

## Chapter 32 - Introduction to Animal Evolution

### Overview: Welcome to Your Kingdom

- Biologists have identified 1.3 million living species of animals.
- Estimates of the total number of animal species run far higher, from 10 million to as many as 200 million.
- This diversity encompasses a huge range of morphological diversity.

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

- There are exceptions to nearly every criterion for distinguishing an animal from other life forms.
- However, several characteristics, taken together, make up a reasonable definition of an animal.
- Animals are multicellular, ingestive heterotrophs.
- Animals take in preformed organic molecules through ingestion, eating other organisms or organic material that is decomposing.
  - In contrast, plants are autotrophic eukaryotes that generate organic molecules by photosynthesis; fungi are absorptive heterotrophs.
- Animal cells lack cell walls that provide structural support for plants and fungi.
- The multicellular bodies of animals are held together by extracellular structural proteins, especially collagen, which is unique to animals.
- Animals have two specialized types of cells found only in animals: nerve cells for impulse conduction and muscle cells for movement.
  - These cells are organized into nervous tissue and muscle tissue.
- Most animals reproduce sexually, with the diploid stage usually dominating the life cycle.
  - In most species, a small flagellated sperm fertilizes a larger, nonmotile egg.
- The zygote undergoes **cleavage**, a succession of mitotic cell divisions, leading to the formation of a multicellular stage called the **blastula**, which takes the shape of a hollow ball in many animals.
- During **gastrulation**, layers of embryonic tissues that will develop into adult body parts are produced.
  - The resulting development stage is called a **gastrula**.
- Some animals develop directly through transient stages into adults, but others have a distinct larval stage or stages.
  - A **larva** is a sexually immature stage that is morphologically distinct from the adult stage, usually eats different foods, and may live in a different habitat from the adult.
  - Animal larvae eventually undergo **metamorphosis**, transforming the animal into an adult.
- Animals share a unique homeobox-containing family of genes known as *Hox* genes.
  - All eukaryotes have genes that regulate the expression of other genes.
  - Many of these regulatory genes contain common modules of DNA sequences called homeoboxes.

- Because all animals share *Hox* genes, this gene family may have arisen in the eukaryotic lineage that gave rise to animals.
- *Hox* genes play important roles in the development of animal embryos, regulating the expression of dozens or hundreds of other genes that influence animal morphology.
  - *Hox* genes in sponges regulate the formation of water channels in the body wall, the primary feature of sponge morphology.
- In the ancestors of more complex animals, the *Hox* gene family underwent further duplication.
  - In vertebrates, insects, and most other animals, *Hox* genes regulate patterning of the anterior-posterior axis.
  - The same conserved genetic network governs the development of a large range of animals.

### **Concept 32.2 The history of animals spans more than half a billion years.**

- The animal kingdom includes not only a great diversity of living species but also the even greater diversity of extinct ones.
  - Some paleontologists have estimated that 99% of all animal species are extinct.
- Various studies suggest that animals began to diversify during the last billion years.
  - Some estimates based on molecular clocks suggest that the ancestors of animals diverged from the ancestors of fungi about a billion years ago.
  - Similar studies suggest that the common ancestor of living animals may have lived 675 million to 875 million years ago.
- A combination of morphological and molecular evidence indicates that the common ancestors of living animals may have been a stationary suspension feeder, similar to present-day choanoflagellates.

#### *Neoproterozoic Era (1 billion–542 million years ago)*

- Despite molecular data that indicate an earlier origin of animals, the oldest generally accepted animal fossils range in age from 565 million to 550 million years old.
- These fossils are known as the **Ediacara fauna**, named for the Ediacara Hills of Australia.
  - Some of the Ediacara fauna are sponges, while others may be related to various groups of living cnidarians.
  - Some do not appear to be closely related to any living plants or animals.
- Neoproterozoic rocks have also yielded microscopic signs of early animals; 575-million-year-old microfossils discovered in China exhibit the basic structural organization of present-day animal embryos.
- Debate continues about whether the fossil embryos are animals or are members of extinct groups that are closely related to animals (but are not actually animals).

#### *Paleozoic Era (542–251 million years ago)*

- Animals underwent considerable diversification between 542 million and 525 million years ago, during the Cambrian period of the Paleozoic Era.
  - During this period, known as the **Cambrian explosion**, about half of extant animal phyla arose, including the first arthropods, chordates, and echinoderms.
  - Fossils of Cambrian animals include the first animals with hard, mineralized skeletons.
- There are three hypotheses regarding the reason for the Cambrian explosion: new predator-prey relationships, atmospheric changes, and developmental flexibility.
- The new predator-prey relationships that emerged in the Cambrian may have generated diversity through natural selection.
  - Predators acquired adaptations, such as new forms of locomotion, that helped them catch prey.

- Prey acquired adaptations, such as protective shells, that helped them resist predation.
- Increased levels of atmospheric oxygen preceded the Cambrian explosion.
  - More oxygen may have provided opportunities for animals with higher metabolic rates and larger body sizes.
- The evolution of the *Hox* gene complex provided the developmental flexibility that resulted in variations in morphology.
- These hypotheses are not mutually exclusive: All may have played a role.
- In the Ordovician, Silurian, and Devonian periods, animal diversity continued to increase, punctuated by episodes of mass extinction.
- Vertebrates (fishes) became the top predators of marine food webs.
- By 460 million years ago, arthropods began to adapt to terrestrial habitats.
  - Millipedes and centipedes appeared on land.
  - Fern galls—enlarged cavities that resident insects stimulate fern plants to form, providing protection for the insects—date back to at least 302 million years ago, suggesting that insects and plants were influencing each other’s evolution by that time.
- Vertebrates moved to land about 360 million years ago and diversified into many lineages.
- Two of these survive today: amphibians and amniotes.

*Mesozoic Era (251–65.5 million years ago)*

- No fundamentally new animal body plans emerged during the Mesozoic era.
- Animal phyla began to spread into new ecological habitats.
  - In the oceans, the first coral reefs formed, providing other animals with new marine habitats.
  - Some reptiles returned to the water and succeeded as large aquatic predators.
  - On land, flight evolved in pterosaurs and birds.
  - Large and small herbivorous and carnivorous dinosaurs evolved.
  - The first mammals—tiny nocturnal insect-eaters—arose.
- During the late Mesozoic, insects and flowering plants also underwent dramatic radiations.

*Cenozoic Era (65.5 million years ago to the present)*

- This era began with mass extinctions of terrestrial and marine animals.
  - Among the groups of species that disappeared were large, nonflying dinosaurs and marine reptiles.
- Large mammalian herbivores and carnivores diversified as mammals exploited vacated ecological niches.
- Some primate species in Africa adapted to open woodlands and savannas as global climates cooled.
  - Our ancestors were among these grassland apes.

**Concept 32.3 Animals can be characterized by their “body plans.”**

- Although animal species show great morphological variation, this diversity can be categorized into a relatively small number of major “body plans.”
- A **body plan** is a set of morphological and developmental traits integrated into a functional whole—the living animal.
- Like all organismal features, animal body plans have evolved over time.
- Some of the evolutionary changes in body plans appear to have occurred early in the history of animal life.

- For example, a key step in the molecular control of gastrulation has remained unchanged for more than 500 million years.
- This early evolutionary innovation was of fundamental importance: Gastrulation helps to explain why most animals are not a hollow ball of cells.
- Other aspects of animal body plans have changed multiple times as various animal lineages evolved and diversified.
- Similar body forms may have evolved independently in two different organisms.
- A group of animal species that share the same level of organizational complexity is called a *grade*.
  - Certain body-plan features shared by a group of animals define a grade.
  - Because these features may evolve independently in separate lineages, a grade is not necessarily equivalent to a *clade* (a group that includes an ancestral species and all of its descendants).
- Animals can be categorized according to the symmetry (or lack of symmetry) of their bodies.
  - Most sponges lack symmetry.
- Some animals, such as sea anemones, have **radial symmetry**. These animals have top (mouth) and bottom sides, but not front and back ends and no left and right sides.
- Many animals have **bilateral symmetry**. A bilateral animal has two axes of orientation: front to back and top to bottom.
  - Bilaterally symmetrical animals have **dorsal** (top) and **ventral** (bottom) sides, left and right sides, and **anterior** (head) and **posterior** (tail) ends.
  - Linked with bilateral symmetry is **cephalization**, an evolutionary trend toward the concentration of nervous and sensory equipment on the anterior end.
- The symmetry of an animal generally fits its lifestyle.
  - Many radial animals are sessile or planktonic and need to meet the environment equally well from all sides.
  - Animals that move actively from place to place are generally bilaterally symmetrical.
  - The central nervous system of bilateral animals allows them to coordinate complex movements involved in crawling, burrowing, flying, and swimming.
- Fossil evidence indicates that these two fundamentally different kinds of symmetry—radial and bilateral—have been present for at least 535 million years.
- Animal body plans also vary according to the organization of the animal's tissues.
  - True tissues are collections of specialized cells isolated from other tissues by membranous layers.
- Sponges and a few other groups lack true tissues.
- In all other animals, the embryo becomes layered through the process of gastrulation.
- As development progresses, *germ layers*, concentric layers of embryonic tissue, form various tissues and organs.
  - **Ectoderm**, the germ layer covering the surface of the embryo, gives rise to the outer covering and, in some phyla, to the central nervous system.
  - **Endoderm**, the innermost germ layer, lines the developing digestive tube, or **archenteron**, and gives rise to the lining of the digestive tract and the organs derived from it, such as the liver and lungs of vertebrates.
- Animals with only two germ layers, such as cnidarians and comb jellies, are **diploblastic**.
- Other animals are **triploblastic** and have three germ layers.
  - In these animals, a third germ layer, the **mesoderm**, lies between the endoderm and the ectoderm.
  - The mesoderm develops into the muscles and most other organs between the digestive tube and the outer covering of the animal.
  - Triploblasts include a broad range of animals, from arthropods to vertebrates.
- Most triploblastic animals possess a **body cavity** (a fluid- or air-filled space separating the digestive tract from the outer body wall) known as a **coelom**.
  - A “true” coelom forms from tissue derived from mesoderm.
  - The inner and outer layers of tissue that surround the coelom connect dorsally and ventrally and form

- structures that suspend the internal organs.
  - Animals that possess a true coelom are known as **coelomates**.
- Some triploblastic animals have a cavity formed from mesoderm and endoderm.
  - Such a cavity is a “pseudocoelom,” and animals that have one are called **pseudocoelomates**.
  - A pseudocoelom is a fully functional body cavity, despite its name.
- Some triploblastic animals lack a coelom. These animals, known as **acoelomates**, have a solid body without a body cavity.
- A body cavity has many functions.
  - Its fluid cushions the suspended organs, helping to prevent internal injury.
  - In soft-bodied coelomates, the noncompressible fluid of the body cavity can function as a hydrostatic skeleton against which muscles can work.
  - The presence of a body cavity enables the internal organs to grow and move independently of the outer body wall.
- Current research suggests that true coeloms and pseudocoeloms have evolved many times in the course of animal evolution.
  - Thus, the terms *coelomate* and *pseudocoelomate* refer to grades, not clades.
- Most animals can be categorized as having one of two developmental modes: **protostome development** or **deuterostome development**.
- The differences between these modes of development center on cleavage pattern, coelom formation, and blastopore fate.
- Many protostomes undergo **spiral cleavage**, in which the planes of cell division are diagonal to the vertical axis of the embryo.
- Some protostomes also show **determinate cleavage**, whereby the developmental fate of each embryonic cell is determined very early.
- Most deuterostomes undergo **radial cleavage**, in which the cleavage planes are parallel or perpendicular to the vertical axis of the embryo.
- Most deuterostomes show **indeterminate cleavage**, whereby each cell in the early embryo retains the capacity to develop into a complete embryo.
  - The indeterminate cleavage of the human zygote makes identical twins possible.
  - Indeterminate cleavage also explains the developmental versatility of embryonic “stem cells,” which may provide new ways to overcome a variety of diseases, including type 1 diabetes, Parkinson’s disease, and Alzheimer’s disease.
- In gastrulation, the developing digestive tube of an embryo initially forms as a blind pouch, the archenteron, which becomes the gut.
  - As the archenteron forms in a protostome, initially solid masses of mesoderm split to form the coelom.
  - In deuterostomes, mesoderm buds off from the wall of the archenteron and hollows to become the coelom.
- Protostome and deuterostome development differ in the fate of the **blastopore**, the indentation during gastrulation that leads to the formation of the archenteron.
  - In most bilaterians, a second opening forms at the opposite end of the gastrula from the archenteron.
  - The blastopore and the second opening become the two openings of the digestive tube (the mouth and anus).
  - In protostome development, the mouth generally develops from the first opening, the blastopore. This is the origin of the term *protostome* (“first mouth”).
  - In deuterostome (“second mouth”) development, the blastopore usually develops into the anus, and the mouth is derived from the secondary opening.

### **Concept 32.4 New views of animal phylogeny are emerging from molecular data.**

- Zoologists currently recognize about 35 animal phyla.
- The relationships among these phyla continue to be debated.
- Traditionally, zoologists have based hypotheses about animal phylogeny on morphological data.
- In the late 1980s, however, zoologists began to study the molecular systematics of animals.
- New studies of lesser-known phyla and fossil analyses help distinguish between ancestral and derived traits in various animal groups.
- Modern phylogenetic systematics is based on the identification of clades, monophyletic sets of taxa defined by shared derived features unique to those taxa and their common ancestor.
  - This study creates a phylogenetic tree, a hierarchy of clades nested within larger clades.
- Defining the shared derived characteristics is key to a particular hypothesis.
  - Whether the data are key morphological characters, embryological similarities, DNA sequences, or some combination, the assumptions and inferences inherent in the tree are the same.
- Two current phylogenetic hypotheses can be compared: one based on morphological data and the other based on recent molecular data.
- The hypotheses agree on five major features of animal phylogeny.
  1. **All animals share a common ancestor.**
    - Both animal trees indicate that the animal kingdom is monophyletic, representing a clade called Metazoa.
  1. **Sponges are basal animals.**
    - Sponges branch from the base of both animal trees.
    - Recent molecular analyses suggest that sponges are paraphyletic.
  1. **Eumetazoa is a clade of animals with true tissues.**
    - All animals except sponges belong to a clade of **eumetazoans**.
    - The common ancestor of living eumetazoans acquired true tissues.
    - Basal members of the eumetazoan clade include the phyla Ctenophora and Cnidaria.
    - These basal eumetazoa are diploblastic and generally feature radial symmetry.
  1. **Most animal phyla belong to the clade Bilateria.**
    - Bilateral symmetry and the presence of three germ layers are shared derived characteristics that help to define the clade of **bilaterians**.
  1. **Chordates and some other phyla belong to the clade Deuterostomia.**
    - The name *deuterostome* refers to an animal development grade and also to a clade that includes vertebrates and other chordates.
- The hypotheses also disagree on some significant points, including the relationships among the bilaterians.
- The morphology-based tree divides the bilaterians into two clades: deuterostomes and protostomes.
  - This division assumes that these two modes of development reflect a phylogenetic pattern.
  - Within the protostomes, arthropods are grouped with annelids because both groups have segmented bodies.
- Molecular phylogenies based on mitochondrial genes, ribosomal genes, *Hox* genes, and dozens of protein-encoding genes suggest a different view.
  - These studies indicate that there are three major clades of bilaterally symmetrical animals: Deuterostomia, Lophotrochozoa, and Ecdysozoa.
  - In this phylogeny, arthropods and annelids are not closely related.
- Traditionally, acoelomate flatworms (the Acoela) were classified with other flatworms in the phylum Platyhelminthes.
- Recent studies indicate that acoel flatworms are basal bilaterians, not members of the phylum Platyhelminthes.

- The basal position of Acoela suggests that bilaterians descended from a common ancestor that resembled living acoel flatworms, with a simple nervous system, a saclike gut, and no excretory system.
- The molecular phylogeny assigns animal phyla not in Deuterostomia to two taxa: the **ecdysozoans** and the **lophotrochozoans**.
- The name *Ecdysozoa* refers to a characteristic shared by nematodes and arthropods, among other taxa.
  - These animals secrete external skeletons (exoskeletons).
  - As the animal grows, it molts the old exoskeleton and secretes a new, larger one, a process called *ecdysis*.
  - Though named for this process, the clade is actually defined mainly by molecular evidence of the common ancestry of its members.
- The name *Lophotrochozoa* refers to two characteristic features of animals in this clade.
  - Some animals, such as brachiopods, develop a **lophophore**, a crown of ciliated tentacles used for feeding.
  - Other phyla, including annelids and mollusks, have a distinctive larval stage called a **trochophore larva**.
- Systematists are conducting large-scale analyses of multiple genes across a wide range of animal phyla in an effort to gain a clearer picture of how the diversity of animal body plans arose.