Cambrian period, occurring between approximately 542–488 million years ago, marks the most rapid evolution of new animal phyla and animal diversity in Earth's history. It is believed that most of the animal phyla in existence today had their origins during this time, often referred to as the **Cambrian explosion** (**Figure 27.16**). Echinoderms, mollusks, worms, arthropods, and chordates arose during this period. One of the most dominant species during the Cambrian period was the trilobite, an arthropod that was among the first animals to exhibit a sense of vision (**Figure 27.17abcd**).

Figure 27.16 An artist's rendition depicts some organisms from the Cambrian period.

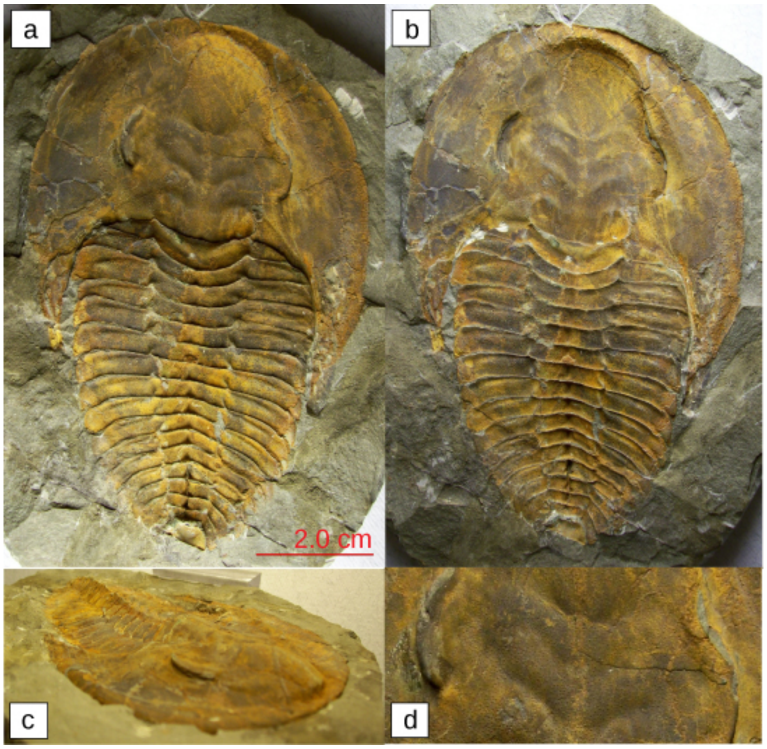


Figure 27.17 These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago.

The cause of the Cambrian explosion is still debated. There are many theories that attempt to answer this question. Environmental changes may have created a more suitable environment for animal life. Examples of these changes include rising atmospheric oxygen levels and large increases in oceanic calcium concentrations that preceded the Cambrian period

(**Figure 27.18**). Some scientists believe that an expansive, continental shelf with numerous shallow lagoons or pools provided the necessary living space for larger numbers of different types of animals to co-exist. There is also support for theories that argue that ecological relationships between species, such as changes in the food web, competition for food and space, and predator-prey relationships, were primed to promote a sudden massive coevolution of species. Yet other theories claim genetic and developmental reasons for the Cambrian explosion. The morphological flexibility and complexity of animal development afforded by the evolution of *Hox* control genes may have provided the necessary opportunities for increases in possible animal morphologies at the time of the Cambrian period. Theories that attempt to explain why the Cambrian explosion happened must be able to provide valid reasons for the massive animal diversification, as well as explain why it happened *when* it did. There is evidence that both supports and refutes each of the theories described above, and the answer may very well be a combination of these and other theories.

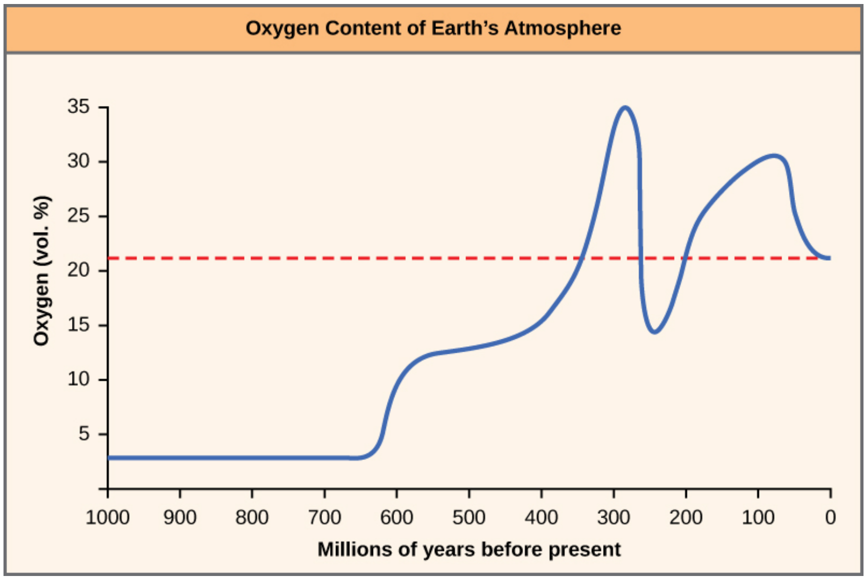


Figure 27.18 The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

However, unresolved questions about the animal diversification that took place during the Cambrian period remain. For example, we do not understand how the evolution of so many species occurred in such a short period of time. Was there really an "explosion" of life at this particular time? Some scientists question the validity of the this idea, because there is increasing evidence to suggest that more animal life existed prior to the Cambrian period and that other similar species' so-called explosions (or radiations) occurred later in history as well. Furthermore, the vast diversification of animal species that appears to have begun during the Cambrian period continued well into the following Ordovician period. Despite some of these arguments, most scientists agree that the Cambrian period marked a time of impressively rapid animal evolution and diversification that is unmatched elsewhere during history.

LINK TO LEARNING

View an **animation (http://openstaxcollege.org/l/ocean_life)** of what ocean life may have been like during the Cambrian explosion.

Post-Cambrian Evolution and Mass Extinctions

The periods that followed the Cambrian during the Paleozoic Era are marked by further animal evolution and the emergence of many new orders, families, and species. As animal phyla continued to diversify, new species adapted to new ecological niches. During the Ordovician period, which followed the Cambrian period, plant life first appeared on land. This change allowed formerly aquatic animal species to invade land, feeding directly on plants or decaying vegetation.

Continual changes in temperature and moisture throughout the remainder of the Paleozoic Era due to continental plate movements encouraged the development of new adaptations to terrestrial existence in animals, such as limbed appendages in amphibians and epidermal scales in reptiles.

Changes in the environment often create new niches (living spaces) that contribute to rapid speciation and increased diversity. On the other hand, cataclysmic events, such as volcanic eruptions and meteor strikes that obliterate life, can result in devastating losses of diversity. Such periods of **mass extinction** (Figure 27.19) have occurred repeatedly in the evolutionary record of life, erasing some genetic lines while creating room for others to evolve into the empty niches left behind. The end of the Permian period (and the Paleozoic Era) was marked by the largest mass extinction event in Earth's history, a loss of roughly 95 percent of the extant species at that time. Some of the dominant phyla in the world's oceans, such as the trilobites, disappeared completely. On land, the disappearance of some dominant species of Permian reptiles made it possible for a new line of reptiles to emerge, the dinosaurs. The warm and stable climatic conditions of the ensuing Mesozoic Era promoted an explosive diversification of dinosaurs into every conceivable niche in land, air, and water. Plants, too, radiated into new landscapes and empty niches, creating complex communities of producers and consumers, some of which became very large on the abundant food available.

Another mass extinction event occurred at the end of the Cretaceous period, bringing the Mesozoic Era to an end. Skies darkened and temperatures fell as a large meteor impact and tons of volcanic ash blocked incoming sunlight. Plants died, herbivores and carnivores starved, and the mostly cold-blooded dinosaurs ceded their dominance of the landscape to more warm-blooded mammals. In the following Cenozoic Era, mammals radiated into terrestrial and aquatic niches once occupied by dinosaurs, and birds, the warm-blooded offshoots of one line of the ruling reptiles, became aerial specialists. The appearance and dominance of flowering plants in the Cenozoic Era created new niches for insects, as well as for birds and mammals. Changes in animal species diversity during the late Cretaceous and early Cenozoic were also promoted by a dramatic shift in Earth's geography, as continental plates slid over the crust into their current positions, leaving some animal groups isolated on islands and continents, or separated by mountain ranges or inland seas from other competitors. Early in the Cenozoic, new ecosystems appeared, with the evolution of grasses and coral reefs. Late in the Cenozoic, further extinctions followed by speciation occurred during ice ages that covered high latitudes with ice and then retreated, leaving new open spaces for colonization.

LINK TO LEARNING

Watch the following video (http://openstaxcollege.org/l/mass_extinction) to learn more about the mass extinctions.

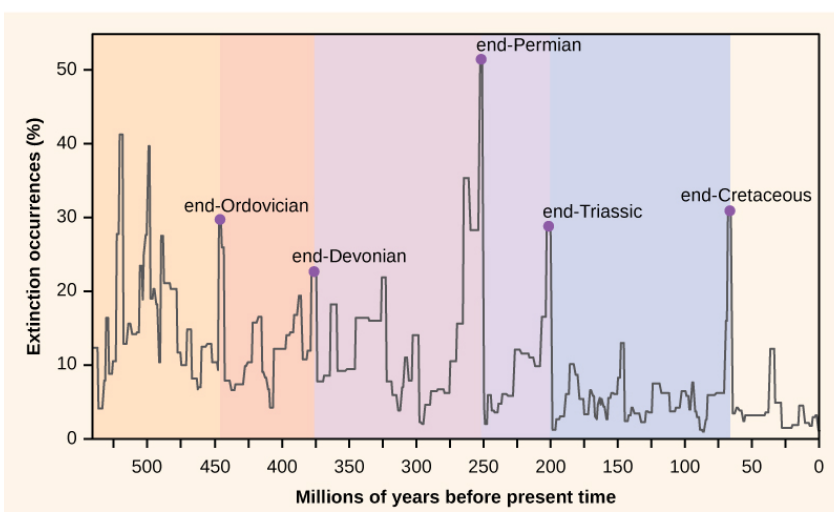


Figure 27.19 Mass extinctions have occurred repeatedly over geological time.

career CONNECTION

Paleontologist

Natural history museums contain the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontogists are scientists who study prehistoric life. They use fossils to observe and explain how life evolved on Earth and how species interacted with each other and with the environment. A paleontologist needs to be knowledgeable in biology, ecology, chemistry, geology, and many other scientific disciplines. A paleontologist's work may involve field studies: searching for and studying fossils. In addition to digging for and finding fossils, paleontologists also prepare fossils for further study and analysis. Although dinosaurs are probably the first animals that come to mind when thinking about paleontology, paleontologists study everything from plant life, fungi, and fish to sea animals and birds.

An undergraduate degree in earth science or biology is a good place to start toward the career path of becoming a paleontologist. Most often, a graduate degree is necessary. Additionally, work experience in a museum or in a paleontology lab is useful.

KEY TERMS

acoelomate animal without a body cavity

bilateral symmetry type of symmetry in which there is only one plane of symmetry, so the left and right halves of an animal are mirror images

blastopore indentation formed during gastrulation, evident in the gastrula stage

blastula 16–32 cell stage of development of an animal embryo

body plan morphology or constant shape of an organism

Cambrian explosion time during the Cambrian period (542–488 million years ago) when most of the animal phyla in existence today evolved

cleavage cell division of a fertilized egg (zygote) to form a multicellular embryo

coelom lined body cavity

Cryogenian period geologic period (850–630 million years ago) characterized by a very cold global climate

determinate cleavage developmental tissue fate of each embryonic cell is already determined

deuterostome blastopore develops into the anus, with the second opening developing into the mouth

diploblast animal that develops from two germ layers

Ecdysozoa clade of protostomes that exhibit exoskeletal molting (ecdysis)

Ediacaran period geological period (630–542 million years ago) when the oldest definite multicellular organisms with tissues evolved

enterocoely mesoderm of deuterostomes develops as pouches that are pinched off from endodermal tissue, cavity contained within the pouches becomes coelom

eucoelomate animal with a body cavity completely lined with mesodermal tissue

Eumetazoa group of animals with true differentiated tissues

gastrula stage of animal development characterized by the formation of the digestive cavity

germ layer collection of cells formed during embryogenesis that will give rise to future body tissues, more pronounced in vertebrate embryogenesis

Hox gene (also, homeobox gene) master control gene that can turn on or off large numbers of other genes during embryogenesis

indeterminate cleavage early stage of development when germ cells or “stem cells” are not yet pre-determined to develop into specific cell types

Lophotrochozoa clade of protostomes that exhibit a trochophore larvae stage or a lophophore feeding structure

mass extinction event that wipes out the majority of species within a relatively short geological time period

Metazoa group containing all animals

organogenesis formation of organs in animal embryogenesis

Parazoa group of animals without true differentiated tissues

protostome blastopore develops into the mouth of protostomes, with the second opening developing into the anus

pseudocoelomate animal with a body cavity located between the mesoderm and endoderm

radial cleavage cleavage axes are parallel or perpendicular to the polar axis, resulting in the alignment of cells between the two poles

radial symmetry type of symmetry with multiple planes of symmetry, with body parts (rays) arranged around a central disk

schizocoely during development of protostomes, a solid mass of mesoderm splits apart and forms the hollow opening of the coelom

spiral cleavage cells of one pole of the embryo are rotated or misaligned with respect to the cells of the opposite pole

triploblast animal that develops from three germ layers

CHAPTER SUMMARY

27.1 Features of the Animal Kingdom

Animals constitute an incredibly diverse kingdom of organisms. Although animals range in complexity from simple sea sponges to human beings, most members of the animal kingdom share certain features. Animals are eukaryotic, multicellular, heterotrophic organisms that ingest their food and usually develop into motile creatures with a fixed body plan. A major characteristic unique to the animal kingdom is the presence of differentiated tissues, such as nerve, muscle, and connective tissues, which are specialized to perform specific functions. Most animals undergo sexual reproduction, leading to a series of developmental embryonic stages that are relatively similar across the animal kingdom. A class of transcriptional control genes called *Hox* genes directs the organization of the major animal body plans, and these genes are strongly homologous across the animal kingdom.

27.2 Features Used to Classify Animals

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

27.3 Animal Phylogeny

Scientists are interested in the evolutionary history of animals and the evolutionary relationships among them. There are three main sources of data that scientists use to create phylogenetic evolutionary tree diagrams that illustrate such relationships: morphological information (which includes developmental morphologies), fossil record data, and, most recently, molecular data. The details of the modern phylogenetic tree change frequently as new data are gathered, and molecular data has recently contributed to many substantial modifications of the understanding of relationships between animal phyla.

27.4 The Evolutionary History of the Animal Kingdom

The most rapid diversification and evolution of animal species in all of history occurred during the Cambrian period of the Paleozoic Era, a phenomenon known as the Cambrian explosion. Until recently, scientists believed that there were only very few tiny and simplistic animal species in existence before this period. However, recent fossil discoveries have revealed that additional, larger, and more complex animals existed during the Ediacaran period, and even possibly earlier, during the Cryogenian period. Still, the Cambrian period undoubtedly witnessed the emergence of the majority of animal phyla that we know today, although many questions remain unresolved about this historical phenomenon.

The remainder of the Paleozoic Era is marked by the growing appearance of new classes, families, and species, and the early colonization of land by certain marine animals. The evolutionary history of animals is also marked by numerous major extinction events, each of which wiped out a majority of extant species. Some species of most animal phyla survived these extinctions, allowing the phyla to persist and continue to evolve into species that we see today.

ART CONNECTION QUESTIONS

1. Figure 27.5 If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

2. Figure 27.6 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.

3. Figure 27.9 Which of the following statements about diploblasts and triploblasts is false?

a. Animals that display radial symmetry 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.

REVIEW QUESTIONS

4. Which of the following is not a feature common to *most* animals?

a. development into a fixed body plan
b. asexual reproduction
c. specialized tissues
d. heterotrophic nutrient sourcing

5. During embryonic development, unique cell layers develop and distinguish during a stage called ________.

a. the blastula stage
b. the germ layer stage
c. the gastrula stage
d. the organogenesis stage

6. Which of the following phenotypes would most likely be the result of a *Hox* gene mutation?

a. abnormal body length or height
b. two different eye colors
c. the contraction of a genetic illness
d. two fewer appendages than normal

7. Which of the following organism is most likely to be a diploblast?

a. sea star
b. shrimp
c. jellyfish
d. insect

8. Which of the following is not possible?

a. radially symmetrical diploblast
b. diploblastic eucoelomate
c. protostomic coelomate
d. bilaterally symmetrical deuterostome

9. An animal whose development is marked by radial cleavage and enterocoely is ________.

a. a deuterostome
b. an annelid or mollusk
c. either an acoelomate or eucoelomate
d. none of the above

10. Consulting the modern phylogenetic tree of animals, which of the following would not constitute a clade?

a. deuterostomes
b. lophotrochozoans
c. Parazoa
d. Bilateria

11. Which of the following is thought to be the most closely related to the common animal ancestor?

a. fungal cells
b. protist cells
c. plant cells
d. bacterial cells

12. As with the emergence of the Acoelomorpha phylum, it is common for ____ data to misplace animals in close relation to other species, whereas ____ data often reveals a different and more accurate evolutionary relationship.

a. molecular : morphological
b. molecular : fossil record
c. fossil record : morphological
d. morphological : molecular

13. Which of the following periods is the earliest during which animals may have appeared?

a. Ordovician period
b. Cambrian period
c. Ediacaran period
d. Cryogenian period

14. What type of data is primarily used to determine the existence and appearance of early animal species?

a. molecular data
b. fossil data
c. morphological data

d. embryological development data

15. The time between 542–488 million years ago marks which period?

a. Cambrian period
b. Silurian period
c. Ediacaran period
d. Devonian period

16. Until recent discoveries suggested otherwise, animals existing before the Cambrian period were believed to be:

a. small and ocean-dwelling
b. small and non-motile
c. small and soft-bodied
d. small and radially symmetrical or asymmetrical

17. Plant life first appeared on land during which of the following periods?

a. Cambrian period
b. Ordovician period
c. Silurian period
d. Devonian period

18. Approximately how many mass extinction events occurred throughout the evolutionary history of animals?

a. 3
b. 4
c. 5
d. more than 5

CRITICAL THINKING QUESTIONS

19. Why might the evolution of specialized tissues be important for animal function and complexity?

20. Describe and give examples of how humans display all of the features common to the animal kingdom.

21. How have *Hox* genes contributed to the diversity of animal body plans?

22. Using the following terms, explain what classifications and groups humans fall into, from the most general to the most specific: symmetry, germ layers, coelom, cleavage, embryological development.

23. Explain some of the advantages brought about through the evolution of bilateral symmetry and coelom formation.

24. Describe at least two major changes to the animal phylogenetic tree that have come about due to molecular or genetic findings.

25. How is it that morphological data alone might lead scientists to group animals into erroneous evolutionary relationships?

26. Briefly describe at least two theories that attempt to explain the cause of the Cambrian explosion.

27. How is it that most, if not all, of the extant animal phyla today evolved during the Cambrian period if so many massive extinction events have taken place since then?