INTRODUCTION TO

## ANIMAL EVOLUTION

# Introduction

* Animal life began in Precambrian seas with the evolution of multicellular forms that lived by eating other organisms.
* Early animals populated the seas, fresh waters, and eventually the land.

**A. What is an animal?**

1. Structure, nutrition and life history define animals

* While there are exceptions to nearly every criterion for distinguishing an animal from other life forms, five criteria, when taken together, create a reasonable definition.

• (1) Animals are multicellular, heterotrophic eukaryotes.

* They must take in preformed organic molecules through **ingestion**, eating other organisms or organic material that is decomposing.

• (2) Animal cells lack cell walls that provide structural supports for plants and fungi.

* The multicellular bodies of animals are held together with the extracellular proteins, especially collagen.
* In addition, other structural proteins create several types of intercellular junctions, including tight junctions, desmosomes, and gap junctions, that hold tissues together.

• (3) Animals have two unique types of tissues: nervous tissue for impulse conduction and muscle tissue for movement.

• (4) Most animals reproduce sexually, with the diploid stage usually dominating the life cycle.

* In most species, a small flagellated sperm fertilizes a larger, nonmotile eggs.
* The zygote undergoes **cleavage**, a succession mitotic cell divisions, leading to the formation of a multicellular, hollow ball of cells called the **blastula**.
* During **gastrulation**, part of the embryo folds inward, forming the blind pouch characteristic of the **gastrula.**
* This produces two tissue layers: the endoderm as the inner layer and the ectoderm as the outer layer.
* Some animals develop directly through transient stages into adults, but others have distinct larval stages.
* The **larva** is a sexually immature stage that is morphologically distinct from the adult, 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.

• (5) The transformation of a zygote to an animal of specific form depends on the controlled expression in the developing embryo of special regulatory genes called *Hox* genes.

* These genes regulate the expression of other genes.
* Many of these *Hox* genes contain common “modules” of DNA sequences, called homeoboxes.
* Only animals possess genes that are both homeobox-containing in structure and homeotic in function.
* All animals, from sponges to the most complex insects and vertebrates have *Hox* genes, with the number of *Hox* genes correlated with the complexity of the animal’s anatomy.

2. The animal kingdom probably evolved from a colonial, flagellated protist

* Most systematists now agree that the animal kingdom is monophyletic.
* If we could trace all the animals lineages back to their origin, they would converge on a common ancestor.
* That ancestor was most likely a colonial flagellated protist that lived over 700 million years ago in the Precambrian era.
* This protist was probably related to choanoflagellates, a group that arose about a billion years ago.
* Modern choanoflagellates are tiny, stalked organisms inhabiting shallow ponds, lakes, and marine environments.
* One hypothesis for the origin of animals from a flagellated protist suggests that a colony of identical cells evolved into a hollow sphere.
* The cells of this sphere then specialized, creating two or more layers of cells.

### B. Two Views of Animal Diversity

* Zoologists recognize about 35 phyla of animals.
* For the past century, there was broad consensus among systematists for the major branches of the animal phylogenetic tree.
* This was based mainly on anatomical features in adults and certain details of embryonic development.
* However, the molecular systematics of the past decade is challenging some of these long-held ideas about the phylogenetic relationships among the animal phyla.

1. The remodeling of phylogenetic trees illustrates the process of scientific inquiry

* It must be frustrating that the phylogenetic trees in textbooks cannot be memorized as fossilized truths.
* On the other hand, the current revolution in systematics is a healthy reminder that science is both a process of inquiry and dynamic.
* Emerging technologies such as molecular biology and fresh approaches such as cladistics produce new data or stimulate reconsideration of old data.
* New hypotheses or refinements of old ones represent the latest versions of what we understand about nature based on the best available evidence.
* *Evidence* is the key word because even our most cherished ideas in science are probationary.
* Science is partly distinguished from other ways of knowing because its ideas *can* be falsified through testing with experiments and observations.
* The more testing that a hypothesis withstands, the more credible it becomes.
* A comparison of the traditional phylogenetic tree of animals with the remodeled tree based on molecular biology shows agreement on some issues and disagreement on others.
* Though the new data from molecular systematics are compelling, the traditional view of animal phylogeny still offers some important advantages for helping us understand the diversity of animal body plans.

2. The traditional phylogenetic tree of animals is based mainly on grades in body “plans”

* The traditional view of relationships among animal phyla is based mainly on key characteristics of body plans and embryonic development.
* Each major branch represents a **grade**, which is defined by certain body-plan features shared by the animals belonging to that branch.
* The major grades are distinguished by structural changes at four deep branches.

• 1) The first branch point splits the **Parazoa** which lack true tissues from the **Eumetazoa** which have true tissues.

* The parazoans, phylum Porifera or sponges, represent an early branch of the animal kingdom.
* Sponges have unique development and a structural simplicity.

• 2) The eumetazoans are divided into two major branches, partly based on body symmetry.

* Members of the phylum Cnidaria (hydras, jellies, sea anemones and their relatives) and phylum Ctenophora (comb jellies) have **radial symmetry** and are known collectively as the **radiata**.
* The other major branch, the **bilateria**, has **bilateral symmetry** with a **dorsal** and **ventral** side, an **anterior** and **posterior** end, and a left and right side.
* Linked with bilateral symmetry is **cephalization**, an evolutionary trend toward the concentration of sensory equipment on the anterior end.
* Cephalization also includes the development of a central nervous system concentrated in the head and extending toward the tail as a longitudinal nerve cord.
* 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 are bilateral, such that the head end is usually first to encounter food, danger, and other stimuli.
* The basic organization of **germ layers**, concentric layers of embryonic tissue that form various tissues and organs, differs between radiata and bilateria.
* The radiata are said to be **diploblastic** because they have two germ layers.
* The **ectoderm**, covering the surface of the embryo, gives rise to the outer covering and, in some phyla, the central nervous system.
* The **endoderm**, the innermost 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.
* The bilateria are **triploblastic.**
* The third germ layer, the **mesoderm** lies between the endoderm and ectoderm.
* The mesoderm develops into the muscles and most other organs between the digestive tube and the outer covering of the animal.

• 3) The Bilateria can be divided by the presence or absence of a **body cavity** (a fluid-filled space separating the digestive tract from the outer body wall) and by the structure the body cavity.

* **Acoelomates** (the phylum Platyhelminthes) have a solid body and lack a body cavity.
* In some organisms, there is a body cavity, but it is not completely lined by mesoderm.
* This is termed a **pseudocoelom**.
* These **pseudocoelomates** include the rotifers (phylum Rotifera) and the roundworms (phylum Nematoda).
* **Coelomates** are organisms with a true **coelom**, a fluid-filled body cavity completely lined by mesoderm.
* The inner and outer layers of tissue that surround the cavity connect dorsally and ventrally to form mesenteries, which suspend the internal organs.
* A body cavity has many functions.
* Its fluid cushions the internal organs, helping to prevent internal injury.
* The noncompressible fluid of the body cavity can function as a hydrostatic skeleton against which muscles can work.
* The presence of the cavity enables the internal organs to grow and move independently of the outer body wall.

(4) The coelomate phyla are divided into two grades based on differences in their development.

* The mollusks, annelids, arthropods, and several other phyla belong to the **protostomes**, while echinoderms, chordates, and some other phyla belong to the **deuterostomes**.
* These differences center on cleavage pattern, coelom formation, and blastopore fate.
* Many protostomes undergo **spiral cleavage**, in which planes of cell division are diagonal to the vertical axis of the embryo.
* Some protostomes also show **determinate cleavage** where the fate of each embryonic cell is determined early in development.
* The zygotes of many deuterostomes undergo **radial cleavage** in which the cleavage planes are parallel or perpendicular to the vertical egg axis.
* Most deuterostomes show **indeterminate cleavage** whereby each cell in the early embryo retains the capacity to develop into a complete embryo.
* Coelom formation begins in the gastrula stage.
* As the archenteron forms in a protostome, solid masses of mesoderm split to form the coelomic cavities, called **schizocoelous** development.
* In deuterostomes, mesoderm buds off from the wall of the archenteron and hollows to become the coelomic cavities, called **enterocoelous** development.
* The third difference centers on the fate of the **blastopore**, the opening of the archenteron.
* In many protosomes, the blastopore develops into the mouth and a second opening at the opposite end of the gastrula develops into the anus.
* In deuterostomes, the blastopore usually develops into the anus and the mouth is derived from the secondary opening.

3. Molecular systematists are moving some branches around on the phylogenetic tree of animals

* Modern phylogenetic systematics is based on the identification of monophyletic clades.
* Clades are defined by shared-derived features unique to those taxa and their common ancestor.
* This creates a phylogenetic tree that is a hierarchy of clades nested within larger clades.
* The traditional phylogenetic tree of animals is based on the assumption that grades in body plan are good indicators of clades.
* Molecular systematics has added a new set of shared-derived characters in the form of unique monomer sequences within certain genes and their products.
* These molecular data can be used to identify the clusters of monophyletic taxa that make up clades.
* In some cases, the clades determined from molecular data reinforce the traditional animal tree based on comparative anatomy and development, but in other cases, a very different pattern emerges.
* This phylogenetic tree is based on nucleotide sequences from the small subunit ribosomal RNA.
* At key places, these two views of animal phylogeny are alike.
* First, both analyses support the traditional hypotheses of the Parazoa-Eumetazoa and Radiata-Bilateria dichotomies.
* Second, the molecular analysis reinforces the hypothesis that the deuterostomes (echinoderms and chordates) form a clade.
* However, the traditional and molecular-based phylogenetic trees clash, especially on the protostome branch.
* The molecular evidence supports two protostome clades: **Lophotrochozoa**, which includes annelids (segmented worms) and mollusks (including clams and snails), and **Ecdysozoa**, which includes the arthropods.
* Traditional analyses have produced two competing hypotheses for the relationships among annelids, mollusks, and arthropods.
* Some zoologists favored an annelid-arthropod lineage, in part because both have segmented bodies.
* Other zoologists argued that certain features favored an annelid-mollusk lineage, especially because they share a similar larval stage, the **trochophore larva**.
* This hypothesis is supported by the molecular data.
* Traditionally, the acoleomate phylum Platyhelminthes (flatworms) branches from the tree before the formation of body cavities.
* The molecular data places the flatworms within the lophotrochozoan clade.
* If this is correct, then flatworms are not primitive “pre-coelomates” but are protostomes that have lost the coelom during their evolution.
* The molecular-based phylogeny splits the pseudoceolomates with the phylum Rotifera (rotifers) clustered with the lophotrochozoan phyla and the phylum Nematoda (nematodes) with the ecdysozoans.
* The name Ecdysozoa (nematodes, arthropods, and other phyla) refers to animals that secrete external skeletons (exoskeleton).
* As the animal grows, it molts the old exoskeleton and secretes a new, larger one, a process called ecdysis.
* While named for this process, the clade is actually defined mainly by molecular evidence.
* In the traditional tree, the assignment of the three lophophorate phyla is problematic.
* These animals have a **lophophore**, a horseshoe-shaped crown of ciliated tentacles used for feeding.
* The lophophorate phyla share some characteristics with protostomes and other features with deuterostomes.
* The molecular data place the lophophorate phyla among the phyla with the trochophore larvae, hence the name lophotrochozoans.
* In summary, the molecular evidence recognizes two distinct clades within the protostomes and distributes the acoelomates, pseudocoelomates, and lophophorate phyla among these two clades.
* Our survey of animal phyla is based on the newer molecular phylogeny, but there are two caveats.
* First, the concept of body-plan grades is still a very useful way to think about the diversity of animal forms that have evolved.
* Second, the molecular phylogeny is a hypothesis about the history of life, and is thus tentative.
* This phylogeny is based on just a few genes - mainly the small subunit ribosomal RNA (SSU-rRNA).
* Ideally, future research, including fossil evidence and traditional approaches, will eventually square the molecular data with data from these other approaches.

**C. The Origins of Animal Diversity**

1. Most animal phyla originated in a relatively brief span of geologic time

* The fossil record and molecular studies concur that the diversification that produced most animal phyla occurred rapidly on the vast scale of geologic time.
* This lasted about 40 million years (about 565 to 525 million years ago) during the late Precambrian and early Cambrian (which began about 543 million years ago).
* The strongest evidence for the initial appearance of multicellular animals is found in the last period of the Precambrian era, the **Ediacaran period**.
* Fossils from the Ediacara Hills of Australia (565 to 543 million years ago) and other sites around the world consist primarily of cnidarians, but soft-bodied mollusks were also present, and numerous fossilized burrows and tracks indicate the presence of worms.
* Recently, fossilized animal embryos in China from 570 million years ago and what could be fossilized burrows from rocks 1.1 billion years ago have been reported.
* Data from molecular systematics suggest an animal origin about a billion years ago.
* Nearly all the major animal body plans appear in Cambrian rocks from 543 to 525 million years ago.
* During this relatively short time, a burst of animal origins, the **Cambrian explosion**, left a rich fossil assemblage.
* It includes the first animals with hard, mineralized skeletons.
* Some Cambrian fossils in the Burgess Shale in British Columbia and other sites in Greenland and China are rather bizarre-looking when compared to typical marine animals today.
* Some of these may represent extinct “experiments” in animal diversity.
* However, most of the Cambrian fossils are simply ancient variations of phyla that are still represented in the modern fauna.
* On the scale of geologic time, animals diversified so rapidly that it is difficult from the fossil record to sort out the sequence of branching in animal phylogeny.
* Because of this, systematists depend largely on clues from comparative anatomy, embryology, developmental genetics, and molecular systematists of extant species.

2. “Evo-devo” may clarify our understanding of the Cambrian diversification

* There are three main hypotheses for what caused the diversification of animals.

• (1) *Ecological Causes*: The emergence of predator-prey relationships led to a diversity of evolutionary adaptations, such as various kinds of protective shells and diverse modes of locomotion.

• (2) *Geological Causes:* Atmospheric oxygen may have finally reached high enough concentrations to support more active metabolism.

• (3) *Genetic causes*: Much of the diversity in body form among animal phyla is associated with variations in the spatial and temporal expression of *Hox* genes within the embryo.

* A reasonable hypothesis is that the diversification of animals was associated with the evolution of the *Hox* regulatory genes, which led to variation in morphology during development.
* Biologists investigating “evo-devo,” the new synthesis of evolutionary biology and developmental biology, may provide insights into the Cambrian explosion.
* These three hypotheses are not mutually exclusive.
* Some systematists studying animal phylogeny interpret the molecular data as supporting three Cambrian explosions, not just one.
* For the three main branches of bilateral animals—Lophotrochozoa, Ecdysozoa, and Deuterostomia—the relationships among phyla *within* each are difficult to resolve, but the differences *between* these three clades are clear, based on their nucleic acid sequences.
* This suggests that these three clades branched apart very early, probably in the Precambrian, perhaps associated with the evolution of the *Hox* complex.
* Rapid diversification within each clade may have been driven by geological and/or ecological changes during the early Cambrian.
* By the end of the Cambrian radiation, the animal phyla were locked into developmental patterns that constrained evolution enough that no additional phyla evolved after that period.
* Variations in developmental patterns continued, allowing subtle changes in body structures and functions, leading to speciation and the origin of taxa below the phylum level.
* In the last half-billion years, animal evolution has mainly generated new variations on old “designs”.