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 modern 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 that the acoels are more closely related to deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

Another example of phylogenetic reorganization involves the identification of the Ctenophora as the basal clade of the animal kingdom. Ctenophora, or comb jellies, were once considered to be a sister group of the Cnidaria, and the sponges (Porifera) were placed as the basal animal group, sister to other animals. The presence of nerve and muscle cells in both the Ctenophores and the Cnidaria and their absence in the Porifera strengthened this view of the relationships among simple animal forms. However, recent molecular analysis has shown that many of the genes that support neural development in other animals are absent from the Ctenophore genome. The muscle cells are restricted to the mouth and tentacles and are derived from cells in the mesoglea. The mitochondrial genome of the Ctenophores is small and lacks many genes found in other animal mitochondrial genomes. These features plus the absence of *Hox* genes from the Ctenophores have been used to argue that the Ctenophores should be considered basal or as a sister group of the Porifera, and that the evolution of specialized nerve and muscle tissue may have occurred more than once in the history of animal life. Although Ctenophores have been shown as basal to other animals in the phylogeny presented in Chapter 27.2, debate on this issue is likely to continue as Ctenophores are more closely studied.

Changes to the phylogenetic tree can be difficult to track and understand, and are evidence of the process of science. Data and analytical methods play a significant role in the development of phylogenies. For this reason – because molecular analysis and reanalysis are not complete -- we cannot necessarily dismiss a former phylogenetic tree as inaccurate. A recent reanalysis of molecular evidence by an international group of evolutionary biologists refuted the proposition that comb jellies are the phylogenetically oldest extant metazoan group. The study, which relied on more sophisticated methods of analyzing the original genetic data, reaffirms the traditional view that the sponges were indeed the first phylum to diverge from the common ancestor of metazoans. The ongoing discussion concerning the location of sponges and comb jellies on the animal "family tree" is an example of what drives science forward.

27.4 The Evolutionary History of the Animal Kingdom

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

- Describe the features that characterized the earliest animals and approximately 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). Ediacaran fossils were first found in the Ediacaran hills of Southern Australia. There are no living representatives of these species, which have left impressions that look like those of feathers or coins (Figure 27.15). It is believed that early animal life, termed *Ediacaran biota*, evolved from protists at this time.

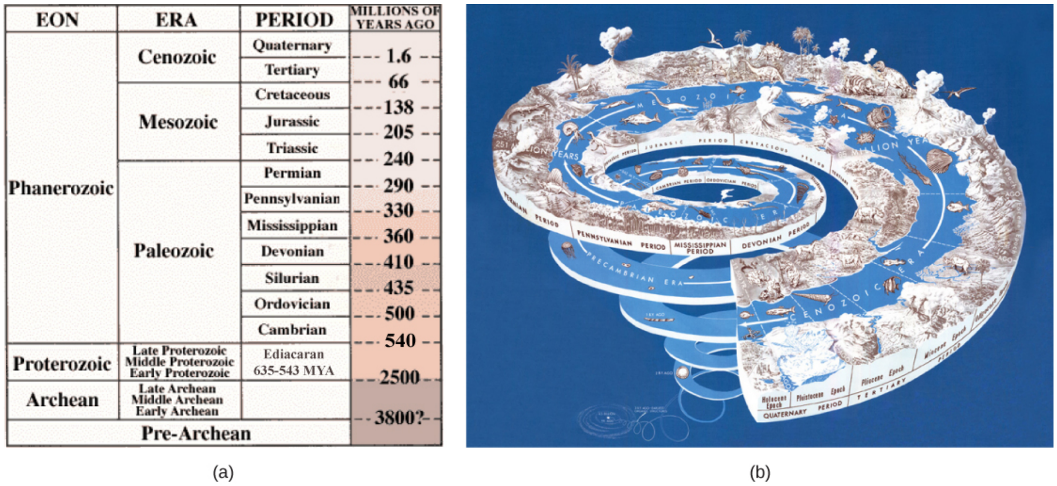

Figure 27.14 An evolutionary timeline. (a) Earth's history is divided into eons, eras, and periods. Note that the Ediacaran period starts in the Proterozoic eon and ends in the Cambrian period of the Phanerozoic eon. (b) Stages on the geological time scale are represented as a spiral. (credit: modification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

Most Ediacaran biota were just a few mm or cm long, but some of the feather-like forms could reach lengths of over a meter. Recently there has been increasing scientific evidence suggesting that more varied and complex animal species lived during this time, and likely 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 thimble-shaped body (estimated about 5 cm long). Other fossils from the Ediacaran period are shown in Figure 27.15a, b, c.

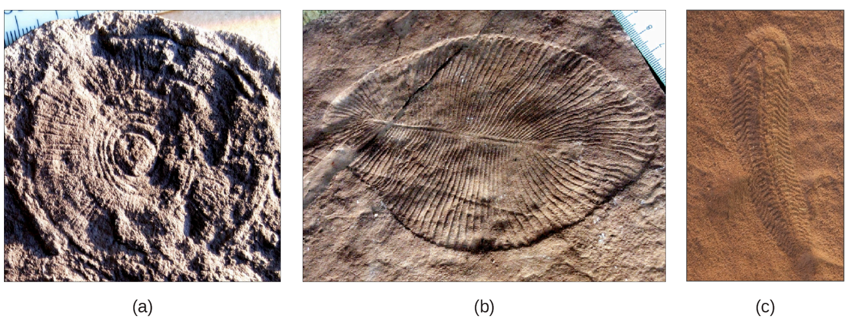

Figure 27.15 Ediacaran fauna. Fossils of (a) *Cyclomedusa (up to 20 cm)*, (b) *Dickinsonia (up to 1.4 m)*, (and (c) *Spriggina* (up to 5 cm) date to the Ediacaran period (543-635 MYA). (credit: modification of work by "Smith609"/Wikimedia Commons)

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, irregularly shaped and with internal tubes or canals. These ancient 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

If the fossils of the Ediacaran and Cryogenian periods are enigmatic, those of the following Cambrian period are far less so, and include body forms similar to those living today. 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. The rapid diversification of animals that appeared during this period, including most of the animal phyla in existence today, is often referred to as the **Cambrian explosion** (Figure 27.16). Animals resembling echinoderms, mollusks, worms, arthropods, and chordates arose during this period. What may have been a top predator of this period was an arthropod-like creature named *Anomalocaris*, over a meter long, with compound eyes and spiky tentacles. Obviously, all these Cambrian animals already exhibited complex structures, so their ancestors must have existed much earlier.

Figure 27.16 Fauna of the Burgess Shale. An artist's rendition depicts some organisms from the Cambrian period. *Anomalocaris* is seen in the upper left quadrant of the picture.

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 27.17a,b,c,d). Trilobites were somewhat similar to modern horseshoe crabs. Thousands of different species have been identified in fossil sediments of the Cambrian period; not a single species survives today.

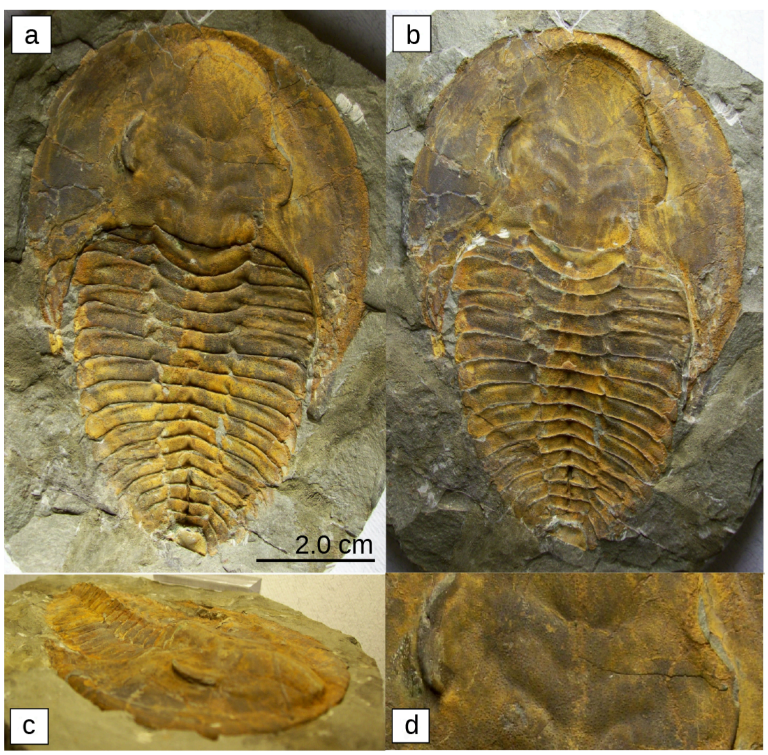

Figure 27.17 Trilobites. These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago.

The cause of the Cambrian explosion is still debated, and in fact, it may be that a number of interacting causes ushered in this incredible explosion of animal diversity. For this reason, there are a number of hypotheses 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 (Figure 27.18) and large increases in oceanic calcium concentrations that preceded the Cambrian period. 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 coexist. There is also support for hypotheses 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 hypotheses 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. Hypotheses 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 hypotheses described above, and the answer may very well be a combination of these and other theories.

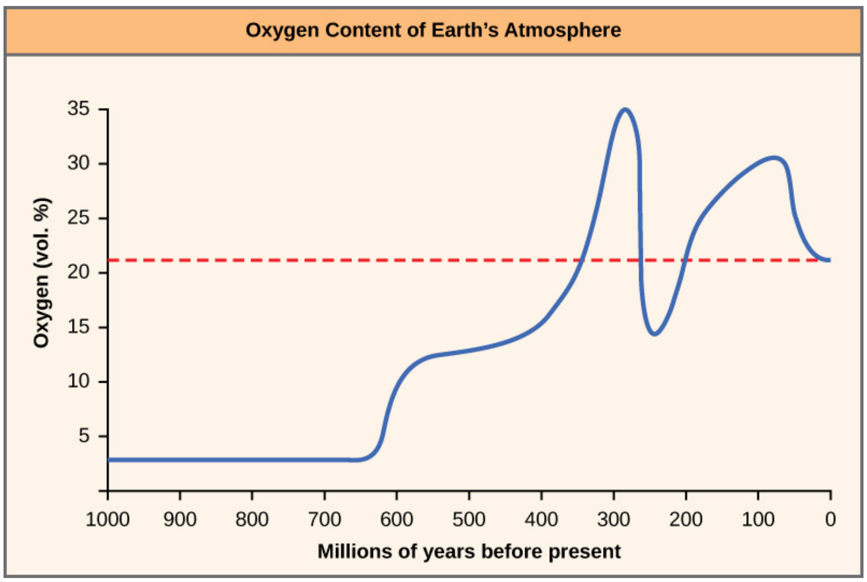

Figure 27.18 Atmospheric oxygen over time. The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

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 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 of body forms that is unmatched for any other time period.

LINK TO LEARNING

View an animation of what ocean life may have been like during the Cambrian explosion.

Click to view content (https://www.openstax.org/l/ocean_life)

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 (diversified living spaces) that invite 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 to some clades, yet provide new opportunities for others to "fill in the gaps" and speciate. 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 an estimated 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 after a large meteor impact and tons of volcanic ash ejected into the atmosphere blocked incoming sunlight. Plants died, herbivores and carnivores starved, and the dinosaurs ceded their dominance of the landscape to the 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 direct descendants 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 pollinating 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://openstax.org/l/mass_extinction) to learn more about the mass extinctions.

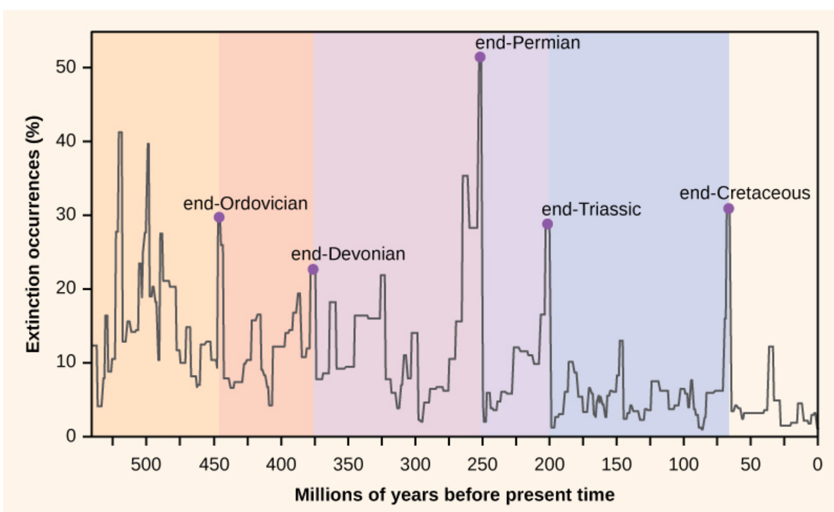

Figure 27.19 Extinctions. Mass extinctions have occurred repeatedly over geological time.

CAREER CONNECTION

Paleontologist

Natural history museums contain the fossils of extinct animals as well as information about how these animals evolved, lived, and died. Paleontologists 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 mathematics, 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 ancient life, paleontologists study a variety of life forms, from plants, fungi and invertebrates to the vertebrate fishes, amphibians, reptiles, birds and mammals.

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 opening into the archenteron that forms during gastrulation
blastula 16–32 cell stage of development of an animal embryo
body plan morphology or defining 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 divisions subdividing 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 cleavage pattern in which developmental fate of each blastomere is tightly defined
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 cleavage pattern in which individual blastomeres have the character of "stem cells," and are not yet predetermined to develop into specific cell types
Lophotrochozoa clade of protostomes that exhibit a trochophore larvae stage or a lophophore feeding structure
mass extinction event or environmental condition 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, their developmental pathways, and their genetic affinities. The relationships between the Eumetazoa and more basal clades (Ctenophora, Porifera, and Placozoa) are still being debated. The Eumetazoa ("true animals") are divided into those with radial versus bilateral symmetry. Generally, the simpler and often nonmotile animals display radial symmetry, which allows them to explore their environment in all directions. 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 embryologic 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 the extent to which mesoderm lines the body cavity. 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, the method of coelom formation, and the rigidity of the developmental fate of blastomeres.

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 documented 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 and semiaquatic arthropods, both freshwater and marine. 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.

VISUAL 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 into specific groups of tissues or organs 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 organisms 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 nonmotile
    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?