Chapter 32

An Introduction to Animal Diversity

Key Concepts

32.1 Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers

32.2 The history of animals may span more than a billion years

32.3 Animals can be characterized by "body plans"

32.4 Leading hypotheses agree on major features of the animal phylogenetic tree

Framework

Animals are multicellular eukaryotic heterotrophs that ingest their food. Fossil evidence for the origin and rapid divergence of animals is limited. A colonial choanoflagellate is the probable ancestor, and most animal phyla diversified during the 20 million years of the Cambrian explosion. The traditional phylogenetic tree of animals is based on body plan grades and includes such characteristics as symmetry, tissue layers, body cavities, and development. Molecular systematics splits the protostomes into clades Ecdysozoa and Lophotrochozoa.

Chapter Review

32.1 Animals are multicellular, heterotrophic eukaryotes with tissues that develop from embryonic layers

Nutritional Mode Most animals ingest their food, eating either other living organisms or nonliving organic matter.

Cell Structure and Specialization Animal cells lack walls and may have desmosomes, gap junctions, and tight junctions connecting adjacent cells. Structural proteins, such as collagen, hold animal bodies together. Muscle and nervous tissues are unique to animals.

Reproduction and Development The diploid stage is usually dominant, and reproduction is primarily sexual, with a flagellated sperm fertilizing a larger, nonmotile egg. The zygote undergoes a series of mitotic divisions, called **cleavage,** usually passing through a **blastula** stage during embryonic development. The process of **gastrulation** produces layers of embryonic tissues, resulting in the **gastrula** stage. The life cycle of many animals includes a **larva**—a free-living, sexually immature form. **Metamorphosis** transforms a larva into an adult.

While other eukaryotes have regulatory genes, many of which contain DNA sequences called homeoboxes, animals share a unique homeobox-containing family of genes, called *Hox* genes, that are involved in regulating gene expression in embryonic development.

32.2 The history of animals may span more than a billion years

The diversity of the animal kingdom includes the estimated 99% of species that are extinct. Some molecular clock calculations indicate that the ancestors of fungi and animals diverged 1.5 billion years ago. The common ancestor of all living animals may have lived 0.8–1.2 billion years ago and probably resembled choanoflagellates—colonial, flagellated protists.

■ INTERACTIVE QUESTION 32.1

List a hypothetical sequence of events that could have led to the origin of animals from a colonial protist.

Neoproterozoic Era (1 Billion–542 Million Years Ago) The earliest generally accepted fossils of animals, known as the **Ediacaran fauna,** are only about 575 million years old. These appear to be related to cnidarians and soft-bodied molluscs, although fossilized burrows indicate that worms may have evolved in this period. Fossilized animal embryos date from 570 million years ago.

Paleozoic Era (542–251 Million Years Ago) Fossils from the **Cambrian explosion** (542 to 525 mya) represent about half of all extant phyla and include the first animals with hard skeletons. There are three main hypotheses to explain the Cambrian explosion: The emergence of new predator-prey relationships may have changed community dynamics and triggered various evolutionary adaptations. The accumulation of atmospheric oxygen may have supported the active metabolisms of mobile and larger animals. The evolution of the *Hox* complex of regulatory genes, and then changes in their spatial and temporal expression during embryonic development, may have produced the body plan differences that appear during the Cambrian explosion.

During the Silurian and Devonian periods, animal diversity continued to increase. Fishes became the top predators of the seas. Arthropods appeared on land by 460 million years ago. Vertebrates began to adapt to land around 360 million years ago. Of the several lineages that diversified, the amphibians and amniotes survive today.

Mesozoic Era (251–65.5 Million Years Ago) The first coral reefs formed; reptiles returned to water; and flight appeared in pterosaurs and birds. Large predatory and herbivorous dinosaurs emerged, as did the first mammals.

Cenozoic Era (65.6 Million Years Ago to the Present) Mass extinctions marked the beginning of this period and included the nonflying dinosaurs and marine reptiles. Mammals began to exploit the vacated niches.

■ INTERACTIVE QUESTION 32.2

Review the three hypotheses for the rapid radiation of animal phyla during the Cambrian period.

32.3 Animals can be characterized by "body plans"

A group of animals that share a similar organizational complexity is called a **grade.** The sets of morphological and developmental traits that define a grade are often referred to as a **body plan.**

Symmetry Sponges lack symmetry. The parts of an animal with **radial symmetry** radiate from the center. Animals with **bilateral symmetry** have distinct **anterior** (head) and **posterior** (tail) ends, and left and right sides. Bilateral animals also have **dorsal** (top) and **ventral** (bottom) sides. Bilateral symmetry is associated with **cephalization,** the concentration of sensory organs and a central nervous system in the head end, which is an adaptation for unidirectional movement.

Tissues True tissues are groups of specialized cells separated from other tissues by membranous layers. Sponges lack true tissues. During gastrulation, an embryo develops concentric layers of cells called **germ layers: Ectoderm** develops into the outer body covering and, in some phyla, into the central nervous system; **endoderm** lines the developing digestive tube, or **archenteron,** and gives rise to the lining of the digestive tract and associated organs. Cnidarians and comb jellies are **diploblastic,** forming only these two germ layers. The bilateria animals are **triploblastic,** producing a middle layer, the **mesoderm,** from which arise muscles and most other organs.

Body Cavities A fluid-filled **body cavity** separating the digestive tract from the outer body wall is called a **coelom.** A "true" coelom is completely lined by mesodermally derived tissue, with mesenteries extending from the dorsal and ventral sides that suspend internal organs. Animals with a true coelom are called **coelomates. Pseudocoelomates** are animals whose body cavity, called a pseudocoelom, is formed from the blastocoel rather than from mesoderm. Triploblastic animals that have solid bodies are called **acoelomates.**

A fluid-filled body cavity cushions internal organs, allows organs to grow and move independently of the outer body wall, and also functions as a hydrostatic skeleton in soft-bodied animals. During animal evolution, coeloms and pseudocoeloms have evolved and been lost many times and cannot be used to distinguish clades.

Protostome and Deuterostome Development Three features distinguish **protostome development** and **deuterostome development.**

Protostome development, typical of molluscs, annelids, and arthropods, is characterized by **spiral cleavage,** in which the planes of cell division are diagonal and newly formed cells fit in the grooves between cells of adjacent tiers. **Determinate cleavage** of some of these animals sets the developmental fate of each embryonic cell very early. Deuterostome development, typical of echinoderms and chordates, involves **radial**

cleavage, in which parallel and perpendicular cleavage planes result in aligned tiers of cells. **Indeterminate cleavage,** present in most animals with deuterostome development, means that cells from early cleavage divisions retain the capacity to develop into complete embryos.

In protostome development, the coelom forms from splits within solid masses of mesoderm, called **schizocoelous** development. In deuterostome development, the mesoderm begins as buds from the archenteron, called **enterocoelous** development.

The **blastopore** is the opening during gastrulation leading to the developing archenteron. In protostome development ("first mouth"), the blastopore develops into the mouth, and a second opening forms at the end of the archenteron to produce an anus. In deuterostome development, the blastopore becomes the anus, and the second opening develops into the mouth.

■ INTERACTIVE QUESTION 32.3

Fill in this table to review some of the differences in the early embryological development of protostomes and deuterostomes.

	Protostomes	Deuterostomes
Cleavage	a.	b.
Coelom formation	c.	d.
Blastopore fate	e.	f.

32.4 Leading hypotheses agree on major features of the animal phylogenetic tree

The relationships of the 35 recognized animal phyla continue to be debated. The traditional animal phylogenetic tree was based on anatomical features. Modern phylogenetic systematics is based on identifying a hierarchy of clades nested within larger clades. Molecular systematics, new studies of lesser-known phyla, and analyses of fossils are contributing to the identification of such clades, defined by shared derived characters unique to the taxa in the clade and their common ancestor. Two current phylogenetic hypotheses are based on systematic analyses of morphological characters or on results from recent molecular studies.

Points of Agreement There are five major points of agreement between the two hypotheses: (1) All animals share a common ancestor. (2) Sponges are basal animals, exhibiting a **parazoan** grade of organization. Phylum Porifera may be paraphyletic. (3) Eumetazoa is a clade of animals with true tissues. The **eumetazoans** include all animals except sponges. Basal members of the clade include the diploblastic, radially symmetrical phylum Cnidaria (which includes jellies) and Ctenophora (comb jellies). These two are often placed in the informal grade called Radiata. (4) Most animal phyla belong to the clade Bilateria. The **bilaterians** are placed in a clade defined by the shared derived character of bilateral symmetry. (5) Vertebrates and some other phyla belong to the clade Deuterostomia.

Disagreement over the Bilaterians The morphology-based tree divides the bilaterians into the deuterostomes and protostomes, assuming that these developmental differences reflect phylogeny. This tree also groups arthropods with annelids, both of which have segmented bodies. Recent molecular studies distinguish two protostome sister taxa: **lophotrochozoans,** which include the annelids and molluscs, and **ecdysozoans,** which include the arthropods and nematodes. The name *Ecdysozoa* refers to the shedding of an exoskeleton, called ecdysis, a trait shared by some edcysozoan phyla. The name *Lophotrochozoa* is based on the feeding apparatus called a **lophophore,** found in the ectoprocts, and the larval stage called the **trochophore larva** shared by other members of the lophotrochozoans.

Future Directions in Animal Systematics Large-scale comparisons of multiple genes across many animal phyla currently being conducted may help systematists to test hypotheses about animal phylogeny.

Word Roots

a- = without; **-koilos** = a hollow (*acoelomate:* the condition of lacking a coelom)

arch- = ancient, beginning (*archenteron:* the endoderm-lined cavity, formed during the gastrulation process, that develops into the digestive tract of an animal)

bi- = two (*Bilateria:* the branch of eumetazoans possessing bilateral symmetry)

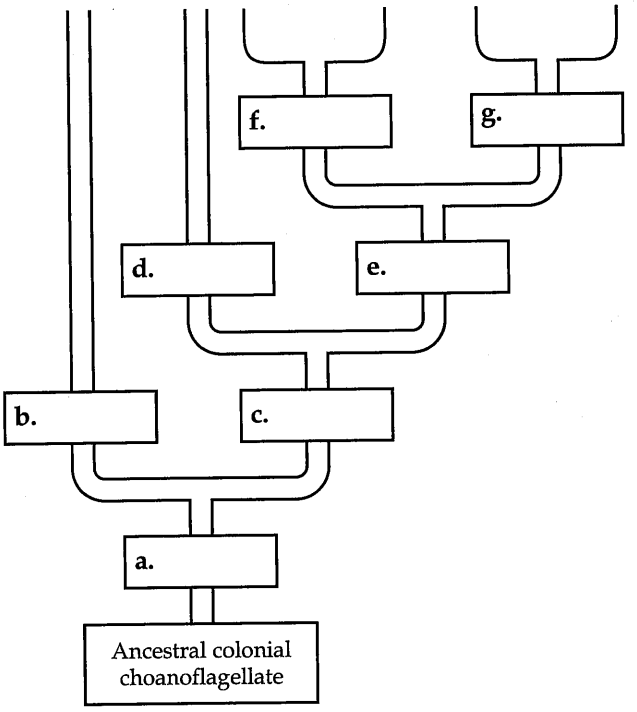
blast- = bud, sprout; **-pore** = a passage (*blastopore:* the opening of the archenteron in the gastrula that develops into the mouth in protostomes and the anus in deuterostomes)

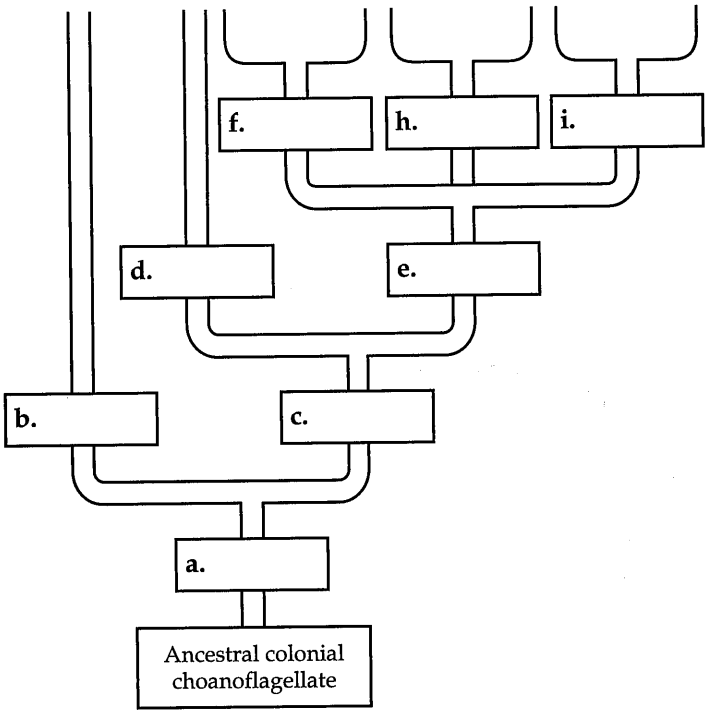
cephal- = head (*cephalization:* an evolutionary trend toward the concentration of sensory equipment on the anterior end of the body)

deutero- = second (*deuterostome:* one of two lines of coelomates characterized by radial, indeterminate cleavage, enterocoelous formation of the coelom, and development of the anus from the blastopore)
di- = two (*diploblastic:* having two germ layers)
ecdys- = an escape (*Ecdysozoa:* one of two proposed clades within the protostomes; it includes the arthropods)
ecto- = outside; **-derm** = skin (*ectoderm:* the outermost of the three primary germ layers in animal embryos)
endo- = within (*endoderm:* the innermost of the three primary germ layers in animal embryos)
entero- = the intestine, gut (*enterocoelous:* the type of development found in deuterostomes; the coelomic cavities form when mesoderm buds from the wall of the archenteron and hollows out)
gastro- = stomach, belly (*gastrulation:* the formation of a gastrula from a blastula)
in- = into; **-gest** = carried (*ingestion:* a heterotrophic mode of nutrition in which other organisms or detritus are eaten whole or in pieces)
lopho- = a crest, tuft; **-trocho** = a wheel; (*Lophotrochozoa:* one of two proposed clades within the protostomes that includes annelids and molluscs)
meso- = middle (*mesoderm:* the middle primary germ layer of an early embryo)
meta- = boundary, turning point; **-morph** = form (*metamorphosis:* the resurgence of development in an animal larva that transforms it into a sexually mature adult)
para- = beside; **-zoan** = animal (*parazoan:* grade of body form lacking symmetry and tissues; describes the sponges)
proto- = first; **-stoma** = mouth (*protostomes:* a member of one of two distinct evolutionary lines of coelomates characterized by spiral, determinate cleavage, schizocoelous formation of the coelom, and development of the mouth from the blastopore)
pseudo- = false (*pseudocoelom:* a body cavity that is not completely lined by mesoderm)
radia- = a spoke, ray (*Radiata:* the radially symmetrical animal phyla, including cnidarians)
schizo- = split (*schizocoelous:* the type of development found in protostomes; initially, solid masses of mesoderm split to form coelomic cavities)
tri- = three (*triploblastic:* having three germ layers)

Structure Your Knowledge

1. These two very abbreviated trees represent two hypotheses of animal phylogeny. In the boxes, fill in the clades or body plan grades for these two trees. In the table on the next page, list some of the shared derived characters that define each group.





Clade or Body Plan Grade	Shared Derived Characters
a.	
b.	
c.	
d.	
e.	
f.	
g.	
h.	
i.	

Test Your Knowledge

MULTIPLE CHOICE: *Choose the one best answer.*

1. Sponges differ from the rest of the animals because
   a. they are completely sessile.
   b. they have radial symmetry and are suspension feeders.
   c. their simple body structure has no true tissues, and they have no symmetry.
   d. they are not multicellular.
   e. they have no flagellated cells.
2. An insect larva
   a. is a miniature version of the adult.
   b. is transformed into an adult by molting.
   c. ensures more genetic variation in the insect life cycle.
   d. is a sexually immature organism specialized for eating and growth.
   e. is all of the above.
3. Cephalization
   a. is the development of bilateral symmetry.
   b. is the formation of a coelom by budding from the archenteron.
   c. is a diagnostic characteristic of deuterostomes.
   d. is common in radially symmetrical animals.
   e. is associated with motile animals that concentrate sensory organs in a head region.
4. A true coelom
   a. has mesenteries extending from the dorsal and ventral sides that support internal organs.
   b. allows organs to grow and move independently of the outer body wall.
   c. is a fluid-filled cavity completely lined by mesoderm.
   d. may be used as a hydrostatic skeleton by soft-bodied coelomates.
   e. is all of the above.
5. Which of the following is descriptive of protostome development?
   a. radial and determinate cleavage, blastopore becomes mouth
   b. spiral and indeterminate cleavage, coelom forms as split in solid mass of mesoderm
   c. spiral and determinate cleavage, blastopore becomes mouth, schizocoelous development
   d. spiral and indeterminate cleavage, blastopore becomes mouth, enterocoelous development
   e. radial and determinate cleavage, enterocoelous development, blastopore becomes anus
6. Which of the following is *not* descriptive of a pseudocoelomate?
   a. a body cavity incompletely lined by mesoderm
   b. bilateral symmetry
   c. triploblastic
   d. true tissues
   e. schizocoelous formation of body cavity
7. Which of the following characteristics is found only in animals?
   a. homeobox-containing genes
   b. flagellated sperm
   c. heterotrophic nutrition
   d. *Hox* genes
   e. All of the above are exclusive animal traits.
8. Some of the oldest known animal fossils are
   a. colonies of flagellated protists.
   b. worms that are 1 billion years old.
   c. sponges, because they were the first animals.
   d. soft-bodied cnidarians of the Ediacaran period.
   e. bizarre-looking animals from the Cambrian explosion.

9. The grade-based and molecular-based phylogenetic trees agree in which of the following ways?
   a. the acoelomate condition as a branch point before the divergence of the two protostome clades
   b. the deepest branch points of the parazoa–eumetazoa and radiata–bilateria, and the deuterostomes as a monophyletic clade
   c. parazoa as the probable ancestor of the animals
   d. the grouping of the segmented annelids and arthropods
   e. the origin of the *Hox* complex as the probable cause of the Cambrian explosion

10. The rapid diversification of animal phyla during the Cambrian explosion is most likely linked with
   a. the movement of animals onto land.
   b. the origin of the triploblastic body plan that allowed for the development of organs.
   c. the origin of the first homeobox-containing genes.
   d. the evolution of bilateral symmetry and cephalization that permitted more efficient movement and processing of sensory data.
   e. ecological changes such as the development of predator-prey relationships and geologic causes such as the accumulation of atmospheric oxygen.