Understanding Organisms: An Evolutionary, Ecological and Comparative Approach

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ROTEL (Remixing Open Textbooks with an Equity Lens) Project

Fitchburg, Massachusetts

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Introduction

I have been utilizing OER (Open Educational Resources) in my courses for several years, understanding that the lack of access and affordability of course materials is a barrier to student success, and a major equity issue that disproportionately impacts underserved populations.

For both introductory and upper-level biology courses, I've been willing to adopt a text or prepare a combination of course resources that were low- or no-cost to students, *even if* they were not ideal because (1) I know through conversations and polling that relief from financial stress is more important to my students than text quality and (2) I saw first-hand the disadvantages to students that were unable to purchase texts, including the "affordable" branded, limited-access electronic versions of popular publishers' biology textbooks.

For introductory biology, which (typically) serves first-year biology majors in our department, I had previously curated custom modules in the course learning management system that brought together various OER texts and other multimodal resources. The ROTEL (Remixing Open Textbooks through an Equity Lens) initiative* provided an opportunity to combine, adapt, and enhance the free materials I had been offering piecemeal to my students, into a single streamlined text that engages readers, aligns with the course learning goals, improves representation and inclusivity in the course resources, and provides students with long-term access.

As a true remix project, this text was adapted from a variety of sources. The original book that forms the 'bones' of this project is OpenStax *Biology* 2e, but many other openly licensed materials were incorporated, including Amanda Simons' ROTEL publication *Chromosomes, Genes, and Traits: An*

Introduction to Genetics, Andrea Bierema's *An Interactive Introduction to Organismal and Molecular Biology*, material from the Khan Academy *College Biology* course, and the University of California Museum of Paleontology's website *Understanding Evolution*. All attributions appear within the modules where they were used.

Understanding Organisms is an 'evergreen' document. This version represents the first phase of this work; plans for a second edition to meet additional project goals and address reviewer and feedback are underway. Future improvements will be focused on representing current science in a rapidly changing world, and ensuring that the content is accessible, inclusive and culturally relevant. Comments and suggestions are welcomed.

What was accomplished in the current version?

- Customized content to align with course learning goals and objectives.
- Embedded or linked multifarious web-based resources like popular science articles, podcasts, short videos and animations, interactive tutorials, simulations and self-check questions into the chapter content.
- Incorporated the work of biologists from diverse backgrounds in the examples used to support biology concepts and highlight connections to research or real-world applications throughout the text.
- Examined all images and media to ensure compliance with current accessibility standards and compatibility with assistive technologies.
- Modified language choices to uphold diversity, equity, and inclusivity, with adapted chapter content to improve accuracy and inclusivity in sex-related topics such as sexual reproduction, sex determination, and sexual selection.

What is planned for a future edition?

- Expanded 'Scientist Spotlight' sections that build on the personal backgrounds, career trajectories, and research projects of diverse biologists, encouraging students to identify as biologists via role models while tying real-world research to core biology concepts.
- Addition or substitution of [special section] within chapters with content that better connects biological concepts to culturally and societally relevant issues.
- Improved chapter summaries or 'key takeaways.'
- Hyperlinking between related content to support the interleaving of key concepts.

I'd like to thank several people for helping to make this project possible:

- Marilyn Billings, Faculty Advisor and Advocate for the ROTEL grant, and the publishing support team, especially Minh Lee, Richard Lizotte and Vicky Gavin.
- My friend and colleague Tess Killpack, for her feedback and encouragement on this project, her partnership in biology course development and redesign, and her tireless work to promote student success and a more equitable, inclusive, and supportive departmental culture.
- The Salem State University Viking OER and Textbook Affordability Initiative for financial and practical support in adopting and developing no-cost or low-cost course resources for our students.
- My partner, family and young children's caretakers. Without them, this text would not exist.

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Land Acknowledgement Statement for the ROTEL Grant

As part of ROTEL Grant's mission to support the creation, management, and dissemination of culturally-relevant textbooks, we must acknowledge Indigenous Peoples as the traditional stewards of the land, and the enduring relationship that exists between them and their traditional territories. We acknowledge that the boundaries that created Massachusetts were arbitrary and a product of the settlers. We honor the land on which the Higher Education Institutions of the Commonwealth of Massachusetts are sited as the traditional territory of tribal nations. We acknowledge the painful history of genocide and forced removal from their territory, and other atrocities connected with colonization. We honor and respect the many diverse indigenous people connected to this land on which we gather, and our acknowledgement is one action we can take to correct the stories and practices that erase Indigenous People's history and culture.

Identified tribes and/or nations of Massachusetts

Historical nations:

- Mahican
- Mashpee
- Massachuset
- Nauset
- Nipmuc
- Pennacook
- Pocomtuc
- Stockbridge
- Wampanoag

Present day nations and tribes:

- Mashpee Wampanoag Tribe
- Wampanoag Tribe of Gay Head Aquinnah
- Herring Pond Wampanoag Tribe
- Assawompsett-Nemasket Band of Wampanoags
- Pocasset Wampanoag of the Pokanoket Nation
- Pacasset Wampanoag Tribe

- Seaconke Wampanoag Tribe
- Chappaquiddick Tribe of the Wampanoag Indian Nation
- Nipmuc Nation (Bands include the Hassanamisco, Natick)
- Nipmuck Tribal Council of Chaubunagungamaug
- Massachusett Tribe at Ponkapoag

In the event that we have an incorrect link or are missing an existing band/nation, please let us know so that we may correct our error.

Suggested readings

Massachusetts Center for Native American Awareness

A guide to Indigenous land acknowledgment

'We are all on Native Land: A conversation about Land Acknowledgements' YouTube video

Native-Land.ca | Our home on native land (mapping of native lands)

Beyond territorial acknowledgments – âpihtawikosisân

Your Territorial Acknowledgment Is Not Enough

I

Introduction to Organisms

This module contains the following chapters:

- What Defines Biological Life?
- Diversity and Organization
- Comparing Prokaryotes and Eukaryotes
- The Origin of Eukaryotes

Adapted from:

What Defines Biological Life?

Section Goals

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

- Formulate a biological definition of “life”
- Identify and describe the universal characteristics of living things

Scientists believe that the first forms of life on Earth were microorganisms that existed for billions of years in the ocean before plants and animals appeared. The mammals, birds, and flowers so familiar to us are all relatively recent, originating 130 to 250 million years ago. The earliest representatives of the genus *Homo*, to which we belong, have inhabited this planet for only the last 2.5 million years, and only in the last 300,000 years have humans started looking like we do today .

It’s hard to grasp the vast amounts of time since Earth formed and life first appeared on its surface. It may help to think of Earth’s history as a 24-hour day, as shown in **Figure 1.**

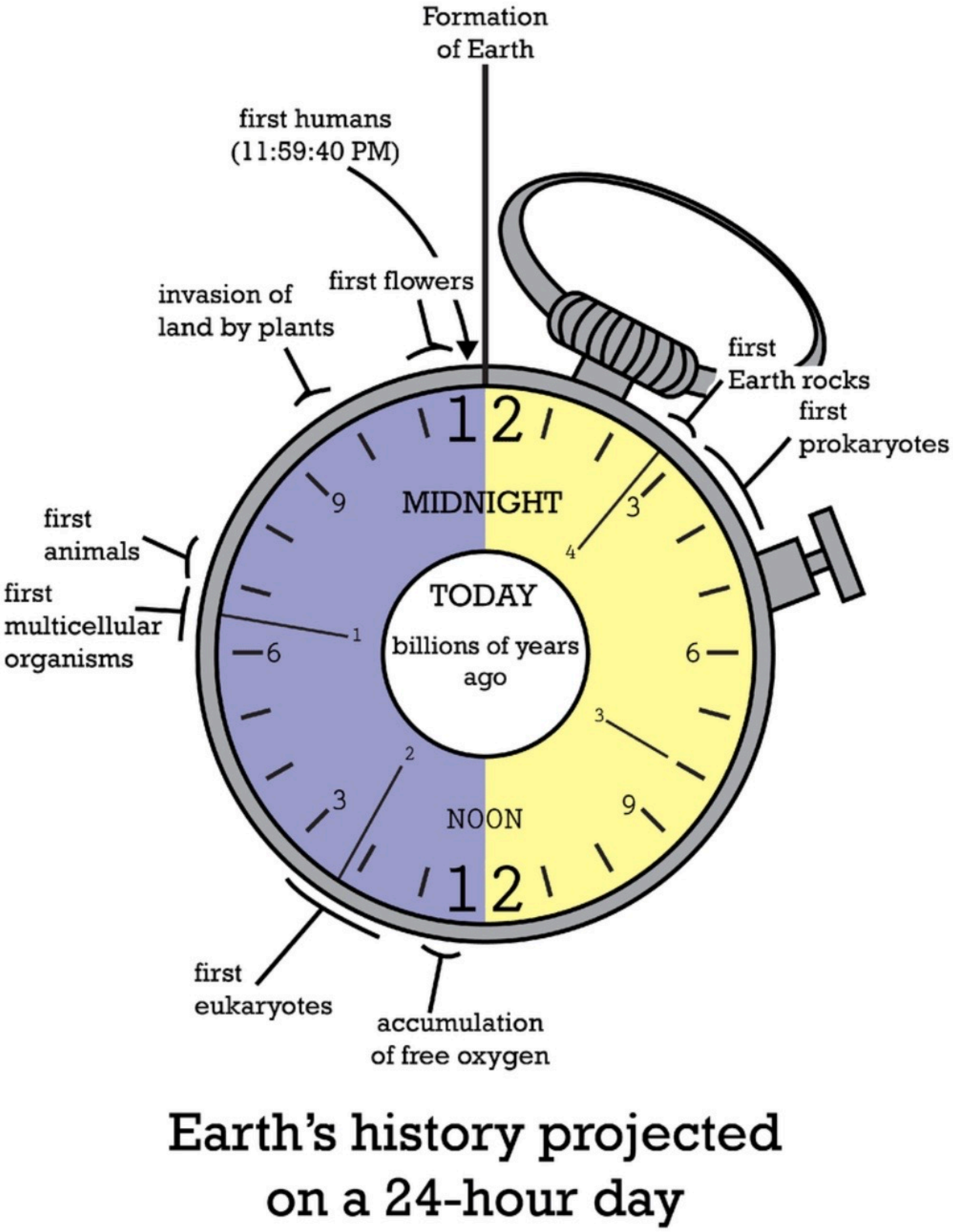
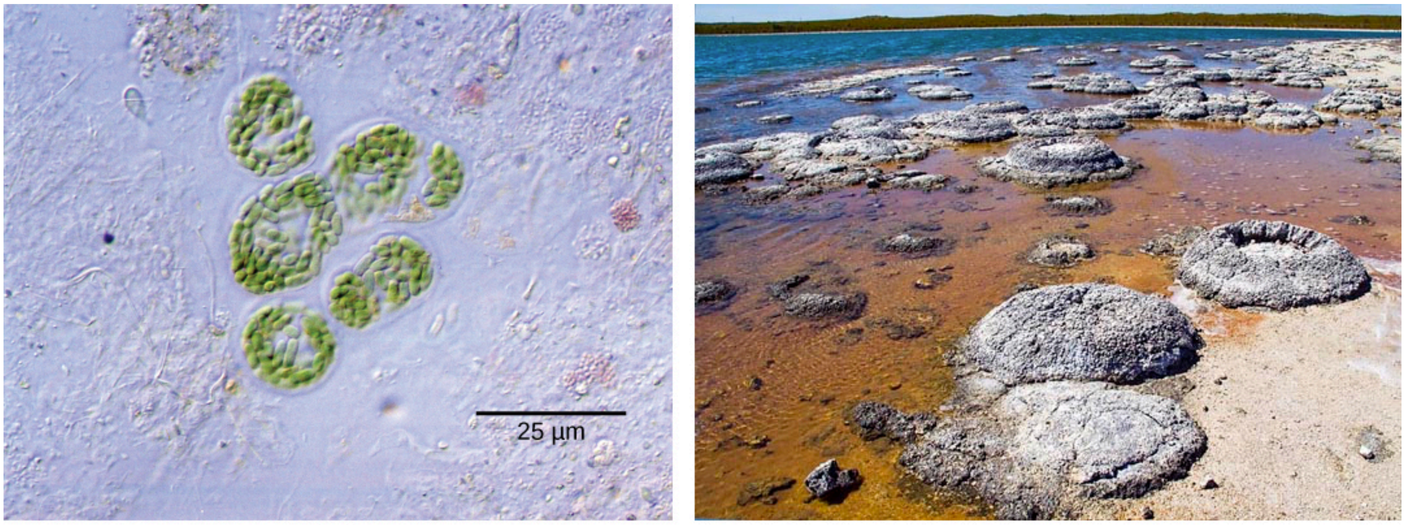


Figure 1. *"History of Earth in a Day"*

What is biology? In simple terms, **biology** is the study of life. This definition is very broad because the scope of biology is vast. Biologists may study anything from the microscopic or submicroscopic view of a cell to ecosystems and the whole living planet (**Figure 2**).



(a) (b)

Figure 2. *Formerly called blue-green algae, these (a) cyanobacteria, magnified 300x under a light microscope, are some of Earth's oldest life forms. These (b) stromatolites along the shores of Lake Thetis in Western Australia are ancient structures formed by layering cyanobacteria in shallow waters. (credit a: modification of work by NASA; credit b: modification of work by Ruth Ellison; scale-bar data from Matt Russell)*

Listening to the daily news, you will quickly realize how many aspects of biology we discuss every day. For example, recent news topics include *Escherichia coli* (**Figure 3**) outbreaks in spinach and *Salmonella* contamination in peanut butter. Other subjects include efforts toward finding a cure for AIDS, Alzheimer's disease, and cancer. On a global scale, many researchers are committed to finding ways to protect the planet, solve environmental issues, and reduce the effects of climate change. All of these diverse endeavors are related to different facets of the discipline of biology.

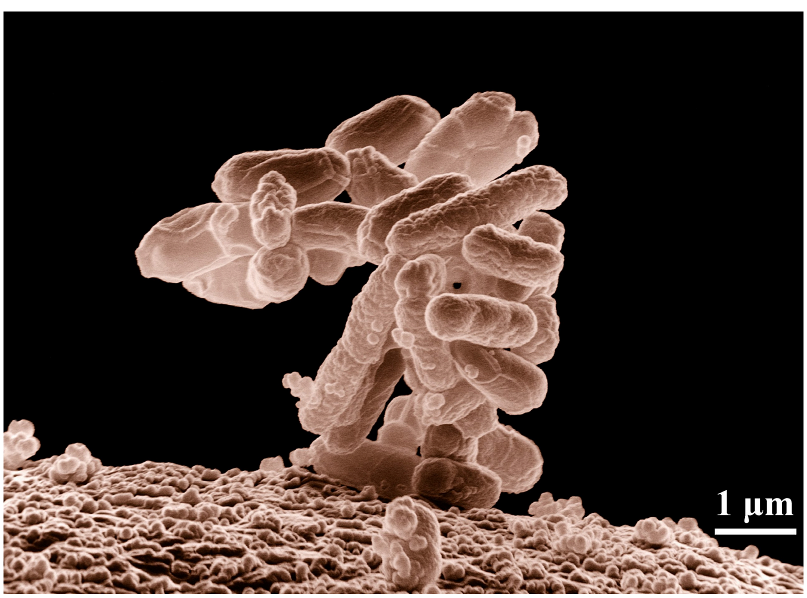


Figure 3. *Escherichia coli (E. coli) bacteria, in this scanning electron micrograph, are normal residents of our digestive tracts that aid in absorbing vitamin K and other nutrients.*

However, virulent strains are sometimes responsible for disease outbreaks.

Biology is the science that studies life, but what exactly is life? This question may sound like a silly question with an obvious response, but it is not always easy to define life. For example, a branch of biology called virology studies viruses, which exhibit some of the characteristics of living entities but lack others. It turns out that although viruses can attack living organisms, cause diseases, and even reproduce, they do not meet the criteria that biologists use to define life. Consequently, virologists are not biologists, strictly speaking. Similarly, some biologists study the early molecular evolution that gave rise to life; since the events that preceded life are not biological events, these scientists are also excluded from biology in the strict sense of the term.

From its earliest beginnings, biology has wrestled with these questions: What are the shared properties that make something "alive"? And once we know something is alive, how do we find meaningful levels of organization in its structure?

All living organisms share several key characteristics or functions: order, sensitivity, or response to the environment, reproduction, growth and development, regulation, homeostasis, and energy processing. When viewed together, these characteristics serve to define life. Each will be described in more detail below.

Order

Figure 4. *A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems.*

Organisms are highly organized, coordinated structures that consist of one or more cells. Even very simple, single-celled organisms are remarkably complex: inside each cell, atoms make up molecules; these, in turn, make up cell organelles and other cellular inclusions.

In multicellular organisms (**Figure 4**), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with distinct functions). Organs work together to form organ systems.

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light, climb on fences and walls, or respond to touch (**Figure 5**). Even tiny bacteria can move toward or away from chemicals (a process called *chemotaxis*) or light (*phototaxis*). Movement toward a stimulus is a positive response, while movement away from a stimulus is a negative response.

Figure 5. *The leaves of this sensitive plant, Mimosa pudica, will instantly droop and fold when touched. After a few minutes, the plant returns to normal. (credit: Alex Lomas)*

Watch this video to see how plants respond to a stimulus—from opening to light to wrapping a tendril around a branch to capturing prey.

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Reproduction

Single-celled organisms reproduce by first duplicating their DNA and then dividing it equally as the cell prepares to divide to form two new cells. Multicellular organisms often produce specialized reproductive germline cells that will form new individuals. When reproduction occurs, DNA containing genes is passed along to an organism's offspring. These genes ensure that the offspring will belong to the same species and will have similar characteristics, such as size and shape.

Adaptation

All living organisms exhibit a "fit" to their environment. Biologists refer to this fit as adaptation, and it is a consequence of evolution by natural selection, which operates in every lineage of reproducing organisms. Examples of adaptations are diverse and unique, from heat-resistant Archaea that live in boiling hot springs to the tongue length of a nectar-feeding moth that matches the size of the flower from which it feeds. All adaptations enhance the reproductive potential of the individuals exhibiting them, including their ability to survive to reproduce. Adaptations are not constant. As an environment changes, natural selection causes the characteristics of the individuals in a population to track those changes.

Growth and Development

Figure 6. *Although no two look alike, these puppies have inherited genes from both parents and share many of the same characteristics.*

Organisms grow and develop following specific instructions coded for by their genes. These genes provide instructions that will direct cellular growth and development, ensuring that a species' young (**Figure 6**) will grow up to exhibit many of the same characteristics as its parents.

Regulation

Even the smallest organisms are complex and require multiple regulatory mechanisms to coordinate internal functions, respond to stimuli, and cope with environmental stresses. Two examples of internal functions regulated in an organism are nutrient transport and blood flow. Organs (groups of tissues working together) perform specific functions, such as carrying oxygen throughout the body, removing wastes, delivering nutrients to every cell, and cooling the body.

Homeostasis

Figure 7. *Polar bears (Ursus maritimus) and other mammals living in ice-covered regions maintain their body temperature by generating heat and reducing heat loss through thick fur and a dense layer of fat under their skin.*

In order to function properly, cells need to have appropriate conditions such as proper temperature, pH, and appropriate concentration of diverse chemicals. These conditions may, however, change from one moment to the next. Organisms are able to maintain internal conditions within a narrow range almost constantly, despite environmental changes, through **homeostasis** (literally, "steady state")—the ability of an organism to maintain constant internal conditions.

For example, an organism needs to regulate body temperature through a process known as thermoregulation. Organisms that live in cold climates, such as the polar bear (**Figure 7**), have body structures that help them withstand low temperatures and conserve body heat. Structures that aid in this type of insulation include fur, feathers, blubber, and fat. In hot climates, organisms have methods (such as perspiration in humans or panting in dogs) that help them to shed excess body heat.

Energy Processing

All organisms use a source of energy for their metabolic activities. Some organisms capture energy from the sun and convert it into chemical energy in food (photosynthesis); others use chemical energy in molecules they take in as food (cellular respiration).

Figure 8. *The California condor (Gymnogyps californianus) uses chemical energy derived from food to power flight. California condors are an endangered species. This bird has a wing tag that helps biologists identify the individual.*

Evolution

The diversity of life on Earth is a result of mutations, or random changes, in hereditary material over time. These mutations allow the possibility for organisms to adapt to a changing environment. An organism that evolves characteristics fit for the environment will have greater reproductive success, subject to the forces of natural selection.

Did I Get It?

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The Diversity and Organization of Life

Section Goals

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

- Describe the levels of organization among living things
- Explain the purpose of phylogenetic trees
- Explain how organismal relationships are indicated by the binomial naming system

Living things are highly organized and structured, following a hierarchy that can be examined on a scale from small to large. The **atom** is the smallest and most fundamental unit of matter. It consists of a nucleus surrounded by electrons. Atoms form molecules. A **molecule** is a chemical structure consisting of at least two atoms held together by one or more chemical bonds. Many biologically important molecules are **macromolecules**, large molecules that are typically formed by polymerization (a polymer is a large molecule that is made by combining smaller units called monomers, which are simpler than macromolecules). An example of a macromolecule is deoxyribonucleic acid (DNA) (**Figure 1**), which contains the instructions for the structure and functioning of all living organisms.

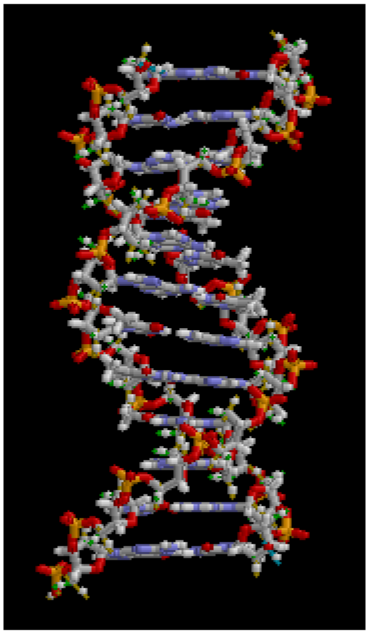

Figure 1. *All molecules, including this DNA molecule, are composed of atoms.*

Some cells contain aggregates of macromolecules surrounded by membranes; these are called **organelles**. Organelles are small structures that exist within cells. Examples of organelles include mitochondria and chloroplasts, which carry out indispensable functions: mitochondria produce energy to power the cell, while chloroplasts enable green plants to utilize the energy in sunlight to make sugars. All living things are made of cells; the **cell** itself is the smallest fundamental unit of structure and function in living organisms. (This requirement is why viruses are not considered living: they are not made of cells. To make new viruses, they have to invade and hijack the reproductive mechanism of a living cell. Only then can they obtain the materials they need to reproduce.) Some organisms consist of a single cell, and others are multicellular. Cells are classified as prokaryotic or eukaryotic. **Prokaryotes** are single-celled or colonial organisms that do not have membrane-bound nuclei or organelles; in contrast, the cells of **eukaryotes** do have membrane-bound organelles and a membrane-bound nucleus.

In larger organisms, cells combine to make **tissues**, which are groups of similar cells carrying out similar or related functions. **Organs** are collections of tissues grouped together performing a common function. Organs are present not only in animals but also in plants. An **organ system** is a higher level of organization that consists of functionally related organs. Mammals have many organ systems. For instance, the circulatory system transports blood through the body and to and from the lungs; it includes organs such as the heart and blood vessels. **Organisms** are individual living entities. For example, each tree in a forest is an organism. Single-celled prokaryotes and single-celled eukaryotes are also considered organisms and are typically referred to as microorganisms.

All the individuals of a species living within a specific area are collectively called a **population**. For example, a forest may include many pine trees. All of these pine trees represent the population of pine trees in this forest. Different populations may live in the same specific area. For example, the forest with the pine trees includes populations of flowering plants and also insects and microbial populations. A **community** is the sum of populations inhabiting a particular area. For instance, all of the trees, flowers, insects, and other populations in a forest form the forest's community. Keep in mind that the community level only consists of living organisms. The forest itself is an ecosystem; this is the first level that contains non-living aspects of a given area that impact the living things in that environment. An **ecosystem** consists of all the living things in a particular area together with the abiotic, non-living parts of that environment, such as nitrogen in the soil or rainwater. At the highest level of organization (**Figure 2**), the **biosphere** is the collection of all ecosystems, and it represents the zones of life on Earth. It includes land, water, and even the atmosphere to a certain extent.

From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy.

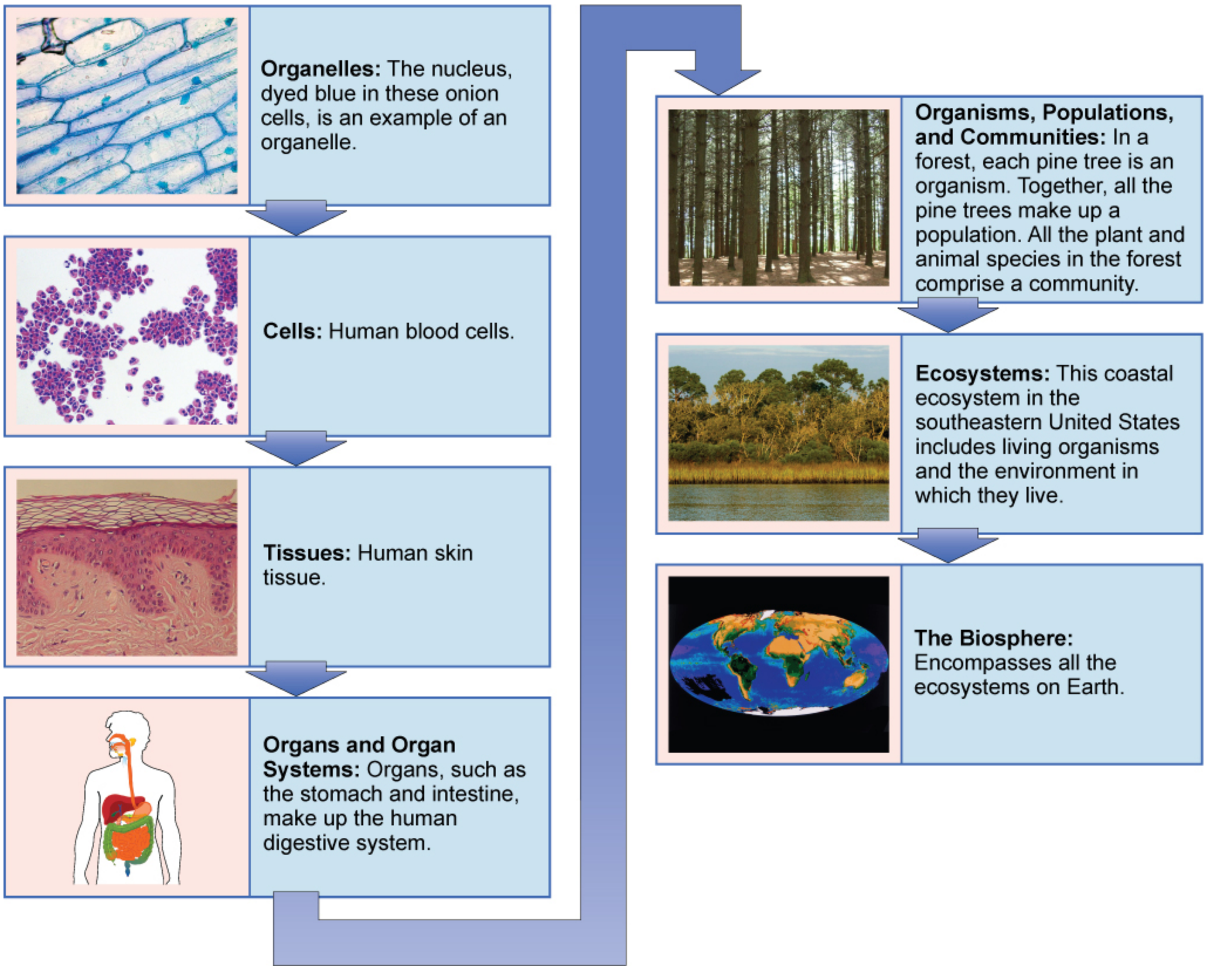

Figure 2. *The biological levels of the organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit "organelles": modification of work by Umberto Salvagnin; credit "cells": modification of work by Bruce Wetzel, Harry Schaefer/ National Cancer Institute; credit "tissues": modification of work by Kilbad; Fama Clamosa; Mikael Häggström; credit "organs": modification of work by Mariana Ruiz Villareal; credit "organisms"*)

Did I Get It?

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The Diversity of Life

When faced with the remarkable diversity of life, how do we organize the different kinds of organisms so that we can better understand them? As new organisms are discovered every day, biologists continue to seek answers to these and other questions. In this outcome, we will discuss *taxonomy*, which both demonstrates the vast diversity of life and tries to organize these organisms in a way we can understand.

Figure 3. *Life on Earth is incredibly diverse.*

Biological diversity is the variety of life on earth. This diversity includes all the different plants, animals, and microorganisms, the genes they contain, and the ecosystems they form on land and in water. Biological diversity is constantly changing. It is increased by new genetic variation and reduced by extinction and habitat degradation.

What Is Biodiversity?

Biodiversity refers to the variety of life and its processes, including the variety of living organisms, the genetic differences among them, and the communities and ecosystems in which they occur. Scientists have identified about 1.9 million species alive today. They are divided into the six kingdoms of life shown in **Figure 3**. Scientists are still discovering new species. Thus, they do not know for sure how many species really exist today. Most estimates range from 5 to 30 million species.

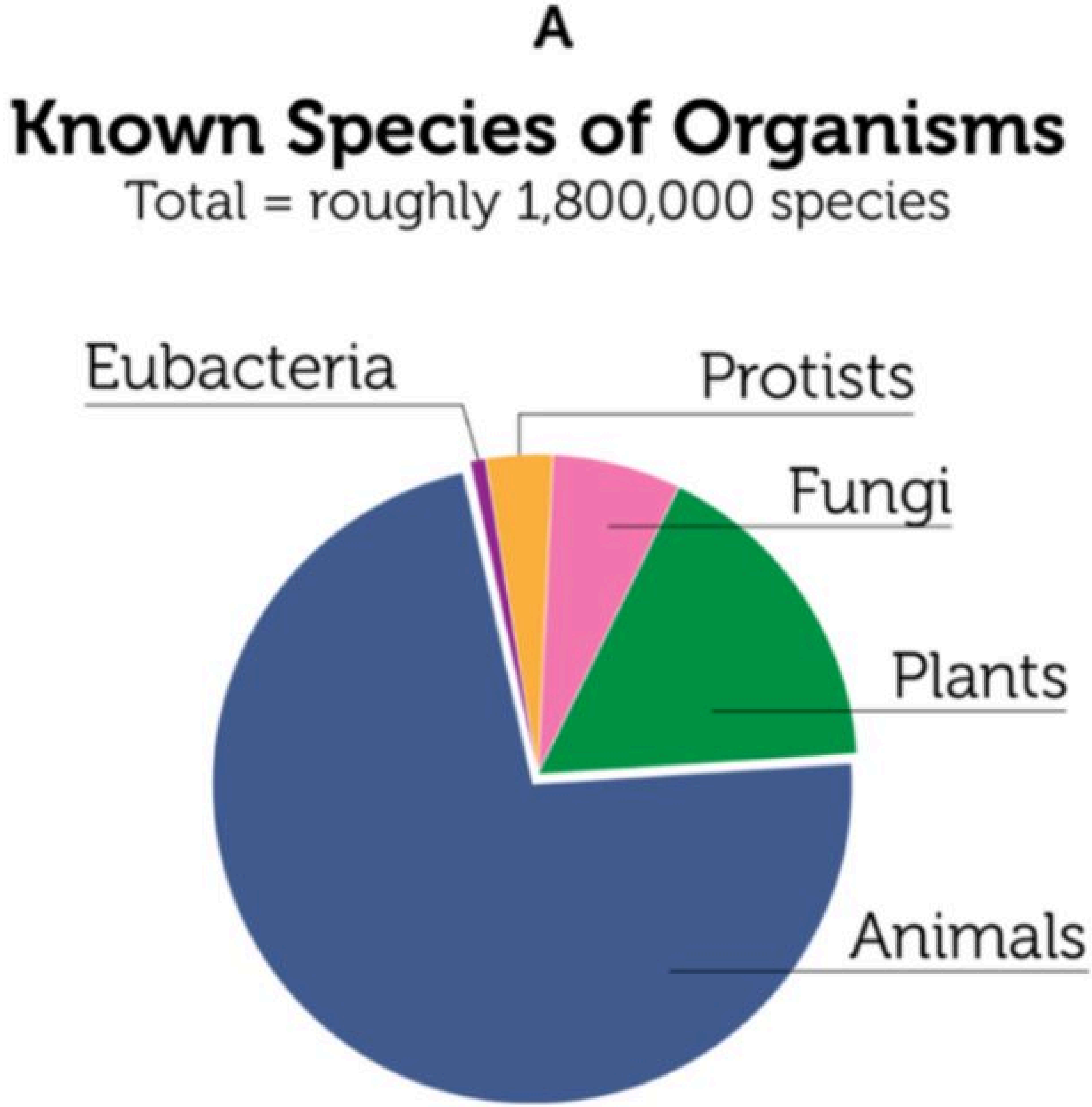


Figure 4. *Known life on Earth.*

Biologists, however, are always alert to levels of organization and have identified three unique measures of life's variation:

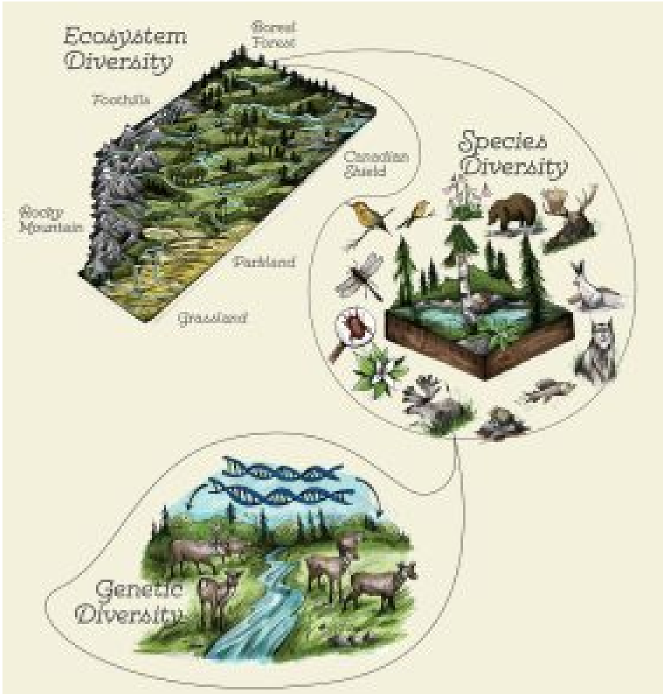
- 

  Figure 5. *Although all three levels of diversity are important, the term biodiversity usually refers to species diversity!*

  The most precise measure of biodiversity is **genetic diversity or genetic variation** within a species. This measure of diversity looks at differences among individuals within a population or at differences across different populations of the same species.

- The level just broader is **species diversity**, which best fits the literal translation of *biodiversity*: the number of different species in a particular ecosystem or on Earth. This type of diversity simply looks at an area and reports what can be found there.
- At the broadest, most encompassing level, we have **ecosystem diversity**. As Leopold clearly understood, the "cogs and wheels" include not only life but also the land, sea, and air that support life. In ecosystem diversity, biologists look at the many types of functional units formed by living communities interacting with their environments.

Although all three levels of diversity are important, the term biodiversity usually refers to ***species diversity!***

Watch this discussion about biodiversity:

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Biodiversity provides us with all of our food. It also provides for many medicines and industrial products, and it has great potential for developing new and improved products for the future. Perhaps most importantly, biological diversity provides and maintains a wide array of ecological "services." These include the provision of clean air and water, soil, food, and shelter. The quality—and the continuation— of our life and our economy is dependent on these "services."

Australia's Biological Diversity

Figure 6. *The short-beaked echidna is endemic to Australia. This animal—along with the platypus and three other species of echidnas—is one of the five surviving species of egg-laying mammals.*

The long isolation of Australia over much of the last 50 million years and its northward movement have led to the evolution of a distinct biota. Significant features of Australia's biological diversity include:

- A high percentage of endemic species (that is, they occur nowhere else):
    - over 80% of flowering plants
    - over 80% of land mammals
    - 88% of reptiles
    - 45% of birds
    - 92% of frogs
- Wildlife groups of great richness. Australia has an exceptional diversity of lizards in the arid zone, many ground orchids, and a total invertebrate fauna estimated at 200,000 species, with more than 4,000 different species of ants alone. Marsupials and monotremes collectively account for about 56% of native terrestrial mammals in Australia.
- Wildlife of major evolutionary importance. For example, Australia has 12 of the 19 known families of primitive flowering plants, two of which occur nowhere else. Some species, such as the Queensland lungfish and peripatus, have remained relatively unchanged for hundreds of millions of years.

Did I Get It?

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Phylogenetic Trees

The fact that biology, as a science, has such a broad scope has to do with the tremendous diversity of life on earth. The source of this diversity is **evolution**, the process of gradual change in a population or species over time. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

In scientific terms, the evolutionary history and relationship of an organism or group of organisms is called phylogeny. **Phylogeny** describes the relationships of one organism to others—such as which organisms it is thought to have evolved from, which species it is most closely related to, and so forth. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, a "tree of life" can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms (**Figure 6**).

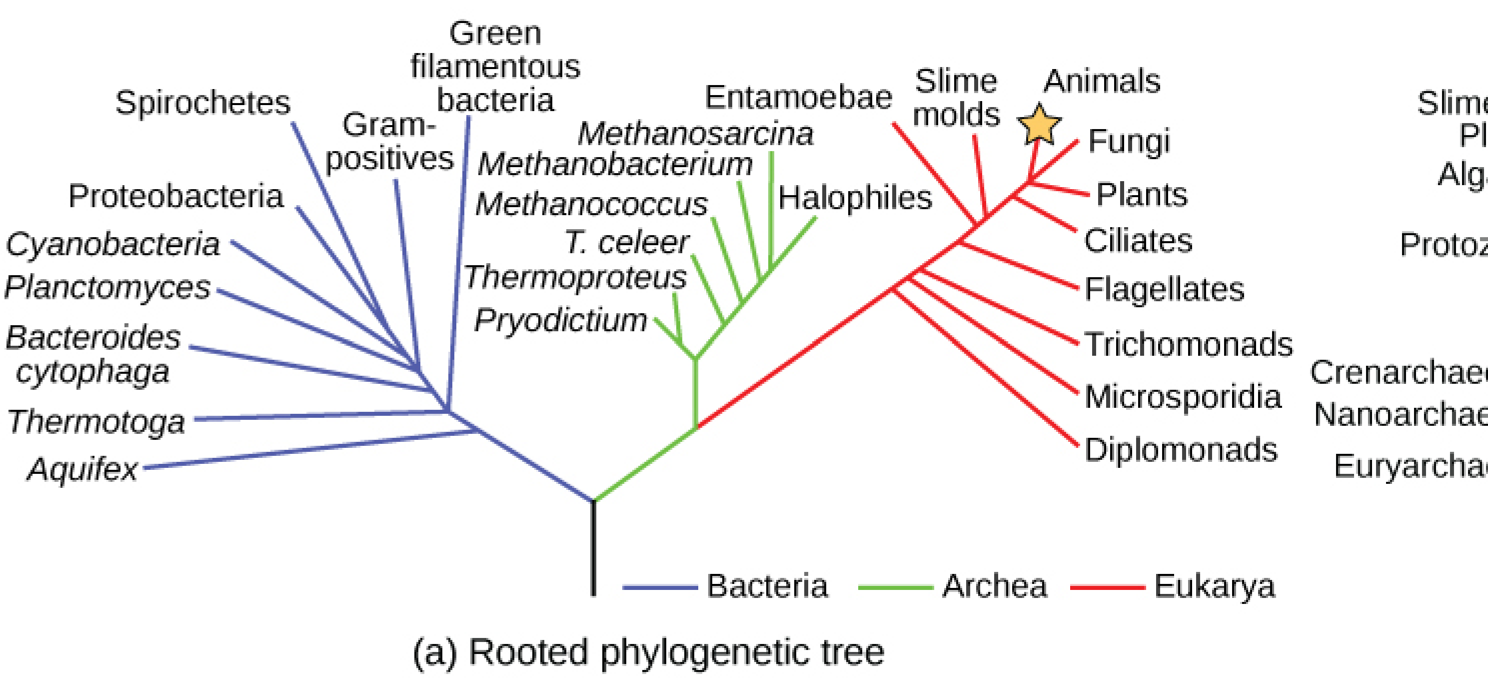

Figure 7. *Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, ar*

when various species diverged from a common ancestor while the (b) unrooted tree does not.

A phylogenetic tree can be read as a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees rooted, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree that the three domains—Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and minuscule these groups are compared with other organisms. Unrooted trees don't show a common ancestor but do show relationships among species.

Did I Get It?

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Taxonomy

Taxonomy (which literally means "arrangement law") is the science of classifying organisms to construct internationally shared classification systems, with each organism placed into more and more inclusive groupings. Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department further divides into aisles, then each aisle into categories and brands, and then finally, a single product. This organization, from larger to smaller, more specific categories, is called a hierarchical system.

The taxonomic classification system (also called the Linnaean system after its inventor, Carl Linnaeus, a Swedish botanist, zoologist, and physician) uses a hierarchical model. Moving from the point of origin, the groups become more specific until one branch ends as a single species. For example, after the common beginning of all life, scientists divide organisms into three large categories called a domain: Bacteria, Archaea, and Eukarya. Within each domain is a second category called a **kingdom**. After kingdoms, the subsequent categories of increasing specificity are **phylum**, **class**, **order**, **family**, **genus**, and **species** (**Figure 7**).

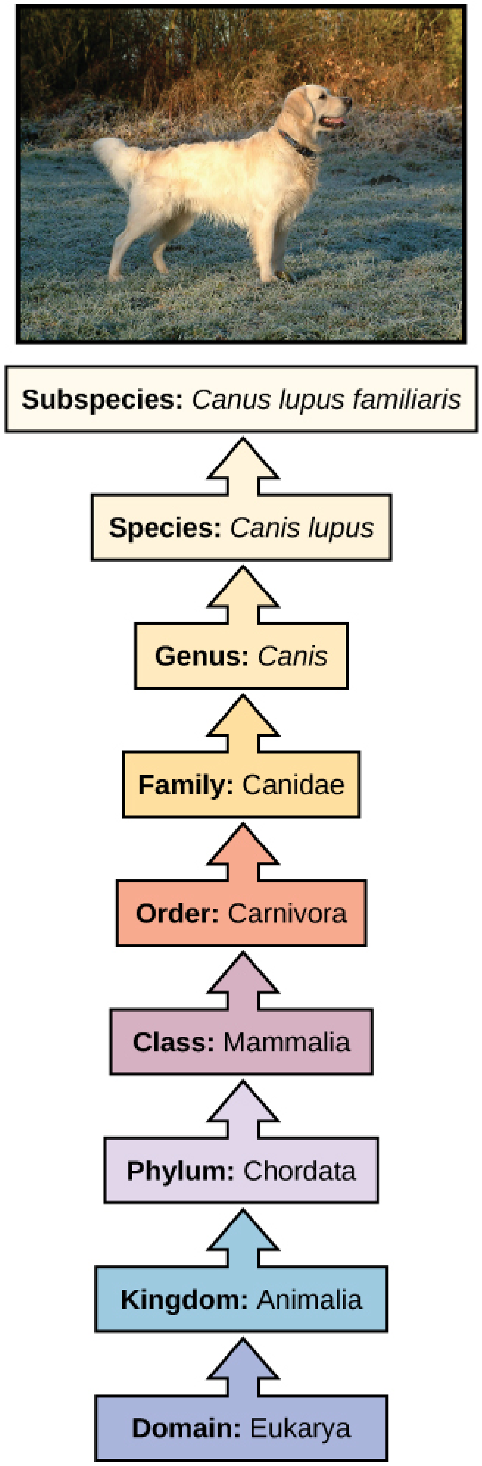

Figure 8. *The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, Canis lupus familiaris, is a subspecies of Canis lupus, which also includes the wolf and dingo.*

The kingdom Animalia stems from the Eukarya domain. For the common dog, the classification levels would be as shown in **Figure 7**. Therefore, the full name of an organism technically has eight terms. For the dog, it is Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis,* and *Lupus*. Notice that each name is capitalized except for species, and the genus and species names are italicized. Scientists generally refer to an organism only by its genus and species, which is its two-word scientific name, in what is called **binomial nomenclature**. Each species has a unique binomial nomenclature to allow for proper identification.

Therefore, the scientific name of the dog is *Canis lupus*.

When calling an organism by its specific binomial, the correct formatting (capitalization and italics) is important.

The name at each level is also called a **taxon**. In other words, dogs are in the order Carnivora. Carnivora is the name of the taxon at the order level; Canidae is the taxon at the family level, and so forth. Organisms also have a common name that people typically use, in this case, dog. Note that the dog is additionally a subspecies: the "*familiaris*" in *Canis lupus familiaris.* Subspecies are members of the same species that are capable of mating and reproducing viable offspring. Still, they are considered separate subspecies due to geographic or behavioral isolation or other factors.

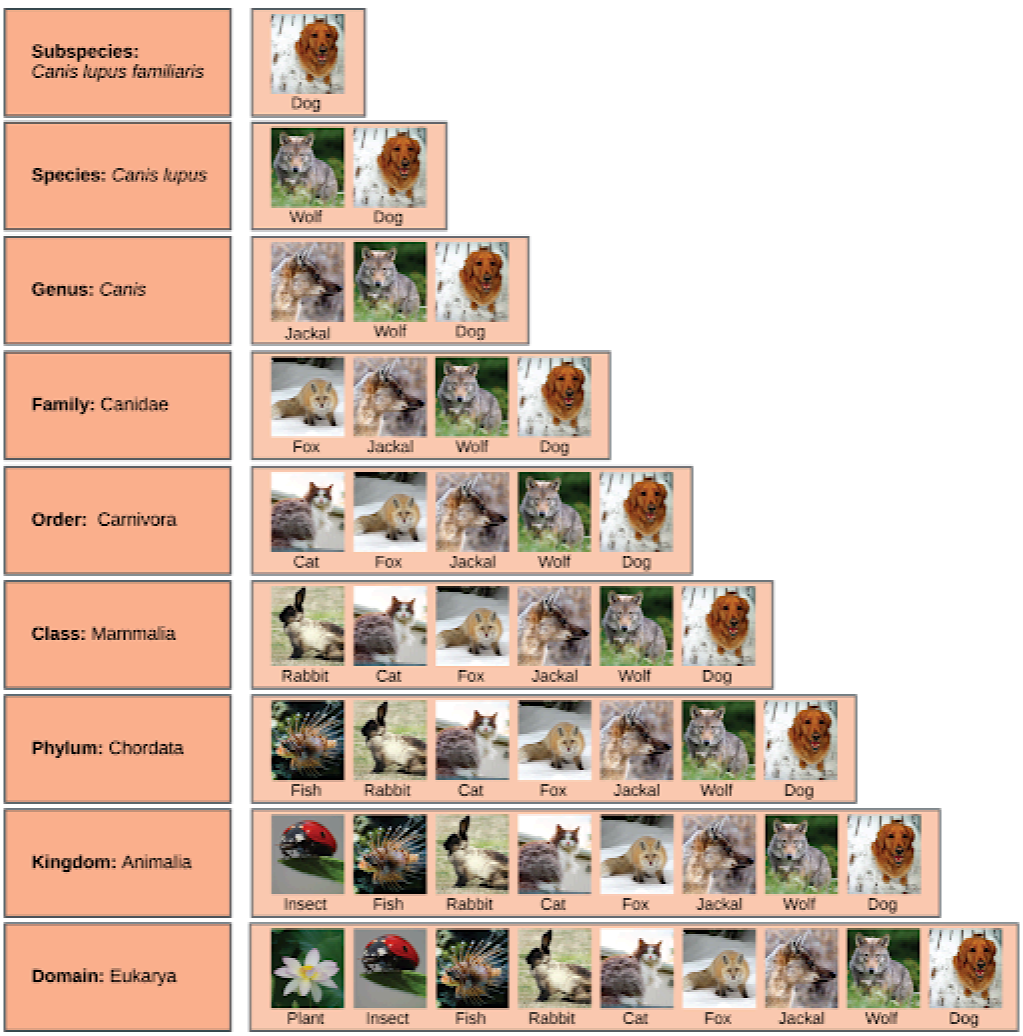

Figure 9. *At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can*

breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work by “berduchwal”/Flickr; credit “insect”: modification of work by Jon Sullivan; credit “fish”: modification of work by Christian Mehlführer; credit “rabbit”: modification of work by Aidan Wojtas; credit “cat”: modification of work by Jonathan Lidbeck; credit “fox”: modification of work by Kevin Bacher, NPS; credit “jackal”: modification of work by Thomas A. Hermann, NBII, USGS; credit “wolf”: modification of work by Robert Dewar; credit “dog”: modification of work by “digital_image_fan”/Flickr)

At what levels are cats and dogs considered to be part of the same group?

Check answer

Cats and dogs are part of the same group at five levels: both are in the domain Eukarya, the kingdom Animalia, the phylum Chordata, the class Mammalia, and the order Carnivora.

Did I Get It?

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Comparing Prokaryotes and Eukaryotes

Section Goals

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

- Describe the role of cells in organisms
- Identify features common to all cells
- Compare and contrast prokaryotic and eukaryotic cells

Close your eyes and picture a brick wall. What is the wall’s basic building block? It is a single brick. Like a brick wall, cells are the building blocks that make up your body.

Your body has many kinds of cells, each specialized for a specific purpose. Just as we use a variety of materials to build a home, the human body is constructed from many cell types. For example, epithelial cells protect the body's surface and cover the organs and body cavities within. Bone cells help to support and protect the body. Immune system cells fight invading bacteria. Additionally, blood and blood cells carry nutrients and oxygen throughout the body while removing carbon dioxide. Each of these cell types plays a vital role during the body's growth, development, and day-to-day maintenance. In spite of their enormous variety, however, cells from all organisms—even ones as diverse as bacteria, onions, and humans—share certain fundamental characteristics.

There are two types of cells: prokaryotic and eukaryotic. In this section, we'll explore the similarities and differences between these two types.

Comparing Prokaryotic and Eukaryotic Cells

The **cell theory** states that one or more cells comprise all living things, that the cell is the basic unit of life, and that new cells arise from existing cells. A cell is the smallest unit of a living thing. Whether composed of one cell (like bacteria) or many cells (like a human), we call it an organism. Thus, cells are the basic building blocks of all organisms.

Several cells of one kind interconnect with each other and perform a shared function to form tissues. These tissues combine to form an organ (your stomach, heart, or brain), and several organs comprise an organ system (such as the digestive system, circulatory system, or nervous system). Several systems that function together form an organism (like a human being). Here, we will examine the structure and function of cells.

There are many types of cells, which scientists group into one of two broad categories: prokaryotic and eukaryotic. The single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (*pro* = before; *karyon–* = nucleus). Animal cells, plant cells, fungi, and protists are eukaryotes (*eu* = true).

Components of Prokaryotic Cells

All cells share four common components: (1) a plasma membrane, an outer covering that separates the cell's interior from its surrounding environment; (2) cytoplasm, consisting of a jelly-like region within the cell in which other cellular components are found; (3) DNA, the genetic material of the cell; and (4) ribosomes, particles that synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

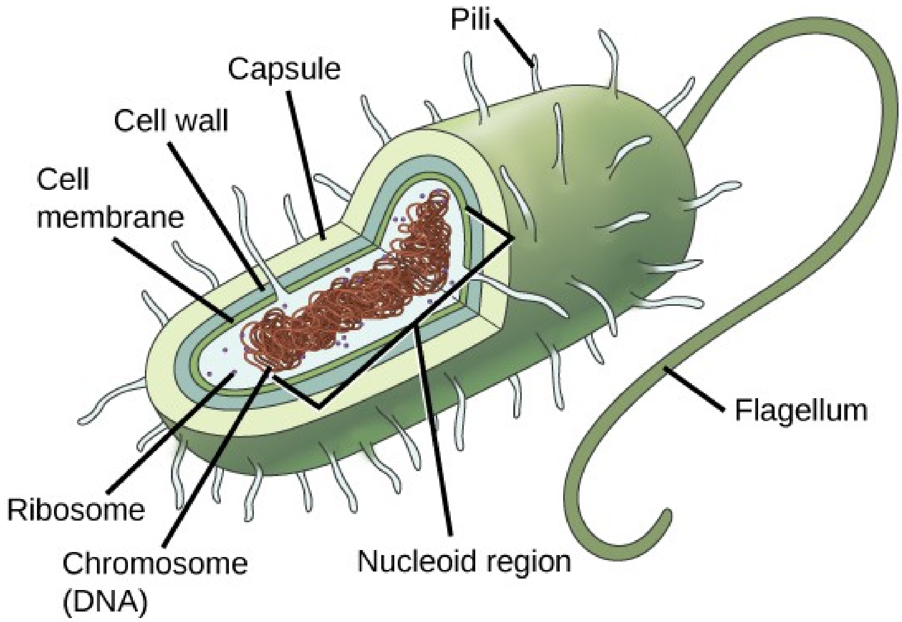

Figure 1. *This figure shows the generalized structure of a prokaryotic cell.*

A **prokaryotic cell** is a simple, single-celled (unicellular) organism that lacks a nucleus or any other membrane-bound organelle. We will shortly come to see that this is significantly different in eukaryotes. Prokaryotic DNA is found in the central part of the cell: a darkened region called the nucleoid (**Figure 1**).

Unlike Archaea and eukaryotes, bacteria have a cell wall made of peptidoglycan, composed of sugars and amino acids, and many have a polysaccharide capsule (**Figure 1**). The cell wall acts as an extra layer of protection, helps the cell maintain its shape, and prevents dehydration. The capsule enables the cell to attach to surfaces in its environment. Some prokaryotes have flagella, pili, or fimbriae. Flagella are used for locomotion, while most pili are used to exchange genetic material during a type of reproduction called conjugation.

Eukaryotic Cells

In nature, the relationship between form and function is apparent at all levels, including the level of the cell, and this will become clear as we explore eukaryotic cells. The principle “form follows function” is found in many contexts. It means that, in general, one can deduce the function of a structure by looking at its form because the two are matched. For example, birds and fish have streamlined bodies that allow them to move quickly through the medium in which they live, be it air or water.

A **eukaryotic cell** is a cell that has a membrane-bound nucleus and other membrane-bound compartments or sacs, called **organelles**, which have specialized functions. The word eukaryotic means “true nucleus,” alluding to the presence of the membrane-bound nucleus in these cells. The word “organelle” means “little organ,” and, as we learned earlier, organelles have specialized cellular functions, just as the organs of your body have specialized functions.

Data from fossils, as well as from the study of living genomes, have led comparative biologists to conclude that living eukaryotes are all descendants of a single common ancestor. Mapping the characteristics found in all major groups of eukaryotes reveals that the following characteristics are present in at least some of the members of each major lineage or during some part of their life cycle and, therefore must have been present in the *last common ancestor*.

1. **Cells with nuclei surrounded by a nuclear envelope with nuclear pores**: This is the single characteristic that is both necessary and sufficient to define an organism as a eukaryote. All extant eukaryotes have cells with nuclei.
2. **Mitochondria**: Most extant eukaryotes have “typical” mitochondria, although some eukaryotes have very reduced mitochondrial “remnants” and a few lack detectable mitochondria.
3. **Cytoskeleton of microtubules and microfilaments**: Eukaryotic cells possess the structural and motility components called *actin microfilaments and microtubules*. All extant eukaryotes have these cytoskeletal elements.
4. **Flagella and cilia**: Organelles associated with cell motility. Some extant eukaryotes lack flagella and/or cilia, but their presence in related lineages suggests that they are descended from ancestors that possessed these organelles.
5. **Chromosomes organized by histones**: Each eukaryotic chromosome consists of a linear DNA molecule coiled around basic (alkaline) proteins called histones. The few eukaryotes with chromosomes lacking histones clearly evolved from ancestors that had them.
6. **Mitosis**: A process of nuclear division in which replicated chromosomes are divided and Separated using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. **Sexual reproduction**: A meiotic process of nuclear division and genetic recombination unique to eukaryotes. During this process, diploid nuclei at one stage of the life cycle undergo meiosis to yield haploid nuclei, which subsequently fuse together (karyogamy) to create a diploid zygote nucleus.
8. **Cell walls**: It is reasonable to conclude that the last common ancestor could make cell walls during some stage of its life cycle because cell walls were present in their prokaryote precursors. However, not enough is known about eukaryotes’ cell walls and their development to know how much homology exists between those of prokaryotes and eukaryotes. If the last common ancestor could make cell walls, it is clear that this ability must have been lost in many groups.

Cell Size

At 0.1–5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10–100 μm (**Figure 2**). The small size of prokaryotes allows ions and organic molecules that enter them to quickly spread to other parts of the cell. Similarly, any waste produced within a prokaryotic cell can quickly move out. However, larger eukaryotic cells have evolved different structural adaptations to enhance cellular transport. Indeed, the large size of these cells would not be possible without these adaptations. In general, cell size is limited because volume increases much more quickly than does cell surface area. As a cell becomes larger, it becomes more and more difficult for the cell to acquire sufficient materials to support the processes inside the cell, because the relative size of the surface area across which materials must be transported declines.

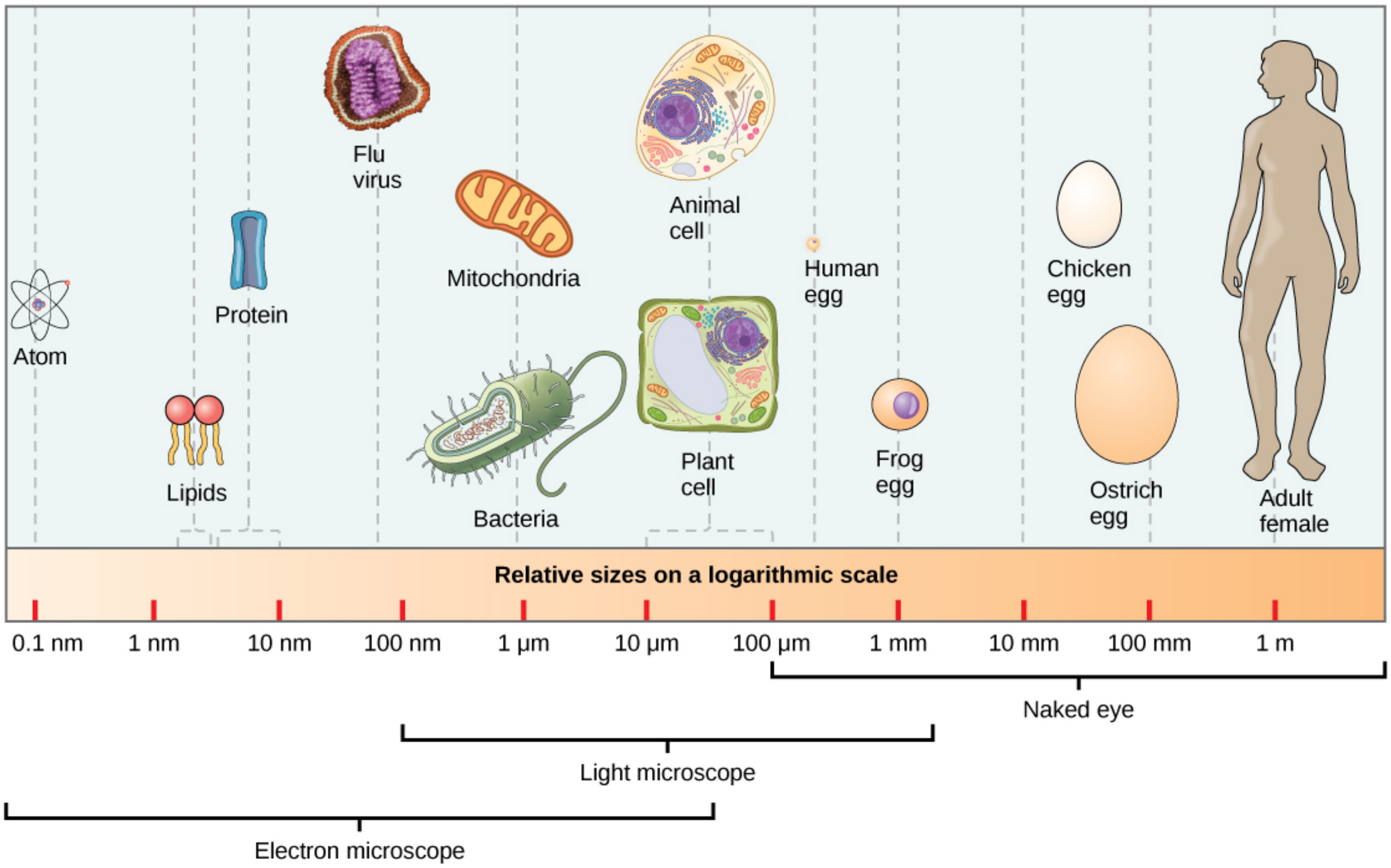

Figure 2. *shows the relative sizes of different kinds of cells and cellular components. An adult human is shown for comparison.*

Did I Get It?

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Summary: Comparing Prokaryotic And Eukaryotic Cells

Prokaryotes are single-celled organisms of the two domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, a cell wall, DNA, and lack membrane-bound organelles. Many also have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1–5.0 µm. Like a prokaryotic cell, a eukaryotic cell has a plasma membrane, cytoplasm, and ribosomes, but a eukaryotic cell is typically larger than a prokaryotic cell, has a true nucleus (meaning its DNA is surrounded by a membrane), and has other membrane-bound organelles that allow for compartmentalization of functions. Eukaryotic cells tend to be 10 to 100 times the size of prokaryotic cells.

The Origin of Eukaryotes

Section Goals

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

- Describe what scientists know about the origins of eukaryotes based on the last common ancestor
- Explain the endosymbiotic theory

Before we discuss the origins of eukaryotes, it is first important to understand that all extant eukaryotes are likely the descendants of a chimera-like organism that was a composite of a host cell and the cell(s) of an alpha-proteobacterium that "took up residence" inside it. This major theme in the origin of eukaryotes is known as **endosymbiosis**, one cell engulfing another such that the engulfed cell survives and both cells benefit. Over many generations, a symbiotic relationship can result in two organisms that depend on each other so completely that neither could survive on its own.

Imagine you swallowed a small bird and suddenly gained the ability to fly, or you ate a cobra and were able to spit poisonous venom! Well, throughout the history of life, and specifically during the evolution of complex eukaryotic cells, things like this happened all the time. In fact, similar endosymbiotic associations are not uncommon even in living eukaryotes!

In the video below, science educator Adam Jacobson explains endosymbiosis.

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Endosymbiotic events likely contributed to the origin of the last common ancestor of today's eukaryotes and to later diversification in certain lineages of eukaryotes. But before explaining endosymbiosis further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Many important metabolic processes arose in prokaryotes; however, some of these processes, such as nitrogen fixation, are never found in eukaryotes. The process of aerobic respiration is found in all major lineages of eukaryotes, and it is localized in the mitochondria. Aerobic respiration is also found in many lineages of prokaryotes, but it is not present in all of them, and a great deal of evidence suggests that such anaerobic prokaryotes never carried out aerobic respiration, nor did their ancestors.

While today's atmosphere is about 20 percent molecular oxygen (O2), geological evidence shows that it originally lacked O2. Without oxygen, aerobic respiration would not be expected, and living things would have relied on anaerobic respiration or the process of fermentation instead. At some point between 3.2 and 3.5 billion years ago, some prokaryotes began using energy from sunlight to power anabolic processes that reduce carbon dioxide to form organic compounds. That is, they evolved the ability to photosynthesize. Hydrogen, derived from various sources, was “captured” using light-powered reactions to reduce fixed carbon dioxide in the Calvin cycle. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O2 as a “waste” product about 2.2 billion years ago.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that posed a risk to living organisms since it can damage many organic compounds. Various metabolic processes evolved that protected organisms from oxygen, one of which, aerobic respiration, also generated high levels of ATP. It became widely present among prokaryotes, including in a free-living group we now call alpha-proteobacteria. Organisms that did not acquire aerobic respiration had to remain in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were abundant and active. Still, by about 2 billion years ago, geological evidence shows that oxygen was building up to higher concentrations in the atmosphere. Oxygen levels similar to today’s levels only arose within the last 700 million years.

Recall that the first fossils that we believe to be eukaryotes date to about 2 billion years old, so they evolved and diversified rapidly as oxygen levels were increasing. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by light microscopists in the late 1800s, where they were worm-shaped structures that were moving around in the cell. Some early observers suggested that they might be bacteria living inside host cells, but these hypotheses remained unknown or rejected in most scientific communities.

Endosymbiotic Theory

As cell biology developed in the twentieth century, it became clear that mitochondria were the organelles responsible for producing ATP using aerobic respiration, in which oxygen was the final electron acceptor.

In the 1960s, American biologist Lynn Margulis of Boston University developed the **endosymbiotic theory**, which states that eukaryotes may have been a product of one cell engulfing another, one living within another, and coevolving over time until the separate cells were no longer recognizable as such and shared genetic control of a mutualistic metabolic pathway to produce ATP (**Figure 3**). In 1967, Margulis introduced new data to support her work on the theory and substantiated her findings through microbiological evidence. Although Margulis’s work initially was met with resistance, this basic component of this once-revolutionary hypothesis is now widely accepted, with work progressing on uncovering the steps involved in this evolutionary process and the key players involved.

While the metabolic organelles and genes responsible for many energy-harvesting processes appear to have had their origins in bacteria, our nuclear genes and the molecular machinery responsible for replication and expression appear to be more closely related to those found in the Archaea. Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of Cooperation and Evolution Discovery in Biology. For instance, it is *not* known whether the endosymbiotic event that led to mitochondria occurred before or after the host cell had a nucleus. Such organisms would be among the extinct precursors of the last common ancestor of eukaryotes.

In this beautiful animation made from paper cutouts, Harvard Professor Rob Lue presents how mitochondria originated through endosymbiosis.

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Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of mitochondria, or their reduced derivatives, in virtually all eukaryotic cells. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption, in humans being most abundant in the liver and skeletal muscles. Each mitochondrion measures 1 to 10 or greater micrometers in length and exists in the cell as an organelle. Although they may have originated as free-living aerobic organisms, mitochondria can no longer survive and reproduce outside the cell.

Mitochondria have several features that suggest their relationship to alpha-proteobacteria. Alpha-proteobacteria are a large group of bacteria that includes species symbiotic with plants, disease organisms that can infect humans via ticks, and many free-living species that use light for energy. Mitochondria have their own genomes, with a circular chromosome. Mitochondria also have special ribosomes and transfer RNAs that resemble these same components in prokaryotes. When mitochondrial genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. In some eukaryotic groups, genes encoding proteins needed for cellular respiration are found in the mitochondria, whereas in other groups, they are found in the nucleus. This placement has been interpreted as evidence that over evolutionary time, genes have been transferred from the endosymbiont chromosome to those of the host genome. This apparent "loss" of genes by the endosymbiont is probably one explanation for why mitochondria cannot live without a host.

Another line of evidence supporting the idea that mitochondria were derived by endosymbiosis comes from the structure of the mitochondrion itself. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes; the inner membrane is bacterial in nature, whereas the outer membrane is eukaryotic. This structure is exactly what one would expect if one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The outer mitochondrial membrane was derived from the enclosing vesicle, while the inner membrane was derived from the plasma membrane of the endosymbiont. The mitochondrial inner membrane is extensive and involves substantial infoldings called **cristae** that resemble the textured outer surface of alpha-proteobacteria (**Figure 1**). The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

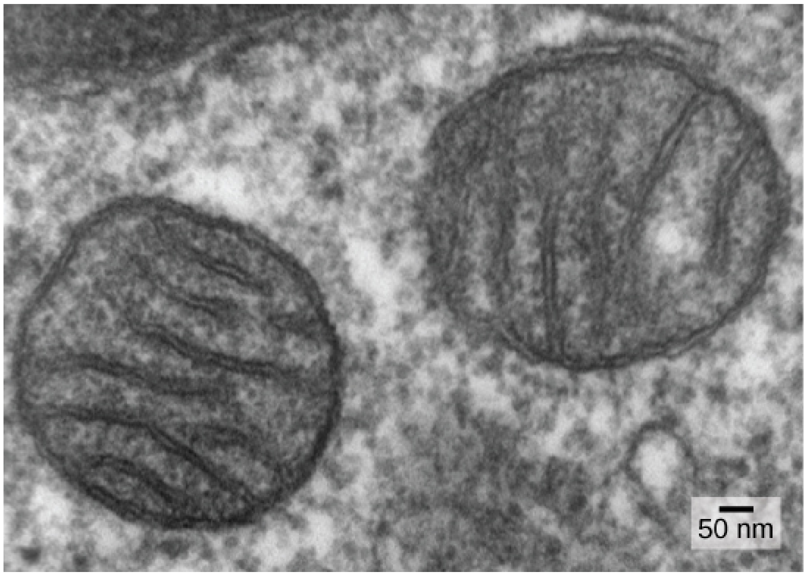


Figure 1. *Mitochondria. In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)*

The third line of evidence comes from the production of new mitochondria. Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Mitochondria arise only from previous mitochondria; they are not formed from scratch (de novo) by the eukaryotic cell. Mitochondria may fuse together, and they may be moved around inside the cell by interactions with the cytoskeleton. They reproduce within their enclosing cell and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they were independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. These features all support the theory that mitochondria were once free-living prokaryotes.

Some living eukaryotes are anaerobic and cannot survive in the presence of too much oxygen. A few appear to lack organelles that could be recognized as mitochondria. In the 1970s and into the early 1990s, many biologists suggested that some of these eukaryotes were descended from ancestors whose lineages had diverged from the lineage of mitochondrion-containing eukaryotes before endosymbiosis occurred. Later findings suggest that *reduced organelles* are found in most if not all, anaerobic eukaryotes and that virtually all eukaryotes appear to carry some genes in their nuclei that are of mitochondrial origin.

In addition to the aerobic generation of ATP, mitochondria have several other metabolic functions. One of these functions is to generate clusters of iron and sulfur that are important cofactors of many enzymes. Such functions are often associated with the reduced mitochondrion-derived organelles of anaerobic eukaryotes. The protist *Monocercomonoides,* an inhabitant of vertebrate digestive tracts, appears to be an exception; it has no mitochondria, and its genome contains neither genes derived from mitochondria nor nuclear genes related to mitochondrial maintenance. However, it is related to other protists with reduced mitochondria and probably represents an end-point in mitochondrial reduction. Although most biologists accept that the last common ancestor of eukaryotes had mitochondria, it appears that the complex relationship between mitochondria and their host cell continues to evolve.

Plastids

Some groups of eukaryotes are photosynthetic. Their cells contain, in addition to the standard eukaryotic organelles, another kind of organelle called a **plastid**. When such cells are carrying out photosynthesis, their plastids are rich in the pigment chlorophyll *a* and a range of other pigments, called *accessory pigments*, which are involved in harvesting energy from light. Photosynthetic plastids are called chloroplasts (**Figure 2**).

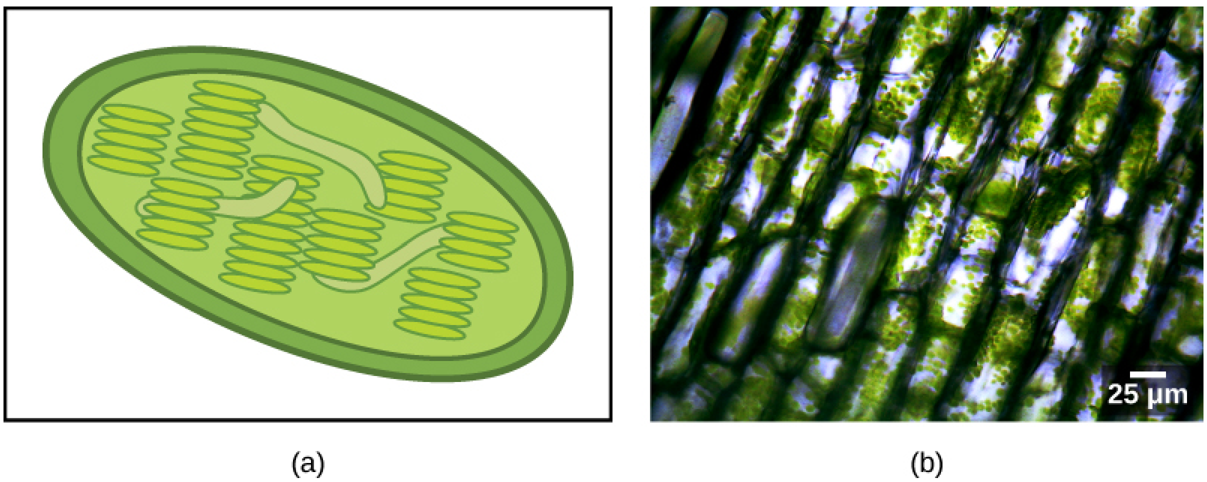


Figure 2. *Chloroplasts. (a) This chloroplast cross-section illustrates its elaborate inner membrane organization. Stacks of thylakoid membranes compartmentalize photosynthetic enzymes and provide scaffolding for chloroplast DNA. (b) In this micrograph of Elodea sp., the chloroplasts can be seen as small green spheres.*

Like mitochondria, plastids have an endosymbiotic origin. This hypothesis was also proposed and championed with the first direct evidence by Lynn Margulis. We now know that plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This arrangement is called primary endosymbiosis, and two membranes surround plastids of primary origin. The common ancestor of the major lineage or “supergroup” Archaeplastida (containing red and green algae) took on a cyanobacterial endosymbiont (**Figure 3**). Almost all photosynthetic eukaryotes are descended from this event.

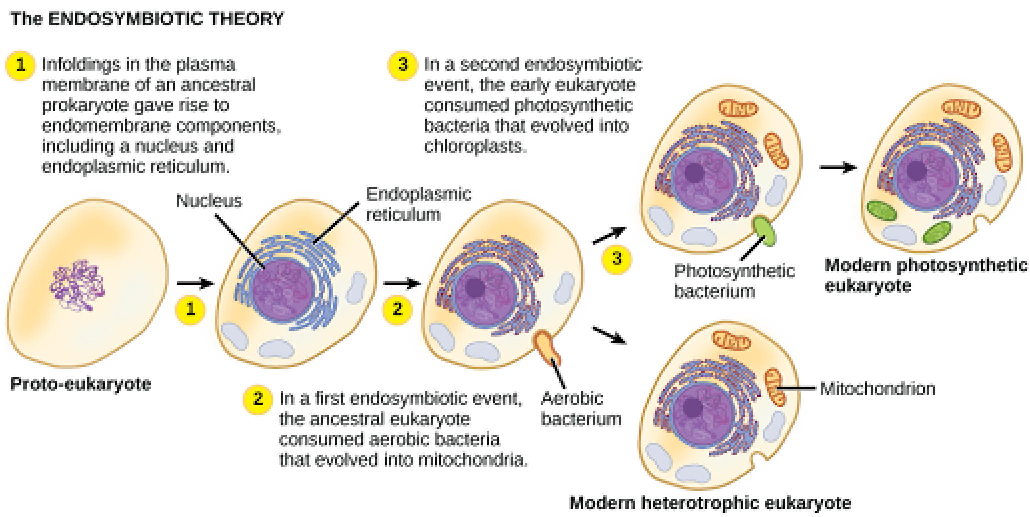


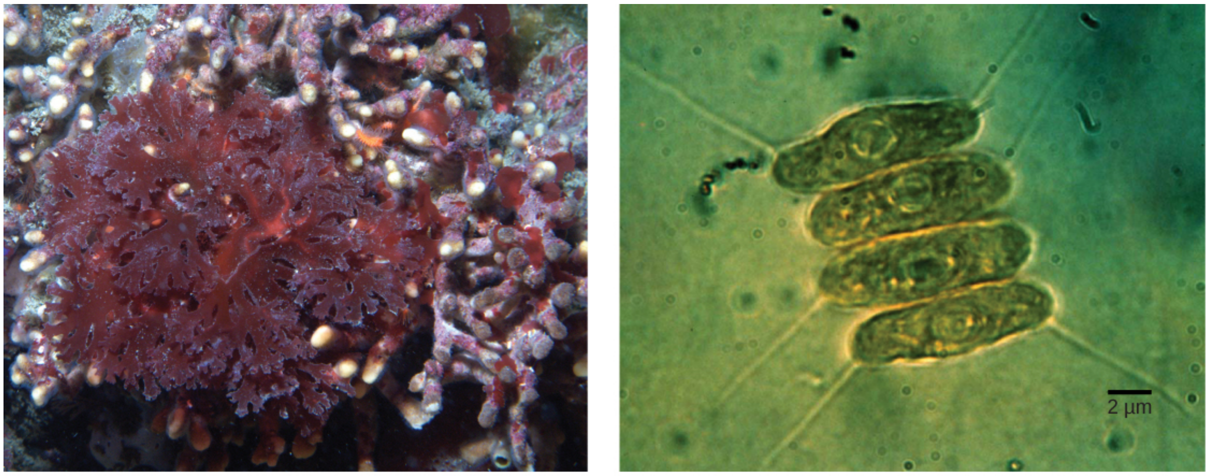
Figure 3. *The Endosymbiotic Theory. The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.*

Cyanobacteria are a group of Gram-negative bacteria with all the conventional structures of the group. However, unlike most prokaryotes, they have extensive, internal membrane-bound sacs called thylakoids. Chlorophyll is a component of these membranes, as are many of the proteins of the light reactions of photosynthesis.

Chloroplasts of primary endosymbiotic origin have thylakoids, a circular DNA chromosome, and ribosomes similar to those of cyanobacteria. As in mitochondria, each chloroplast is surrounded by two membranes. The outer membrane is thought to be derived from the enclosing vacuole of the host, and the inner membrane is thought to be derived from the plasma membrane of the cyanobacterial endosymbiont.

There is also, as with the case of mitochondria, strong evidence that many of the genes of the endosymbiont were transferred to the nucleus. Plastids, like mitochondria, cannot live independently outside the host. In addition, like mitochondria, plastids are derived from the division of other plastids and are never built from scratch. Researchers have suggested that the endosymbiotic event that led to the Archaeplastida occurred 1 to 1.5 billion years ago, at least five hundred million years after the fossil record suggests that eukaryotes were present.

Not all plastids in eukaryotes are derived directly from primary endosymbiosis. Some of the major groups of algae became photosynthetic by secondary endosymbiosis, that is, by taking in either green algae or red algae (both from the group Archaeplastida) as endosymbionts (**Figure 4**). Numerous microscopic and genetic studies have supported this conclusion. Secondary plastids are surrounded by three or more membranes, and some secondary plastids even have clear remnants of the nucleus (nucleomorphs) of endosymbiotic algae. There are even cases where tertiary or higher-order endosymbiotic events are the best explanations for the features of some eukaryotic plastids.



(a) (b)

Figure 4. *Algae. (a) Red algae and (b) green algae (seen here by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts.*

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II

How Organisms Get Energy

This module contains the following chapters:

Adapted from:

Biology 2e. **Authors**: Mary Ann Clark, Matthew Douglas and Jung Choi. **Provided by**: OpenStax CNX.

Energy and Metabolism

Section Goals

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

- Explain metabolic pathways and describe the two major types
- Discuss how chemical reactions play a role in energy transfer
- Describe how cells store and transfer free energy using ATP

Virtually every task performed by living organisms requires energy. Organisms require energy to perform heavy labor and exercise, but humans also use considerable energy while thinking and even during sleep. Every organism's living cells constantly use energy. Organisms import nutrients and other molecules. They metabolize (break down) and may be synthesized into new molecules. If necessary, molecules modify, move around the cell, and may distribute themselves to the entire organism. For example, the large proteins that make up muscles are actively built from smaller molecules. Complex carbohydrates break down into simple sugars that the cell uses for energy. Just as energy is required to both build and demolish a building, energy is required to synthesize and break down molecules. Additionally, signaling molecules such as hormones and neurotransmitters transport between cells. Cells ingest and break down bacteria and viruses. Cells must also export waste and toxins to stay healthy, and many cells must swim or move surrounding materials via the beating motion of cellular appendages like cilia and flagella.

The cellular processes that we listed above require a steady supply of energy. From where and in what form, does this energy come? How do living cells obtain energy, and how do they use it? Fortunately for us, our cells—and those of other living organisms—are excellent at harvesting energy from glucose and other organic molecules, such as fats and amino acids. Here, we'll go through an overview of how cells use energy and replenish it.

Scientists use the term **bioenergetics** to discuss the concept of energy flow (**Figure 1**) through living systems, such as cells. Cellular processes such as building and breaking down complex molecules occur through stepwise chemical reactions. Some of these chemical reactions are spontaneous and release energy, whereas others require energy to proceed. Just as living things must continually consume food to replenish what they have used, cells must continually obtain more energy to replenish that which the many energy-requiring chemical reactions that constantly take place use. All of the chemical reactions that transpire inside cells, including those that use and release energy, are the cell's **metabolism**.

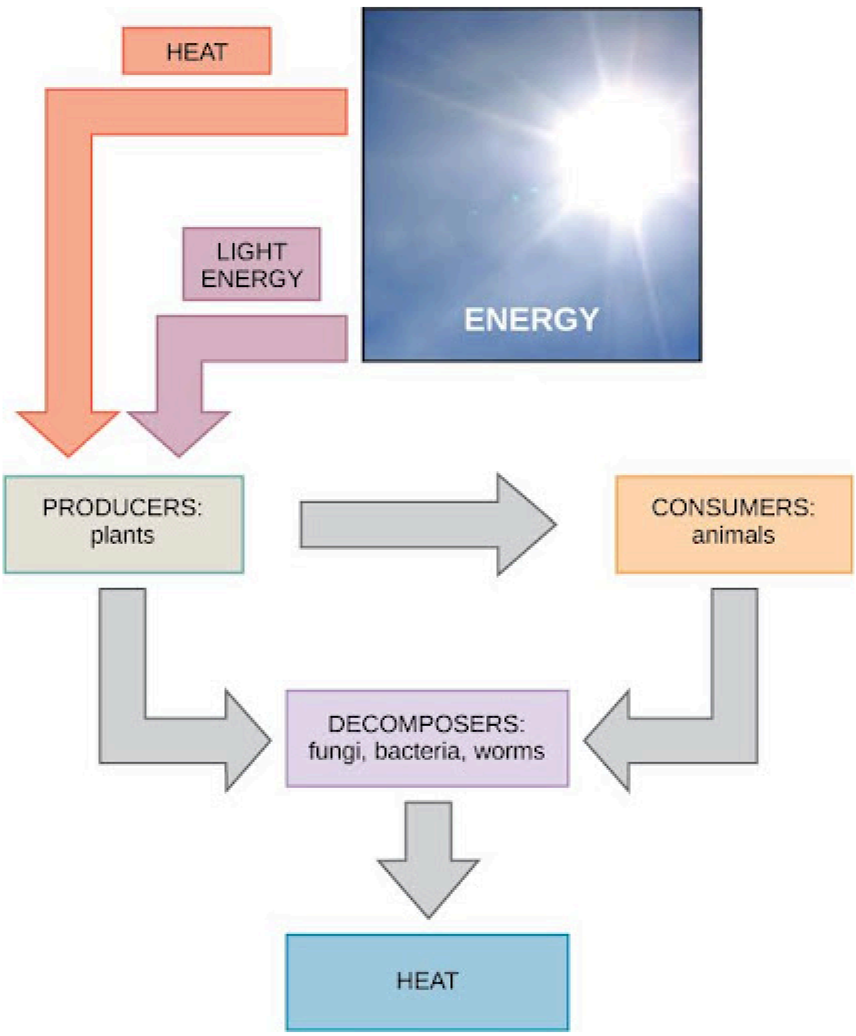

Figure 1. *Most life forms on Earth obtain their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat those plants to obtain energy. Carnivores eat the herbivores, and decomposers digest plant and animal matter.*

Carbohydrate Metabolism

Sugar (a simple carbohydrate) metabolism (chemical reactions) is a classic example of the many cellular processes that use and produce energy. Living things consume sugar as a major energy source because sugar molecules have considerable energy stored within their bonds. The following equation describes the breakdown of glucose, a simple sugar:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O + \text{energy}$$

Consumed carbohydrates have their origins in photosynthesizing organisms like plants (**Figure 2**). During photosynthesis, plants use the energy of sunlight to convert carbon dioxide gas (CO_2) into sugar molecules, like glucose ($C_6H_{12}O_6$). Because this process involves synthesizing a larger, energy-storing molecule, it requires an energy input to proceed. The following equation (notice that it is the reverse of the previous equation) describes the synthesis of glucose:

$$6CO_2 + 6H_2O + \text{energy} \rightarrow C_6H_{12}O_6 + 6O_2.$$

During the chemical reactions in the process of photosynthesis, energy is in the form of a very high-energy molecule scientists call ATP, or adenosine triphosphate. ATP is the primary energy currency of all cells. Just as the dollar is the currency we use to buy goods, cells use ATP molecules as energy currency to perform immediate work. The sugar (glucose) is stored as starch or glycogen. Energy-storing polymers like these break down into glucose to supply ATP molecules.

Figure 2. *Plants, like this oak tree and acorn, use energy from sunlight to make sugar and other organic molecules. Both plants and animals (like this squirrel) use cellular respiration to derive energy from the organic molecules that plants originally produced.*

Solar energy is required to synthesize a glucose molecule during the photosynthesis reactions. In photosynthesis, light energy from the sun initially transforms into chemical energy that temporarily stores itself in the energy carrier molecules ATP and NADPH (nicotinamide adenine dinucleotide phosphate). Photosynthesis later uses the stored energy in ATP and NADPH to build one glucose molecule from six molecules of CO_2. This process is analogous to eating breakfast in the morning to acquire energy for your body that you can use later in the day. Under ideal conditions, energy from 18 molecules of ATP is required to synthesize one glucose molecule during photosynthesis reactions. Glucose molecules can also combine with and convert into other sugar types. When an organism consumes sugars, glucose molecules eventually make their way into each organism's living cell. Inside the cell, each sugar molecule breaks down through a complex series of chemical reactions. The goal of these reactions is to harvest the energy stored inside the sugar molecules. The harvested energy makes high-energy ATP molecules, which perform work, powering many chemical reactions in the cell. The amount of energy needed to make one glucose molecule from six carbon dioxide molecules is 18 ATP molecules and 12 NADPH molecules (each one of which is energetically equivalent to three ATP molecules), or a total of 54 molecule equivalents required for synthesizing one glucose molecule. This process is a fundamental and efficient way for cells to generate the molecular energy that they require.

Metabolic Pathways

The processes of making and breaking down sugar molecules illustrate two types of metabolic pathways. A metabolic pathway is a series of interconnected biochemical reactions that convert a substrate molecule or molecules, step-by-step, through a series of metabolic intermediates, eventually yielding a final product or products.

In the case of sugar metabolism, the first metabolic pathway synthesizes sugar from smaller molecules, and the other pathway breaks sugar down into smaller molecules. Scientists call these two opposite processes—the first requiring energy and the second producing energy—**anabolic** (building) and **catabolic** (breaking down) pathways, respectively (**Figure 3**).

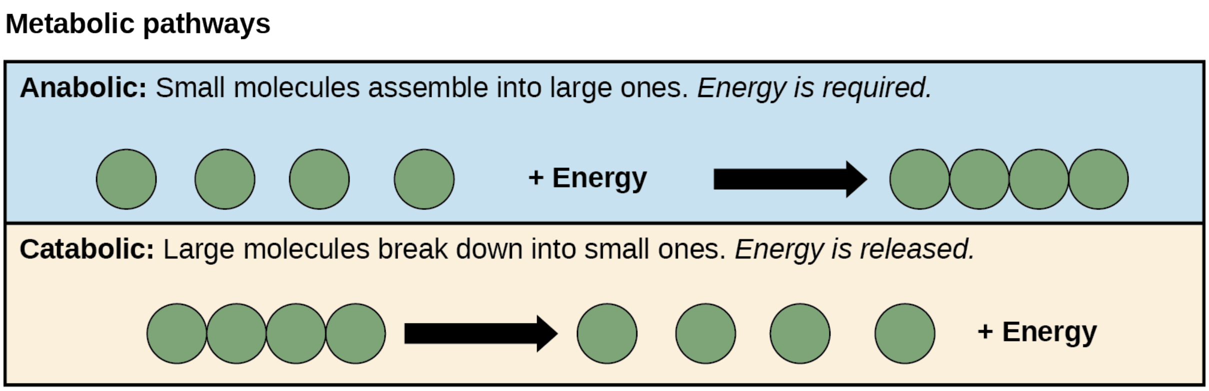

Figure 3. *There are two different kinds of metabolic pathways. Anabolic pathways are those that require energy to synthesize larger molecules. Catabolic pathways are those that generate energy by breaking down larger molecules. Both types of pathways are required for maintaining the cell's energy balance.*

The reactions that allow energy to be extracted from molecules such as glucose, fats, and amino acids are catabolic because they involve breaking a larger molecule into smaller pieces. For example, when glucose is broken down in the presence of oxygen, it's converted into six carbon dioxide molecules and six water molecules:

$$C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$$

The above reaction, as written, is simply a combustion reaction, similar to what takes place when you burn a piece of wood in a fireplace or gasoline in an engine. Does this mean that glucose is continually combusting inside your cells? Thankfully, not quite! The combustion reaction describes the overall process that takes place, but inside the cell, this process is broken down into many smaller steps. The energy contained in the bonds of glucose is released in small bursts, and some of it can be captured in the form of adenosine triphosphate (ATP), a small molecule that is used to power reactions in the cell. Much of the energy from glucose is still lost as heat, but enough is captured to keep the metabolism of the cell running.

As a glucose molecule is gradually broken down, some of the breakdown steps release energy that is captured directly as ATP. In these steps, a phosphate group is transferred from a pathway intermediate straight to ADP, a process known as **substrate-level phosphorylation**. Many more steps, however, indirectly produce ATP. In these steps, electrons from glucose are transferred to small molecules known as electron carriers. The electron carriers take the electrons to a group of proteins in the inner membrane of the mitochondrion, called the electron transport chain. As electrons move through the electron transport chain, they go from a higher to a lower energy level and are ultimately passed to oxygen (forming water). The energy released in the electron transport chain is captured as a proton gradient, which powers the production of ATP by a membrane protein called ATP synthase. This process is known as **oxidative phosphorylation**. A simplified diagram of oxidative and substrate-level phosphorylation is shown below.

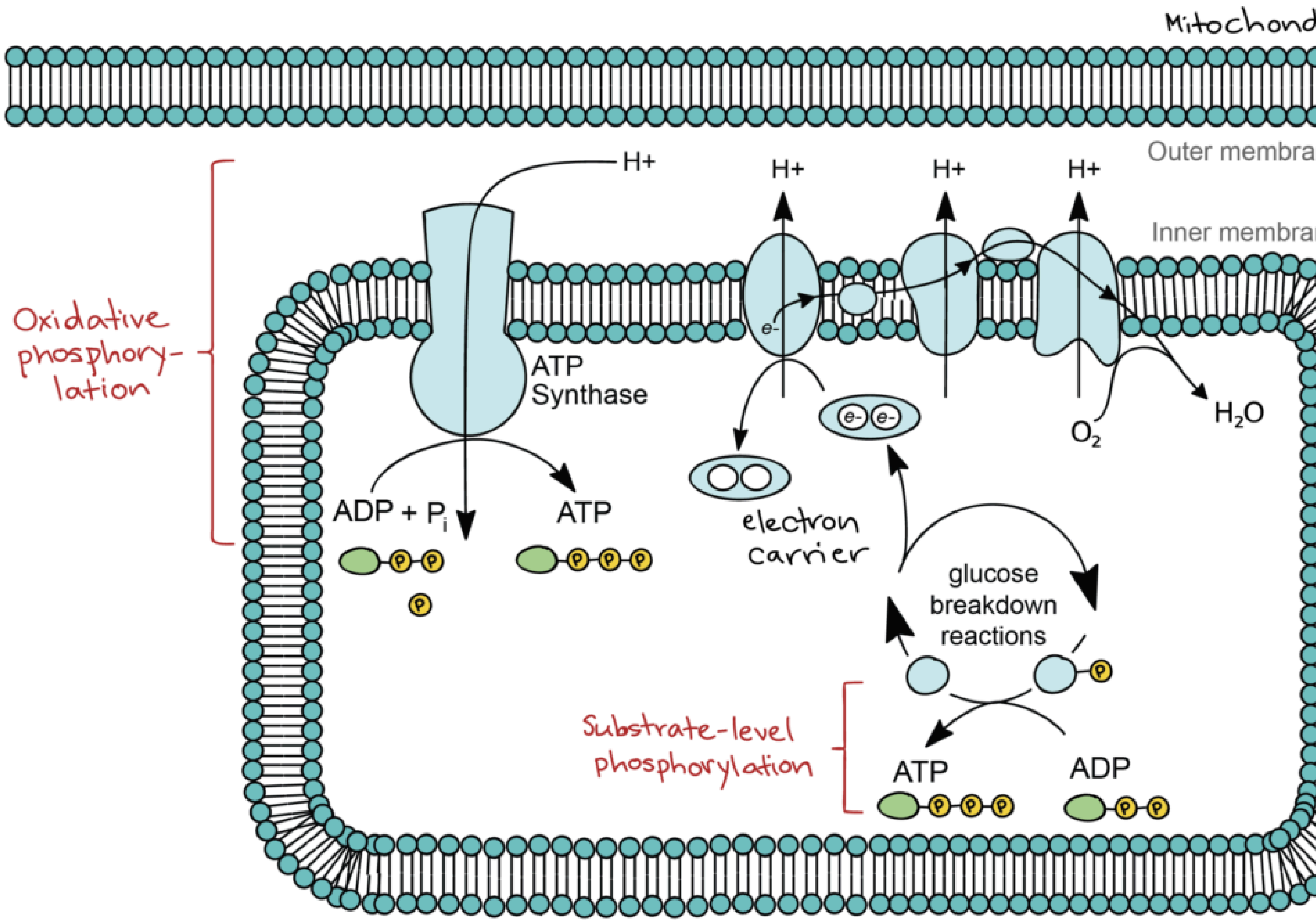

Figure 4. *Image modified from "Etc4" by Fvasconcellos (public domain).*

When organic fuels like glucose are broken down using an electron transport chain that ends with oxygen, the breakdown process is known as **aerobic respiration** (aerobic = oxygen-requiring). Most eukaryotic cells, as well as many bacteria and other prokaryotes, can carry out aerobic respiration. Some prokaryotes have pathways similar to aerobic respiration but with a different inorganic molecule, such as sulfur, substituted for oxygen. These pathways are not oxygen-dependent, so the breakdown process is called **anaerobic respiration** (anaerobic = non-oxygen-requiring). Officially, both processes are examples of **cellular respiration**, the breakdown of organic fuels using an electron transport chain. However, cellular respiration is commonly used as a synonym for aerobic respiration.

ATP in Living Systems

A living cell cannot store significant amounts of free energy. Excess free energy would result in an increase of heat in the cell, which would result in excessive thermal motion that could damage and then destroy the cell. Rather, a cell must be able to handle that energy in a way that enables the cell to store energy safely and release it for use only as needed. Living cells accomplish this by using the compound adenosine triphosphate (ATP). ATP is often called the "energy currency" of the cell, and, like currency, this versatile compound can be used to fill any energy need of the cell. How? It functions similarly to a rechargeable battery.

When ATP is broken down, usually by the removal of its terminal phosphate group, energy is released. The energy is used to do work by the cell, usually by the released phosphate binding to another molecule, activating it. For example, in the mechanical work of muscle contraction, ATP supplies the energy to move the contractile muscle proteins. Recall the active transport work of the sodium-potassium pump in cell membranes. ATP alters the structure of the integral protein that functions as the pump, changing its affinity for sodium and potassium. In this way, the cell performs work, pumping ions against their electrochemical gradients.

ATP Structure and Function

At the heart of ATP is a molecule of adenosine monophosphate (AMP), which is composed of an adenine molecule bonded to a ribose molecule and a single phosphate group (**Figure 5**).

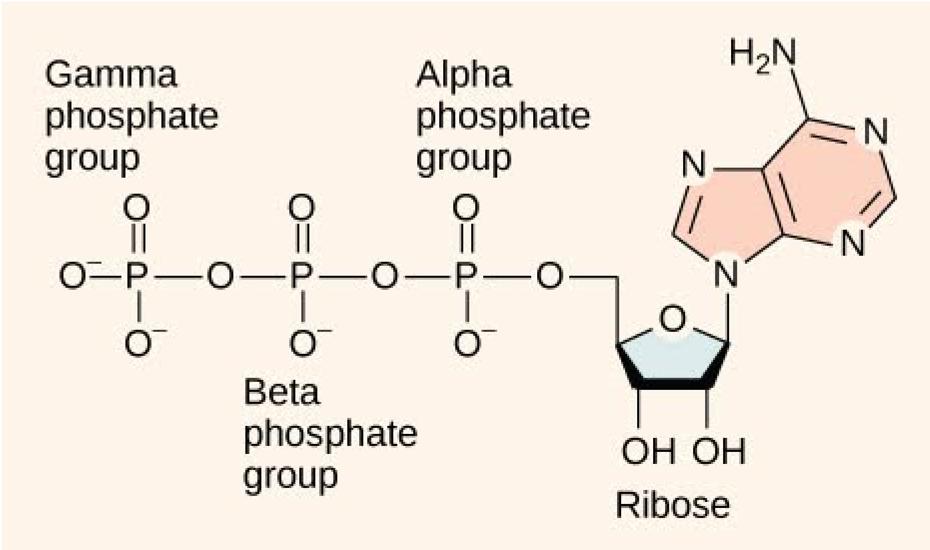

Figure 5. *ATP (adenosine triphosphate) has three phosphate groups that can be removed by hydrolysis to form ADP (adenosine diphosphate) or AMP (adenosine monophosphate).The negative charges on the phosphate group naturally repel each other, requiring energy to bond them together and releasing energy when these bonds are broken.*

Ribose is a five-carbon sugar found in RNA, and AMP is one of the nucleotides in RNA. The addition of a second phosphate group to this core molecule results in the formation of adenosine diphosphate (ADP); the addition of a third phosphate group forms adenosine triphosphate (ATP). The addition of a phosphate group to a molecule requires energy. Phosphate groups are negatively charged and thus repel one another when they are arranged in series, as they are in ADP and ATP. This repulsion makes the ADP and ATP molecules inherently unstable. The release of one or two phosphate groups from ATP, a process called dephosphorylation, releases energy.

Energy from ATP

Hydrolysis is the process of breaking complex macromolecules apart. During hydrolysis, water is split or lysed, and the resulting hydrogen atom (H+) and a hydroxyl group (OH–) are added to the larger molecule. The hydrolysis of ATP produces ADP, together with an inorganic phosphate ion (P*i*), and the release of free energy. To carry out life processes, ATP is continuously broken down into ADP, and like a rechargeable battery, ADP is continuously regenerated into ATP by the reattachment of a third phosphate group. Water, which was broken down into its hydrogen atom and hydroxyl group during ATP hydrolysis, is regenerated when a third phosphate is added to the ADP molecule, reforming ATP.

Obviously, energy must be infused into the system to regenerate ATP. Where does this energy come from? In nearly every living thing on earth, the energy comes from the metabolism of glucose. In this way, ATP is a direct link between the limited set of exergonic pathways of glucose catabolism and the multitude of endergonic pathways that power living cells.

Phosphorylation

Recall that, in some chemical reactions, enzymes may bind to several substrates that react with each other on the enzyme, forming an intermediate complex. An intermediate complex is a temporary structure, and it allows one of the substrates (such as ATP) and reactants to react with each other more readily; in reactions involving ATP, ATP is one of the substrates, and ADP is a product. During an endergonic chemical reaction, ATP forms an intermediate complex with the substrate and enzyme in the reaction. This intermediate complex allows the ATP to transfer its third phosphate group, with its energy, to the substrate, a process called phosphorylation. **Phosphorylation** refers to the addition of the phosphate (~P). This process is illustrated by the following generic reaction:

A + enzyme + ATP → [A − enzyme − ~P] → B + enzyme + ADP + phosphate ion

When the intermediate complex breaks apart, the energy is used to modify the substrate and convert it into a reaction product. The ADP molecule and a free phosphate ion are released into the medium and are available for recycling through cell metabolism.

Substrate Phosphorylation

ATP is generated through two mechanisms during the breakdown of glucose. A few ATP molecules are generated (that is, regenerated from ADP) as a direct result of the chemical reactions that occur in the catabolic pathways. A phosphate group is removed from an intermediate reactant in the pathway, and the free energy of the reaction is used to add the third phosphate to an available ADP molecule, producing ATP (**Figure 6**). This very direct method of phosphorylation is called **substrate-level phosphorylation**.

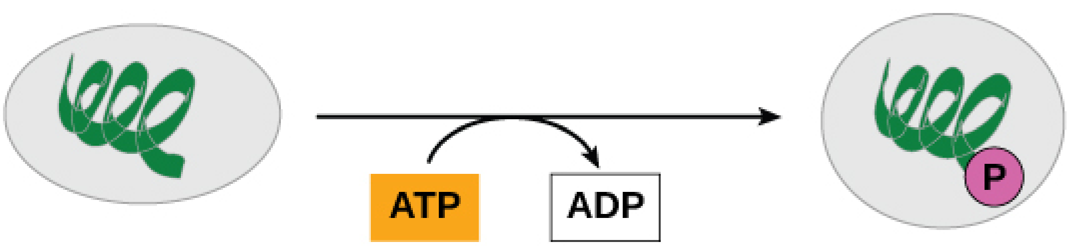

Figure 6. *In phosphorylation reactions, the gamma phosphate of ATP is attached to a protein.*

Oxidative Phosphorylation

Most of the ATP generated during glucose catabolism, however, is derived from a much more complex process, chemiosmosis, which takes place in mitochondria (**Figure 7**) within a eukaryotic cell or the plasma membrane of a prokaryotic cell.

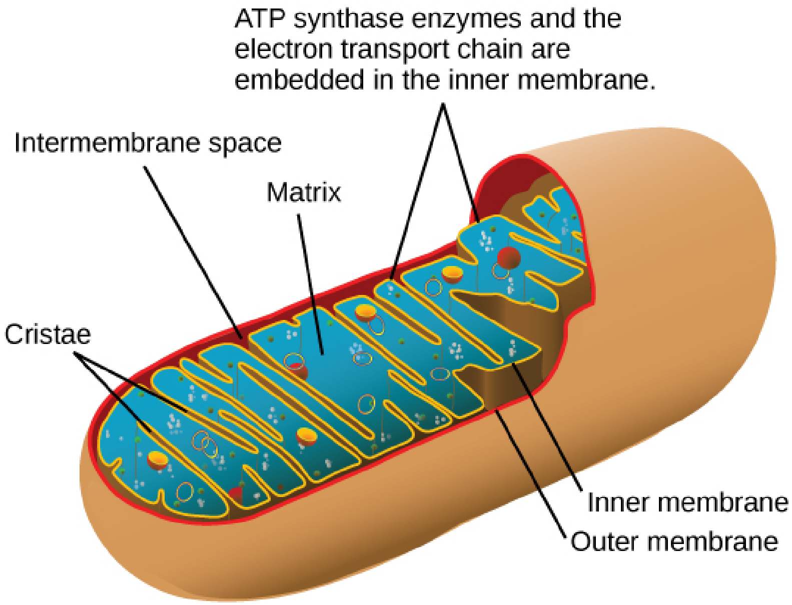

Figure 7. *The mitochondria*

Chemiosmosis, a process of ATP production in cellular metabolism, generates 90 percent of the ATP made during glucose catabolism. It is also the method used in the light reactions of photosynthesis to harness the energy of sunlight. The production of ATP using the process of chemiosmosis is called **oxidative phosphorylation** because oxygen is involved in the process.

Did I Get It?

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Mitochondrial Disease Physician
What happens when the critical reactions of cellular respiration do not proceed correctly? Mitochondrial diseases are genetic disorders of metabolism. Mitochondrial disorders can arise from mutations in nuclear or mitochondrial DNA, and they result in the production of less energy than is normal in body cells. In type 2 diabetes, for instance, the oxidation efficiency of NADH is reduced, impacting oxidative phosphorylation but not the other steps of respiration. Symptoms of mitochondrial diseases can include muscle weakness, lack of coordination, stroke-like episodes, and loss of vision and hearing. Most affected people are diagnosed in childhood, although there are some adult-onset diseases. Identifying and treating mitochondrial disorders is a specialized medical field. The educational preparation for this profession requires a college education, followed by medical school with a specialization in medical genetics. Medical geneticists can be board-certified by the American Board of Medical Genetics and go on to become associated with professional organizations devoted to the study of mitochondrial diseases, such as the Mitochondrial Medicine Society and the Society for Inherited Metabolic Disease.
Summary: Energy, Metabolism and ATP

Cells perform the functions of life through various chemical reactions. A cell's metabolism refers to the chemical reactions that take place within it. There are metabolic reactions that involve breaking down complex chemicals into simpler ones, such as breaking down large macromolecules. Scientists refer to this process as catabolism, and we associate such reactions with an energy release. On the other end of the spectrum, anabolism refers to metabolic processes that build complex molecules out of simpler ones, such as macromolecule synthesis. Anabolic processes require energy. Glucose synthesis and glucose breakdown are examples of anabolic and catabolic pathways, respectively.

ATP functions as the energy currency for cells. It allows the cell to store energy briefly and transport it within the cell to support endergonic chemical reactions. The structure of ATP is that of an RNA nucleotide with three phosphates attached. As ATP is used for energy, a phosphate group or two is detached, and either ADP or AMP is produced. Energy derived from glucose catabolism is used to convert ADP into ATP. When ATP is used in a reaction, the third phosphate is temporarily attached to a substrate in a process called phosphorylation. The two processes of ATP regeneration that are used in conjunction with glucose catabolism are substrate-level phosphorylation and oxidative phosphorylation through the process of chemiosmosis.

A Photosynthesis Primer

Section Goals

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

- Explain the significance of photosynthesis to other living organisms
- Describe the main structures involved in photosynthesis
- Identify the substrates and products of photosynthesis
- Explain how chloroplasts evolved via endosymbiosis

Photosynthesis is essential to all life on earth; both plants and animals depend on it. It is the only biological process that can capture the energy that originates from sunlight and convert it into chemical compounds (carbohydrates) that every organism uses to power its metabolism. It is also a source of oxygen necessary for many living organisms. In brief, the energy of sunlight is "captured" to energize electrons, whose energy is then stored in the covalent bonds of sugar molecules. How long-lasting and stable are those covalent bonds? The energy extracted today by the burning of coal and petroleum products represents the energy of sunlight captured and stored by photosynthesis 350 to 200 million years ago during the Carboniferous Period.

Plants, algae, and a group of bacteria called cyanobacteria are the only organisms capable of performing photosynthesis (**Figure 1**). Because they use light to manufacture their food, they are called **photoautotrophs** (literally, “self-feeders using light”). Other organisms, such as animals, fungi, and most other bacteria, are termed **heterotrophs** (“other feeders”)because they must rely on the sugars produced by photosynthetic organisms for their energy needs. A third very interesting group of bacteria synthesize sugars, not by using sunlight’s energy but by extracting energy from inorganic chemical compounds. For this reason, they are referred to as **chemoautotrophs**.

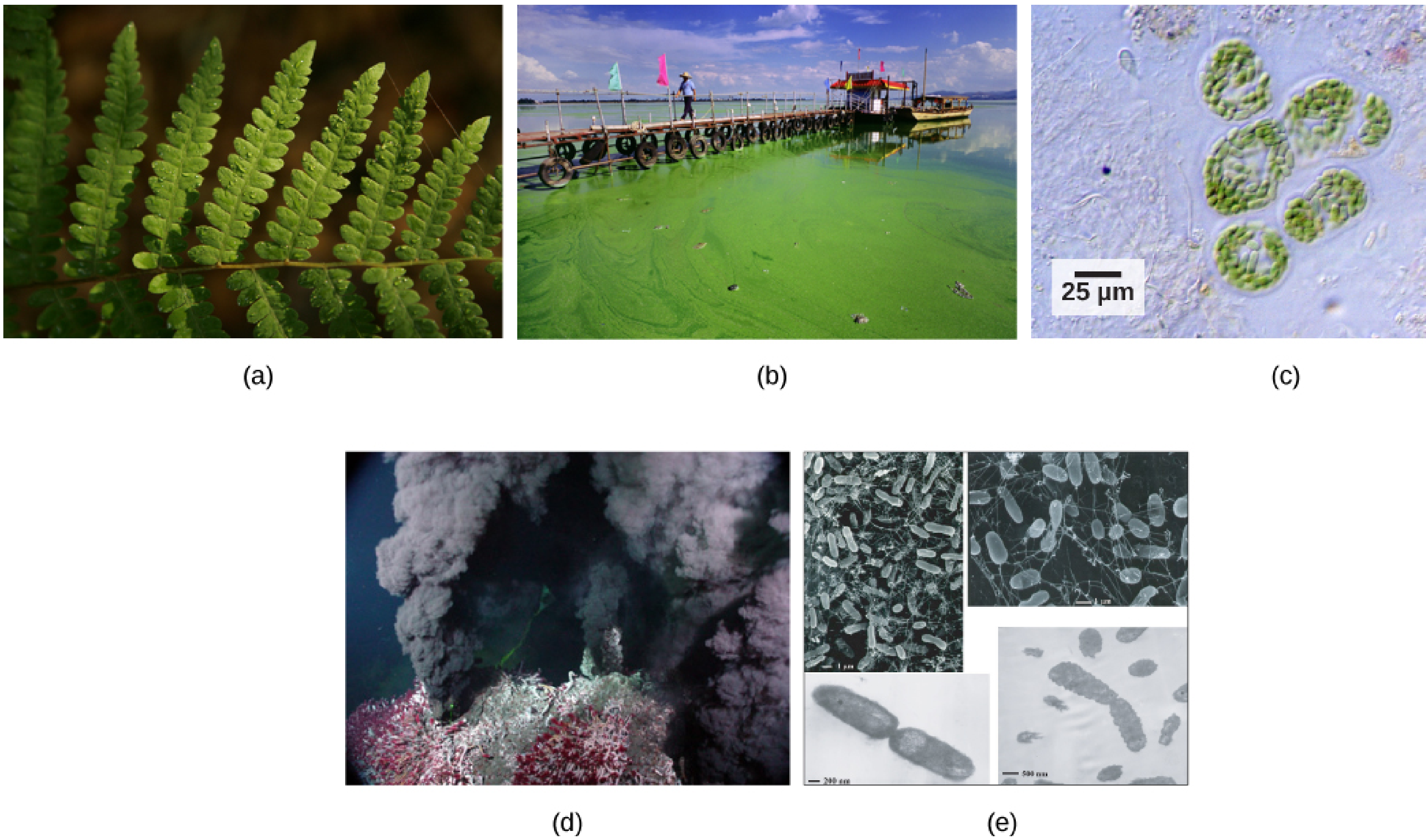

Figure 1. *Photoautotrophs, including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compoun photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous ar water, at times completely covering the surface. In a deep sea vent (d), chemoautotrophs, such as these (e) thermoph bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the has a diverse array of animals, such as tubeworms, crustaceans, and octopuses that derive energy from the bacteria*

The importance of photosynthesis is not just that it can capture sunlight’s energy. After all, a lizard sunning itself on a cold day can use the sun’s energy to warm up in a process called *behavioral thermoregulation*. In contrast, photosynthesis is vital because it evolved as a way to *store the energy from solar radiation (the “photo-” part) to energy in the carbon-carbon bonds of carbohydrate molecules (the “-synthesis” part).* Those carbohydrates are the energy source that heterotrophs use to power the synthesis of ATP via respiration. Therefore, photosynthesis powers 99 percent of Earth’s ecosystems. When a top predator, such as a wolf, preys on a deer (**Figure 2**), the wolf is at the end of an energy path that went from nuclear reactions on the surface of the sun, to visible light, to photosynthesis, to vegetation, to deer, and finally to the wolf.

Figure 2. *The energy stored in carbohydrate molecules from photosynthesis passes through the food chain. The predator that eats these deer receives a portion of the energy that originated in the photosynthetic vegetation that the deer consumed.*

Main Structures and Summary of Photosynthesis

Photosynthesis is a multi-step process that requires specific wavelengths of visible sunlight, carbon dioxide (which is low in energy), and water as substrates (**Figure 3**). After the process is complete, it releases oxygen and produces glyceraldehyde-3-phosphate (G3P), as well as simple carbohydrate molecules (high in energy) that can then be converted into glucose, sucrose, or any of dozens of other sugar molecules. These sugar molecules contain energy and the energized carbon that all living things need to survive.

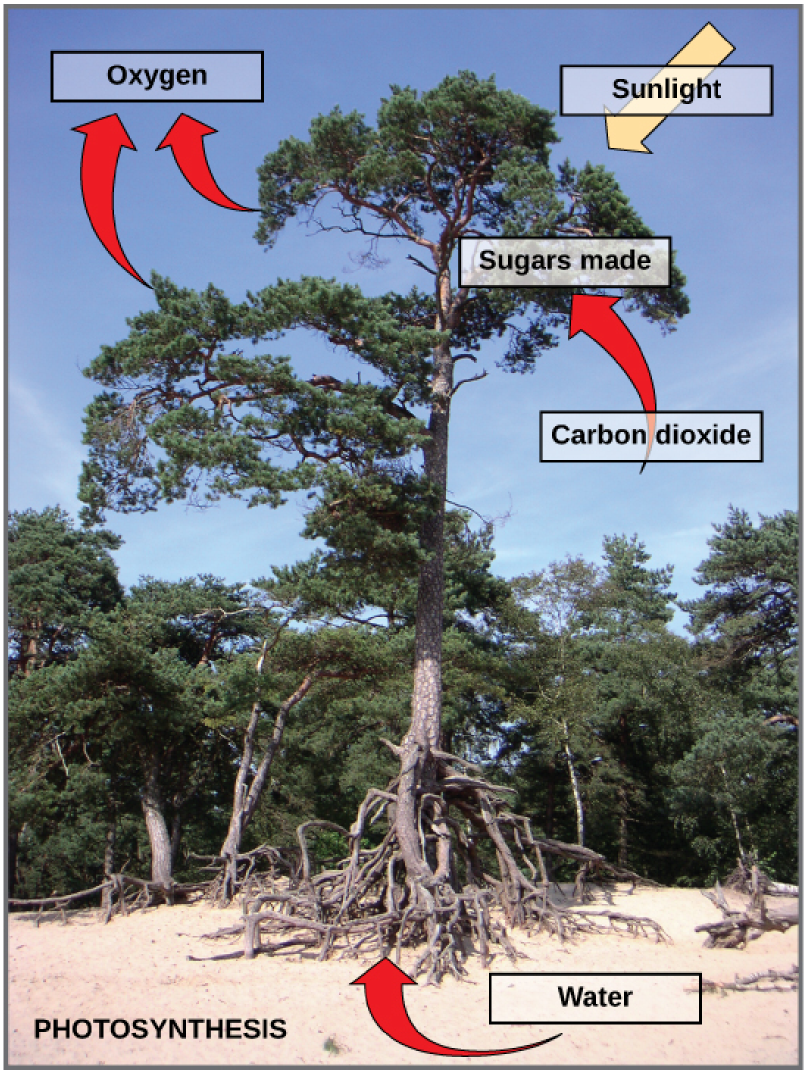

Figure 3. *Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.*

The following is the chemical equation for photosynthesis (**Figure 4**):

Photosynthesis Equation							
Carbon dioxide	+	Water	SUNLIGHT →	Sugar	+	Oxygen	
$6CO_2$		$6H_2O$		$C_6H_{12}O_6$		$6O_2$	

Figure 4. *The basic equation for photosynthesis is deceptively simple. In reality, the process takes place in many steps involving intermediate reactants and products. Glucose, the primary energy source in cells, is made from two three-carbon G3Ps.*

Although the equation looks simple, the many steps that take place during photosynthesis are actually quite complex. Before learning the details of how photoautotrophs turn sunlight into food, it is important to become familiar with the structures involved.

Basic Photosynthetic Structures

In plants, photosynthesis generally takes place in leaves, which consist of several layers of cells. The process of photosynthesis occurs in a middle layer called the **mesophyll**. The gas exchange of carbon dioxide and oxygen occurs through small, regulated openings called **stomata** (singular: stoma), which also play roles in the regulation of gas exchange and water balance. The stomata are typically located on the underside of the leaf, which helps to minimize water loss due to high temperatures on the upper surface of the leaf. Each stoma is flanked by guard cells that regulate the opening and closing of the stomata by swelling or shrinking in response to osmotic changes.

In all autotrophic eukaryotes, photosynthesis takes place inside an organelle called a **chloroplast** (**Figure 5**). For plants, chloroplast-containing cells exist mostly in the mesophyll. Chloroplasts have a double membrane envelope (composed of an outer membrane and an inner membrane), and are ancestrally derived from ancient free-living cyanobacteria. Within the chloroplast are stacked, disc-shaped structures called **thylakoids**. Embedded in the thylakoid membrane is chlorophyll, a **pigment** (molecule that absorbs light) responsible for the initial interaction between light and plant material, and numerous proteins that make up the electron transport chain. The thylakoid membrane encloses an internal space called the **thylakoid lumen**. A stack of thylakoids is called a **granum**, and the liquid-filled space surrounding the granum is called **stroma** or "bed" (not to be confused with stoma or "mouth," an opening on the leaf epidermis).

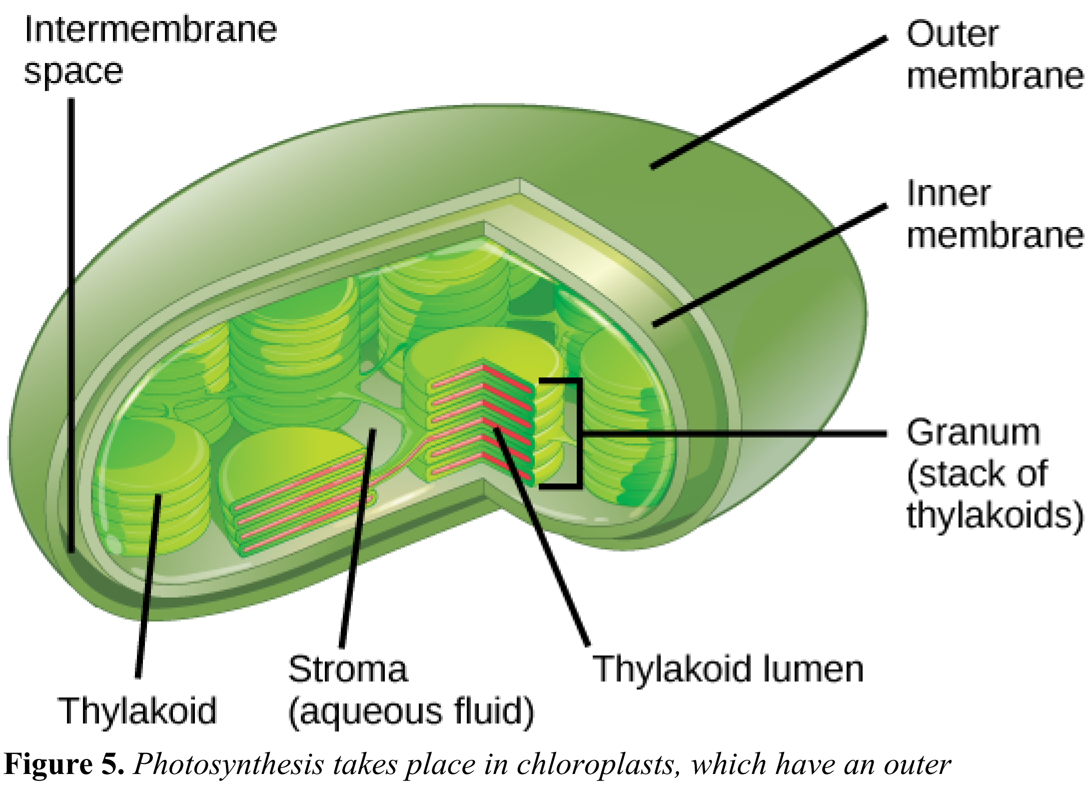

Figure 5. *Photosynthesis takes place in chloroplasts, which have an outer*

membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

Did I Get It?

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The Two Parts of Photosynthesis

Photosynthesis takes place in two sequential stages: the light-dependent reactions and the light-independent reactions. In the **light-dependent reactions**, energy from sunlight is absorbed by chlorophyll and that energy is converted into stored chemical energy. In the **light-independent reactions**, the chemical energy harvested during the light-dependent reactions drives the assembly of sugar molecules from carbon dioxide. Therefore, although the light-independent reactions do not use light as a reactant, they require the products of the light-dependent reactions to function. In addition, however, several enzymes of the light-independent reactions are activated by light. The light-dependent reactions utilize certain molecules to temporarily store the energy: These are referred to as *energy carriers*. The energy carriers that move energy from light-dependent reactions to light-independent reactions can be thought of as "full" because they are rich in energy. After the energy is released, the "empty" energy carriers return to the light-dependent reaction to obtain more energy. **Figure 6** illustrates the components inside the chloroplast where the light-dependent and light-independent reactions take place.

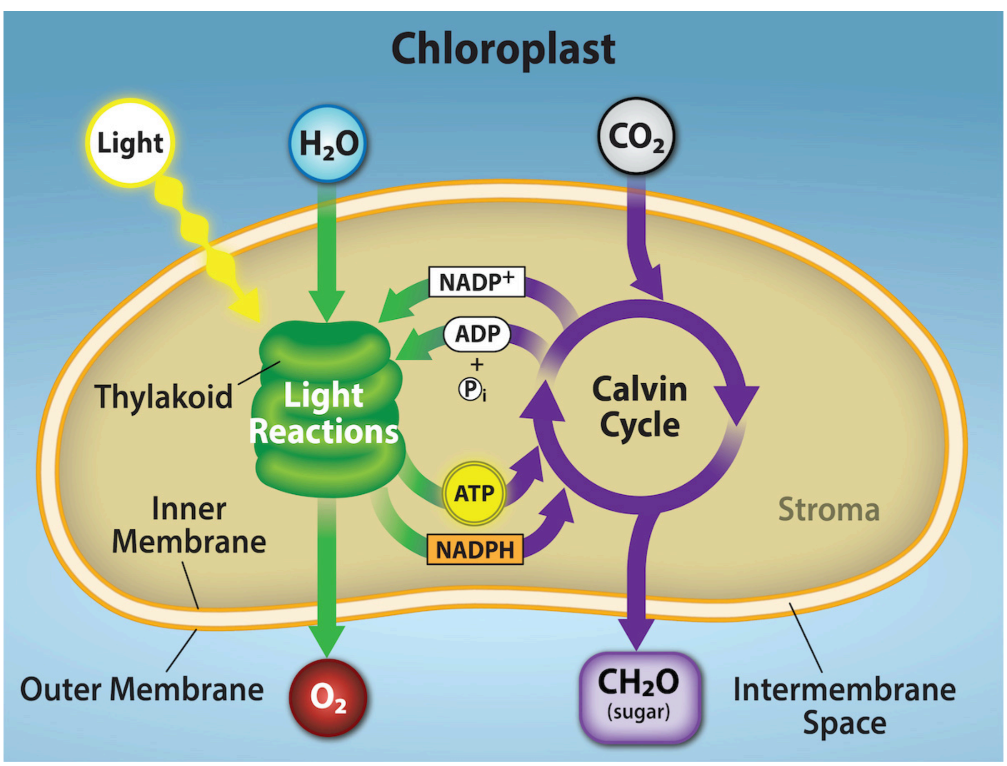

Figure 6. *Photosynthesis takes place in two stages: light-dependent reactions and the Calvin cycle. Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make G3P from CO2.*

Did I Get It?

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The Evolution of Photosynthesis

Ancient cyanobacteria produced oxygen as a byproduct of photosynthesis, changing the composition of the atmosphere over time in the Great Oxygenation Event. Recall that these cyanobacteria also led to the evolution of chloroplasts when they started living inside other cells through a process called endosymbiosis. The cyanobacteria provided the larger cell with sugars from photosynthesis, and the larger cell gave protection and nutrients.

Watch the animation below that highlights how the ancestors of cyanobacteria, and the evolution of photosynthesis changed the world– creating the conditions on the planet that could support complex life.

One or more interactive elements has been excluded from this version of the text. You can view them online here: https://rotel.pressbooks.pub/understanding-organisms/?p=192#oembed-1

The evolution of photosynthesis was crucially important to the biosphere for the following reasons:

1. Photosynthesis generates oxygen, which is important for two reasons. Photosynthetic organisms created the molecular oxygen in Earth's atmosphere; without photosynthesis there would be no oxygen to support aerobic cellular respiration needed by complex, multicellular life. Photosynthetic bacteria were likely the first organisms to perform photosynthesis billions of years ago. Thanks to their activity, and a diversity of present-day photosynthesizing organisms, Earth's atmosphere is currently about 21% oxygen. Also, this oxygen is vital for the creation of the ozone layer, which protects life from harmful ultraviolet radiation emitted by the sun. Ozone (O3) is created from the breakdown and reassembly of O2.
2. Photosynthesis provides energy for nearly all ecosystems. By transforming light energy into chemical energy, photosynthesis provides the energy used by organisms, whether those organisms are plants, grasshoppers, wolves, or fungi. The only exceptions are found in very rare and isolated ecosystems, such as near deep-sea hydrothermal vents where organisms harness energy that originally came from minerals and other chemicals rather than the sun.
3. Photosynthesis provides the carbon needed for organic molecules. Organisms are primarily made of two things: water and organic, carbon-based molecules. Through the process of

carbon fixation, photosynthesis takes carbon from CO2 and converts it into sugars. Carbon in these sugars can be repurposed to create the other types of organic molecules that organisms need, such as lipids, proteins, and nucleic acids. For example, the carbon used to make your DNA was once CO2 absorbed by photosynthetic organisms.

Summary: An Overview Of Photosynthesis

The process of photosynthesis transformed life on Earth. By harnessing energy from the sun, photosynthesis evolved to allow living things access to enormous amounts of energy, and because of photosynthesis, living things gained access to sufficient energy that allowed them to build new structures and achieve the biodiversity evident today.

Only certain organisms, called photoautotrophs, can perform photosynthesis; they require the presence of chlorophyll, a specialized pigment that absorbs certain portions of the visible spectrum and can capture energy from sunlight. Photosynthesis uses carbon dioxide and water to assemble carbohydrate molecules and release oxygen as a waste product into the atmosphere. Eukaryotic autotrophs, such as plants and algae, have organelles called chloroplasts in which photosynthesis takes place and starch accumulates. In prokaryotes, such as cyanobacteria, the process is less localized and occurs within folded membranes, extensions of the plasma membrane, and in the cytoplasm.

Photosynthetic prokaryotes called cyanobacteria led to the evolution of chloroplasts when they started living inside other cells, in a process known as endosymbiosis.

Putting it Together: Metabolic Pathways

Whether the organism is a bacterium, plant, or animal, all living things access energy by breaking down carbohydrate molecules. But if plants make carbohydrate molecules, why would they need to break them down, especially when it has been shown that the gas organisms release as a “waste product” (CO_2) acts as a substrate for the formation of more food in photosynthesis? Remember, living things need energy to perform life functions. An organism can either make its own food or eat another organism—either way, the food still needs to be converted to a form cells can actually use. In that process of conversion, called cellular respiration, organisms release needed energy and produce “waste” in the form of CO_2 gas. These two metabolic processes that are crucial to life on earth– those that build sugars, and those that break them down– are deeply connected.

Breaking down glucose: Cellular respiration

As an example of an energy-releasing pathway, let’s see how one of your cells might break down a sugar molecule (say, from that candy you had for dessert).

Many cells, including most of the cells in your body, get energy from glucose ($C_6H_{12}O_6$) in a process called cellular respiration. During this process, a glucose molecule is broken down gradually, in many small steps. However, the process has an overall reaction of:

$$C_6H_{12}0_6 + 6O_2 \rightarrow 6CO_2 + 6H_20 + \text{energy}$$

Breaking down glucose releases energy, which is captured by the cell in the form of ATP (adenosine triphosphate). ATP gives cells a convenient way to briefly store energy.

Once it’s made, ATP can be used by other reactions in the cell as an energy source. Much as we humans use money because it’s easier than bartering each time we need something, so the cell uses ATP to have a standardized way to transfer energy. Because of this, ATP is sometimes described as the “energy currency” of the cell.

Building up glucose: Photosynthesis

As an example of an energy-requiring metabolic pathway, let’s flip that last example around and see how a sugar molecule is built.

Sugars like glucose are made by plants in a process called photosynthesis. In photosynthesis, plants use the energy of sunlight to convert carbon dioxide gas into sugar molecules. Photosynthesis takes place in many small steps, but its overall reaction is just the cellular respiration reaction flipped backwards:

$$6CO_2 + 6H_20 + \text{energy} \rightarrow C_6H_{12}O_6 + 6O_2$$

Like us, plants need energy to power their cellular processes, so some of the sugars are used by the plant itself. They can also provide a food source for animals that eat the plant, like the giraffe below (**Figure 1**). In both cases, the glucose will be broken down through cellular respiration, generating ATP to keep cells running.

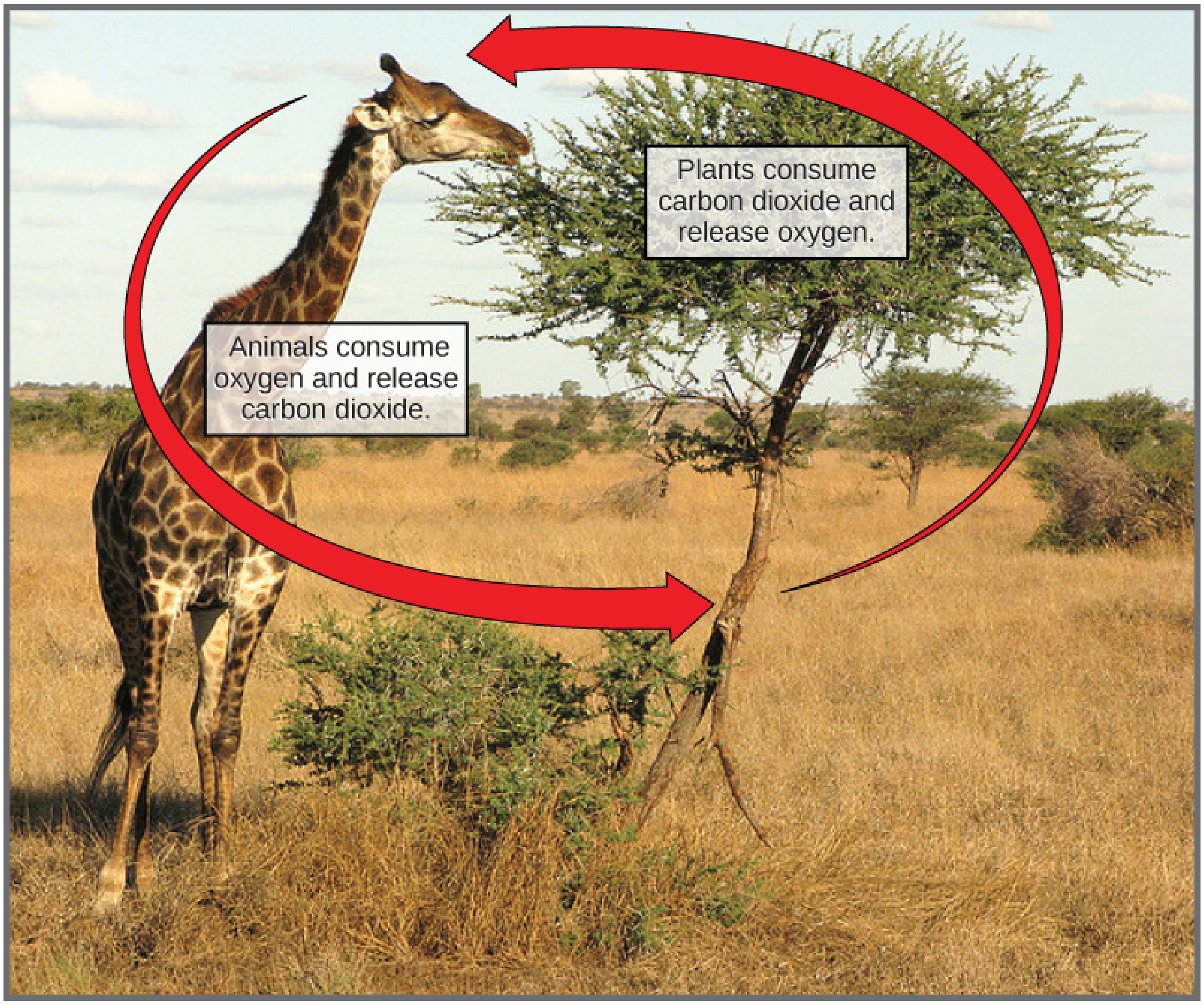

Figure 1. *Photosynthesis consumes carbon dioxide and produces oxygen. Aerobic respiration consumes oxygen and produces carbon dioxide. These two processes play an important role in the carbon cycle.*

In nature, there is no such thing as waste. Every single atom of matter and energy is conserved, recycling over and over infinitely. Substances change form or move from one type of molecule to another, but their constituent atoms never disappear (**Figure 1**).

While you may be tempted to call CO_2 a waste product, you should remember that oxygen is a “waste product” of photosynthesis: CO_2 and oxygen are byproducts of reactions that move on to other reactions. Photosynthesis absorbs light energy to build carbohydrates in chloroplasts, and aerobic cellular respiration releases energy by using oxygen to metabolize carbohydrates in the cytoplasm and mitochondria. Both processes use electron transport chains to capture the energy necessary to drive other reactions. These two powerhouse processes, photosynthesis and cellular respiration, function in biological, cyclical harmony to allow organisms to access life-sustaining energy that originates millions of miles away in a burning star humans call the sun.

III

Plant Form and Physiology

This module contains the following chapters:

- The Plant Body
- Transport of Water in Plants
- Transport of Food in Plants

The Plant Body

Section Goals

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

- Identify the different tissue types and organ systems in plants
- Describe the main function and basic structure of stems, roots, and leaves

Plants are as essential to human existence as land, water, and air. Without plants, our day-to-day lives would be impossible because, without oxygen from photosynthesis, aerobic life cannot be sustained. From providing food and shelter to serving as a source of medicines, oils, perfumes, and industrial products, plants provide humans with numerous valuable resources.

Watch Botany Without Borders, a video produced by the Botanical Society of America about the importance of plants.

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When you think of plants, most of the organisms that come to mind are vascular plants. These plants have tissues that conduct food and water, and most of them have seeds. Seed plants are divided into gymnosperms and angiosperms. Gymnosperms include the needle-leaved conifers—spruce, fir, and pine—as well as less familiar plants, such as ginkgos and cycads. Their seeds are not enclosed by a fleshy fruit. Angiosperms, also called flowering plants, constitute the majority of seed plants. They include broadleaved trees (such as maple, oak, and elm), vegetables (such as potatoes, lettuce, and carrots), grasses, and plants known for the beauty of their flowers (roses, irises, and daffodils, for example).

While individual plant species are unique, all share a common structure: a plant body consisting of stems, roots, and leaves. They all transport water, minerals, and sugars produced through photosynthesis through the plant body in a similar manner. All plant species also respond to environmental factors, such as light, gravity, competition, temperature, and predation.

Like animals, plants contain cells with organelles in which specific metabolic activities take place. Unlike animals, however, plants use energy from sunlight to form sugars during photosynthesis. In addition, plant cells have cell walls, plastids, and a large central vacuole: structures that are not found in animal cells. Each of these cellular structures plays a specific role in plant structure and function.

Plant Tissues

Plants are multicellular eukaryotes with tissue systems made of various cell types that carry out specific functions. Plant tissue systems fall into one of two general types: meristematic tissue and permanent (or non-meristematic) tissue. Cells of the meristematic tissue are found in **meristems**, which are plant regions of continuous cell division and growth. **Meristematic tissue** cells are either undifferentiated or incompletely differentiated, and they continue to divide and contribute to the growth of the plant. In contrast, permanent tissue consists of plant cells that are no longer actively dividing.

Meristematic tissues consist of three types based on their location in the plant. **Apical meristems** contain meristematic tissue located at the tips of stems and roots, which enable a plant to extend in length. **Lateral meristems** facilitate growth in thickness or girth in a maturing plant. **Intercalary meristems** occur only in monocots, at the bases of leaf blades, and at nodes (the areas where leaves attach to a stem). This tissue enables the monocot leaf blade to increase in length from the leaf base; for example, it allows lawn grass leaves to elongate even after repeated mowing.

Meristems produce cells that quickly differentiate or specialize and become permanent tissue. Such cells take on specific roles and lose their ability to divide further. They differentiate into three main types: dermal, vascular, and ground tissue. **Dermal tissue** covers and protects the plant, and **vascular tissue** transports water, minerals, and sugars to different parts of the plant. **Ground tissue** serves as a site for photosynthesis, provides a supporting matrix for the vascular tissue, and helps to store water and sugars.

Secondary tissues are either simple (composed of similar cell types) or complex (composed of different cell types). Dermal tissue, for example, is a simple tissue that covers the outer surface of the plant and controls gas exchange. Vascular tissue is an example of a complex tissue and is made of two specialized conducting tissues: xylem and phloem. Xylem tissue transports water and nutrients from the roots to different parts of the plant. It includes three different cell types: vessel elements and tracheids (both of which conduct water), and xylem parenchyma. Phloem tissue, which transports organic compounds from the site of photosynthesis to other parts of the plant, consists of four different cell types: sieve cells (which conduct photosynthates), companion cells, phloem parenchyma, and phloem fibers. Unlike xylem-conducting cells, phloem-conducting cells are alive at maturity. The xylem and phloem always lie adjacent to each other (**Figure 1**). In stems, the xylem and the phloem form a structure called a **vascular bundle**.

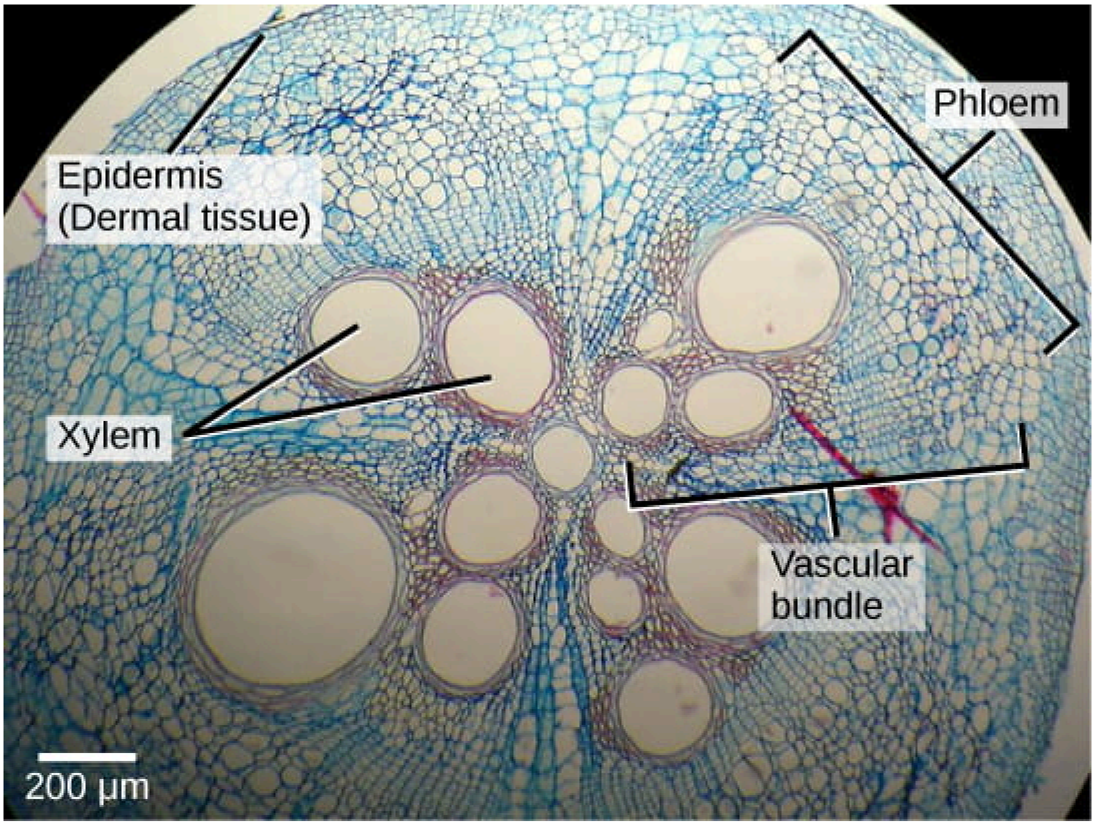

Figure 1. *This light micrograph shows a cross section of a squash (Curcurbita maxima) root. Each teardrop-shaped vascular bundle consists of large xylem vessels toward the inside and smaller phloem cells toward the outside. Xylem cells, which transport water and nutrients from the roots to the rest of the plant, are dead at functional maturity. Phloem cells, which transport sugars and other organic compounds from photosynthetic tissue to the rest of the plant, are living. The vascular bundles are encased in ground tissue and surrounded by dermal tissue.*

Dermal Tissue

The dermal tissue of the stem consists primarily of epidermis, a single layer of cells covering and protecting the underlying tissue. Woody plants have a tough, waterproof outer layer of cork cells commonly known as bark, which further protects the plant from damage. Epidermal cells are the most numerous and least differentiated of the cells in the epidermis. The epidermis of a leaf also contains openings known as stomata, through which the exchange of gasses takes place (**Figure 2**). Two cells, known as guard cells, surround each leaf stoma, controlling its opening and closing and thus regulating the uptake of carbon dioxide and the release of oxygen and water vapor. Some leaves may have small hairs (trichomes) on the leaf surface. Trichomes help to deter herbivory by restricting insect movements, or by storing toxic or bad-tasting compounds; they can also reduce the rate of transpiration by blocking air flow across the leaf surface.

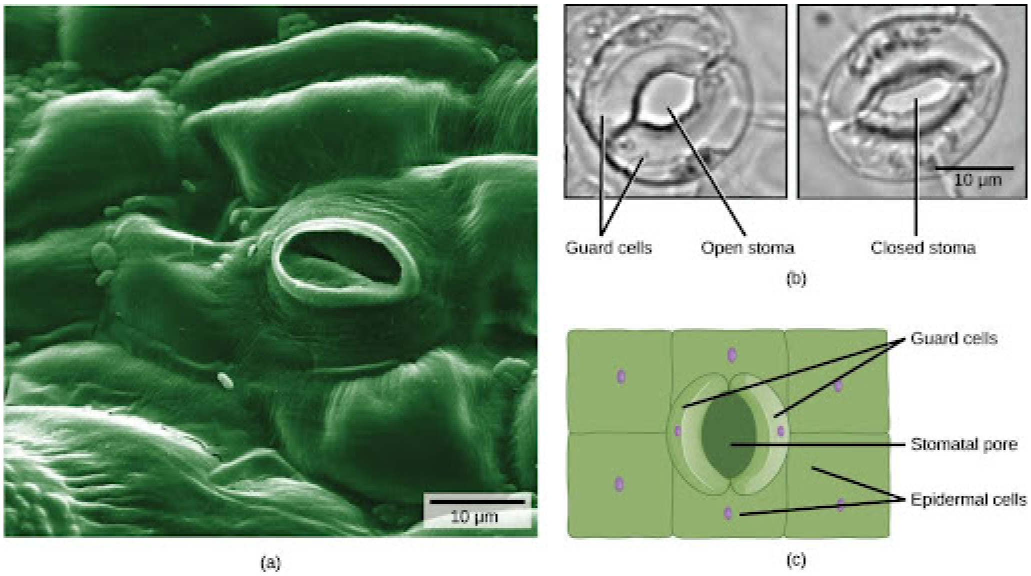

Figure 2. *Openings called stomata (singular: stoma) allow a plant to take up carbon dioxide and release oxygen and water vapor. The (a) colorized scanning-electron micrograph shows a closed stoma of a dicot. Each stoma is flanked by two guard cells that regulate its (b) opening and closing. The (c) guard cells sit within the layer of epidermal cells*

Vascular Tissue

The xylem and phloem that make up the vascular tissue of the stem are arranged in distinct strands called vascular bundles, which run up and down the length of the stem. When the stem is viewed in cross-section, the vascular bundles of dicot stems are arranged in a ring. In plants with stems that live for more than one year, the individual bundles grow together and produce the characteristic growth rings. In monocot stems, the vascular bundles are randomly scattered throughout the ground tissue (**Figure 3**).

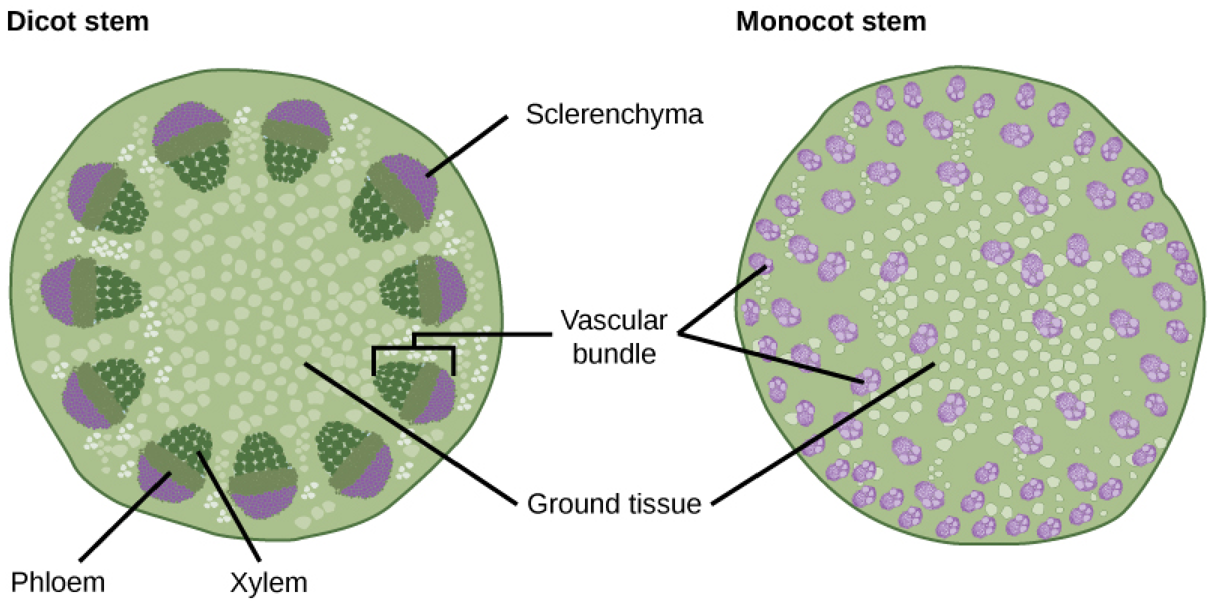

Figure 3. *In (a) dicot stems, vascular bundles are arranged around the periphery of the ground tissue. The xylem tissue is located toward the interior of the vascular bundle, and phloem is located toward the exterior. Sclerenchyma fibers cap the vascular bundles. In (b) monocot stems, vascular bundles composed of xylem and phloem tissues are scattered throughout the ground tissue.*

Xylem tissue has three types of cells: xylem parenchyma, tracheids, and vessel elements. The latter two types conduct water and are dead at maturity. **Tracheids** are xylem cells with thick secondary cell walls that are lignified. Water moves from one tracheid to another through regions on the side walls known as pits, where secondary walls are absent. **Vessel elements** are xylem cells with thinner walls; they are shorter than tracheids. Each vessel element is connected to the next by means of a perforation plate at the end walls of the element. Water moves through the perforation plates to travel up the plant. Phloem tissue is composed of sieve-tube cells, companion cells, phloem parenchyma, and phloem fibers. A series of **sieve-tube cells** (also called sieve-tube elements) are arranged end to end to make up a long sieve tube, which transports organic substances such as sugars and amino acids. The sugars flow from one sieve-tube cell to the next through perforated sieve plates, which are found at the end junctions between two cells. Although still alive at maturity, the nucleus and other cell components of the sieve-tube cells have disintegrated. **Companion cells** are found alongside the sieve-tube cells, providing them with metabolic support. The companion cells contain more ribosomes and mitochondria than the sieve-tube cells, which lack some cellular organelles.

Ground Tissue

Ground tissue is mostly made up of parenchyma cells but may also contain collenchyma and sclerenchyma cells that help support the stem. The ground tissue towards the interior of the vascular tissue in a stem or root is known as **pith**, while the layer of tissue between the vascular tissue and the epidermis is known as the **cortex**.

Plant Organ Systems

In plants, just as in animals, similar cells working together form a tissue. When different types of tissues work together to perform a unique function, they form an organ; organs working together form organ systems. Vascular plants have two distinct organ systems: a shoot system, and a root system. The **shoot system** consists of two portions: the vegetative (non-reproductive) parts of the plant, such as the leaves and the stems, and the reproductive parts of the plant, which include flowers and fruits. The shoot system generally grows above ground, where it absorbs the light needed for photosynthesis. The **root system**, which supports the plants and absorbs water and minerals, is usually underground. **Figure 4** shows the organ systems of a typical plant.

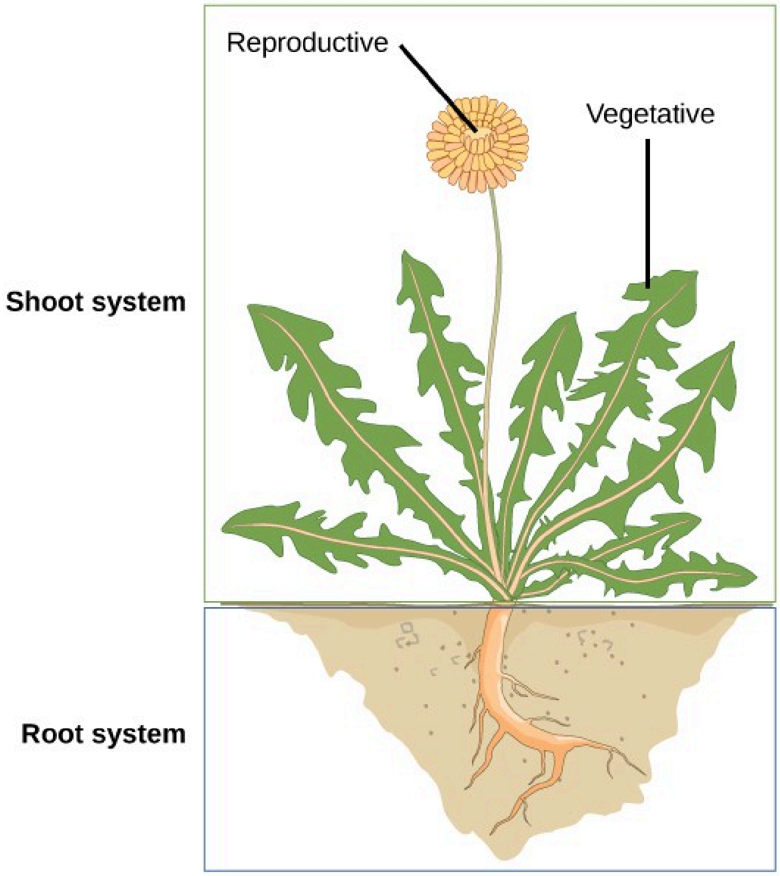

Figure 4. *The shoot system of a plant consists of leaves, stems, flowers, and fruits. The root system anchors the plant while absorbing water and minerals from the soil.*

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Stems

The stem of a plant bears the leaves, flowers, and fruits. Plant stems, whether above or below ground, are characterized by the presence of nodes and internodes. **Nodes** are points of attachment for leaves, aerial roots, and flowers. The stem region between two nodes is called an **internode**. The stalk that extends from the stem to the base of the leaf is the petiole (**Figure 5**).

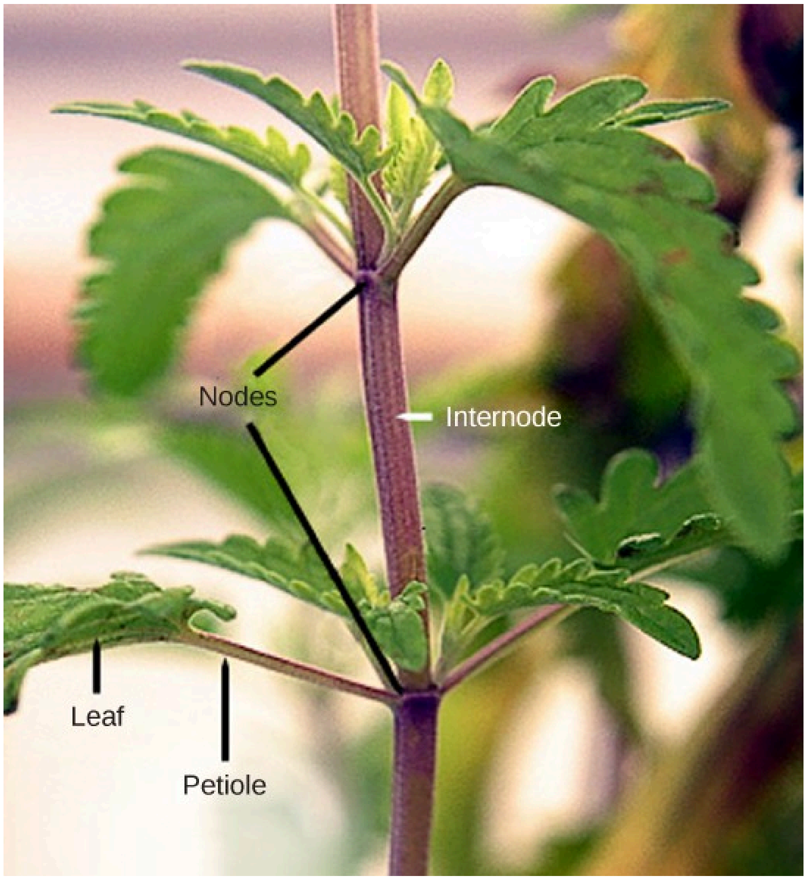

Figure 5. *Leaves are attached to the plant stem at areas called nodes. An internode is the stem region between two nodes. The petiole is the stalk connecting the leaf to the stem.*

Plant organs are made up of simple and complex tissues. The stem has three tissue systems: dermal, vascular, and ground tissue. Dermal tissue is the outer covering of the plant. It contains epidermal cells, stomata, guard cells, and trichomes. Vascular tissue is made up of xylem and phloem tissues and conducts water, minerals, and photosynthetic products. Ground tissue is responsible for photosynthesis and support.

Primary growth occurs at the tips of roots and shoots, causing an increase in length. Woody plants may also exhibit secondary growth or increase in thickness. In woody plants, especially trees, annual rings may form as growth slows at the end of each season. Some plant species have modified stems that help to store food, propagate new plants, or discourage predators. Rhizomes, corms, stolons, runners, tubers, bulbs, tendrils, and thorns are examples of modified stems (**Figure 6**).

Figure 6. *Stem modifications enable plants to thrive in a variety of environments. Shown are (a) ginger (Zingiber of rhizomes, (b) a carrion flower (Amorphophallus titanum) corm (c) Rhodes grass (Chloris gayana) stolons, (d) straw (Fragaria ananassa) runners, (e) potato (Solanum tuberosum) tubers, and (f) red onion (Allium) bulbs.*

In the next video, watch botanist Wendy Hodgson of Desert Botanical Garden in Phoenix, Arizona, explain how agave plants were cultivated for food hundreds of years ago in the Arizona desert.

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Some aerial modifications of stems are tendrils and thorns (**Figure 7**). Tendrils are slender, twining strands that enable a plant (like a vine or pumpkin) to seek support by climbing on other surfaces. Thorns are modified branches appearing as sharp outgrowths that protect the plant; common examples include roses, Osage orange and devil's walking stick.

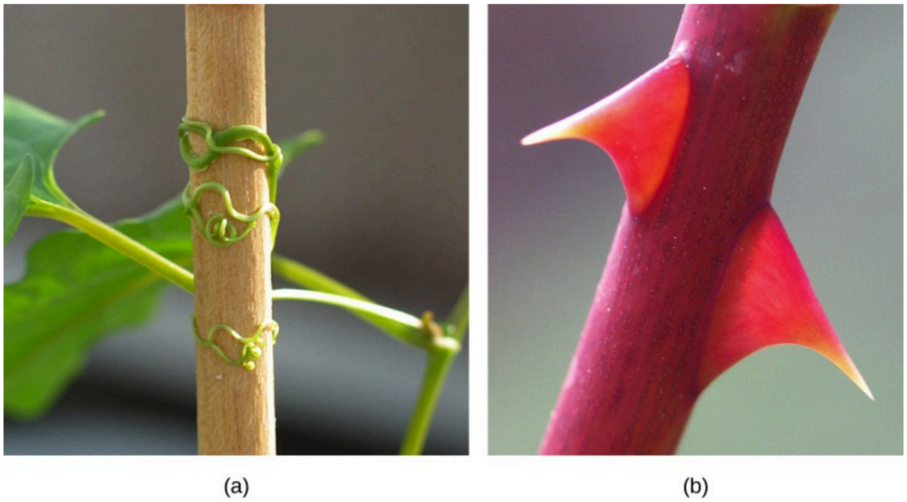

Figure 7. *Found in southeastern United States, (a) buckwheat vine (Brunnichia ovata) is a weedy plant that climbs with the aid of tendrils. This one is shown climbing up a wooden stake. (b) Thorns are modified branches.*

Roots

The roots of seed plants have three major functions: anchoring the plant to the soil, absorbing water and minerals and transporting them upwards, and storing the products of photosynthesis. Some roots are modified to absorb moisture and exchange gasses.

Taproots and **fibrous** roots are the two main types of root systems (**Figure 8**). In a taproot system, a main root grows vertically downward with a few lateral roots. Fibrous root systems arise at the base of the stem, where a cluster of roots forms a dense network that is shallower than a taproot.

Figure 8. *(a) Tap root systems have a main root that grows down, while (b) fibrous root systems consist of many small roots.*

The root has an outer layer of cells called the epidermis, which surrounds areas of ground tissue and vascular tissue. The epidermis provides protection and helps in absorption. **Root hairs**, which are extensions of root epidermal cells, increase the surface area of the root, greatly contributing to the absorption of water and minerals. Root vascular tissue conducts water, minerals, and sugars.

Inside the root, the ground tissue forms two regions: the cortex and the pith. Both regions include cells that store photosynthetic products. The cortex is between the epidermis and the vascular tissue, whereas the pith lies between the vascular tissue and the center of the root.

Root structures may be modified for specific purposes. For example, some roots are bulbous and store starch. Aerial roots and prop roots are two forms of aboveground roots that provide additional support to anchor the plant. Tap roots, such as carrots, turnips, and beets, are examples of roots that are modified for food storage (**Figure 9**).

Figure 9. *Many vegetables are modified roots.*

Epiphytic roots enable a plant to grow on another plant. The banyan tree (*Ficus* sp.) begins as an epiphyte, germinating in the branches of a host tree; aerial roots develop from the branches and eventually reach the ground, providing additional support (**Figure 10**).

Figure 10. *The banyan tree, also known as the strangler fig, begins life as an epiphyte in a host tree. Aerial roots extend to the ground and support the growing plant, which eventually strangles the host tree.*

Leaves

Leaves are the main site of photosynthesis. Most leaves are usually green, due to the presence of chlorophyll in the leaf cells. However, some leaves may have different colors, caused by other plant pigments that mask the green chlorophyll. A typical leaf consists of a lamina (the broad part of the leaf, also called the blade) and a petiole (the stalk that attaches the leaf to a stem).

The thickness, shape, and size of leaves are adapted to the environment. Each variation helps a plant species maximize its chances of survival in a particular habitat. Usually, the leaves of plants growing in tropical rainforests have larger surface areas than those of plants growing in deserts or very cold conditions, which are likely to have a smaller surface area to minimize water loss.

The arrangement of leaves on a stem, known as phyllotaxy, enables maximum exposure to sunlight. Each plant species has a characteristic leaf arrangement and form. The pattern of leaf arrangement may be alternate, opposite, or spiral, while leaf form may be simple or compound (**Figure 11**).

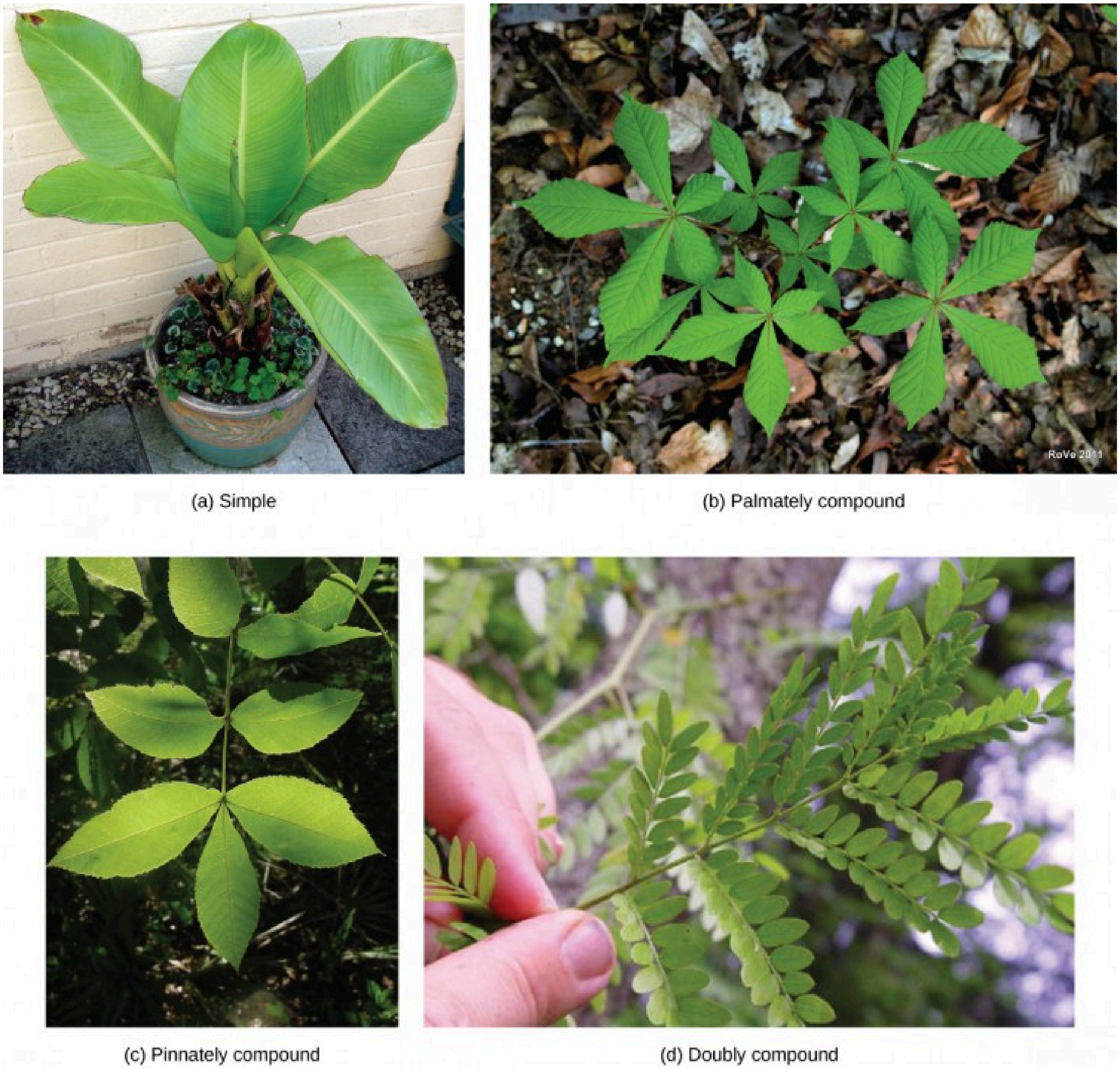

Figure 11. *Leaves may be simple or compound. In simple leaves, the lamina is continuous. The (a) banana plant (Musa sp.) has simple leaves. In compound leaves, the lamina is separated into leaflets. Compound leaves may be palmate or pinnate. In (b) palmately compound leaves, such as those of the horse chestnut (Aesculus hippocastanum), the leaflets branch from the petiole. In (c) pinnately compound leaves, the leaflets branch from the midrib, as on a scrub hickory (Carya floridana). The (d) honey locust has double compound leaves, in which leaflets branch from the veins.*

Leaf tissue consists of the epidermis, which forms the outermost cell layer, and mesophyll and vascular tissue, which make up the inner portion of the leaf. The epidermis helps in the regulation of gas exchange. It contains stomata (**Figure 12**), openings through which the exchange of gasses takes place. Two guard cells surround each stoma, regulating its opening and closing.

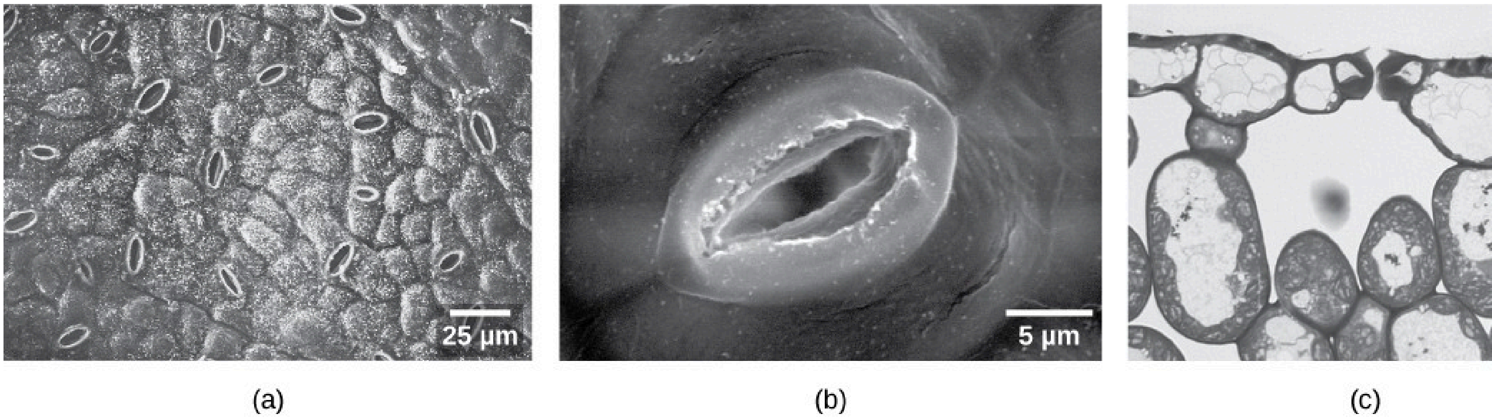

Figure 12. *Visualized at 500x with a scanning electron microscope, several stomata are clearly visible on (a) the su this sumac (Rhus glabra) leaf. At 5,000x magnification, the guard cells of (b) a single stoma from lyre-leaved sand c (Arabidopsis lyrata) have the appearance of lips that surround the opening. In this (c) light micrograph cross-sectio A. lyrata leaf, the guard cell pair is visible along with the large, sub-stomatal air space in the leaf.*

In the leaf drawing (**Figure 13a**), the central mesophyll is sandwiched between an upper and lower epidermis. The mesophyll has two layers: an upper palisade layer composed of tightly packed columnar cells, and a lower spongy layer, composed of loosely packed, irregularly shaped cells. Stomata on the leaf underside allow gas exchange. A waxy layer known as the **cuticle** covers the leaves of all plant species. The cuticle reduces the rate of water loss from the leaf surface. These leaf layers are clearly visible in the scanning electron micrograph (**Figure 13b**).

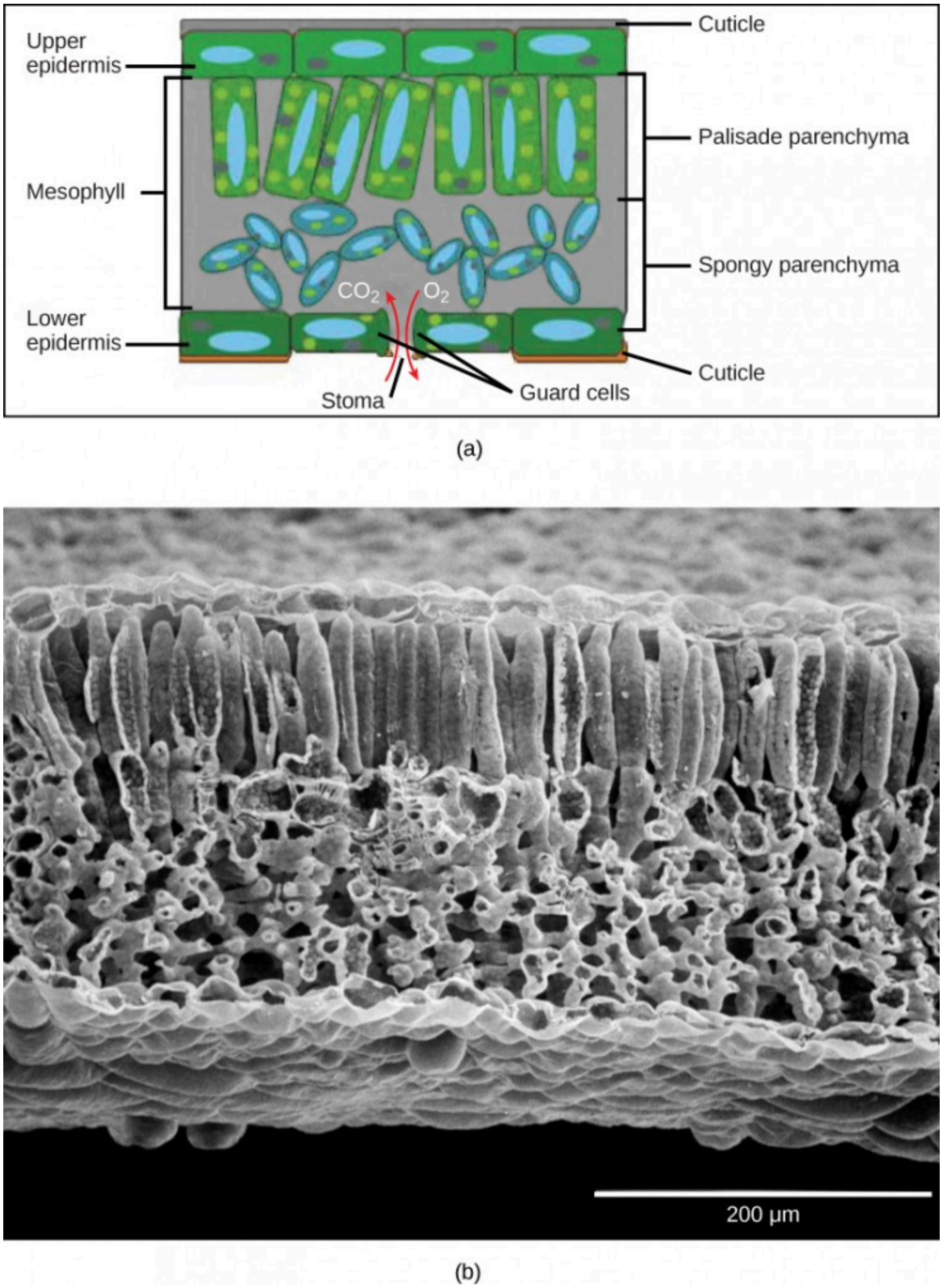

Figure 13. *(a) Leaf drawing (b) Scanning electron micrograph of a leaf. (credit b: modification of work by Robert R. Wise)*

Like the stem, the leaf contains vascular bundles composed of xylem and phloem (**Figure 14**). The xylem consists of tracheids and vessels, which transport water and minerals to the leaves. The phloem transports the photosynthetic products from the leaf to the other parts of the plant. A single vascular bundle, no matter how large or small, always contains both xylem and phloem tissues.

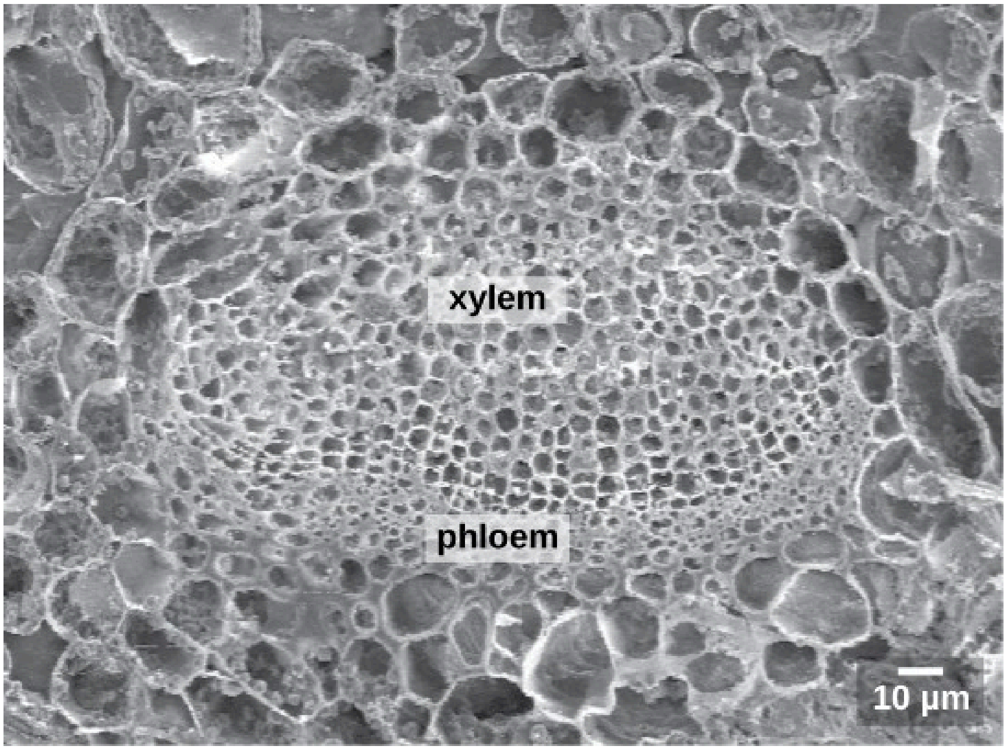

Figure 14. *This scanning electron micrograph shows xylem and phloem in the leaf vascular bundle from the lyre-leaved sand cress (Arabidopsis lyrata). (credit: modification of work by Robert R. Wise; scale-bar data from Matt Russell)*

In some plant species, leaf form is modified to form structures such as tendrils, spines, bud scales, and needles. Coniferous plant species that thrive in cold environments, like spruce, fir, and pine, have leaves that are reduced in size and needle-like in appearance. These needle-like leaves have sunken stomata and a smaller surface area, two attributes that aid in reducing water loss. In hot climates, plants such as cacti have leaves that are reduced to spines, which, in combination with their succulent stems, help to conserve water. Many aquatic plants have leaves with wide lamina that can float on the surface of the water and a thick waxy cuticle on the leaf surface that repels water.

Watch "The Pale Pitcher Plant" episode of the video series Plants Are Cool, Too, a Botanical Society of America video about a carnivorous plant species found in Louisiana.

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Transport of Water in Plants

Section Goals

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

- Describe how water potential, transpiration, and stomatal regulation influence how water is transported in plants.

The structure of plant roots, stems, and leaves facilitates the transport of water, nutrients, and photosynthates throughout the plant. The phloem and xylem are the main tissues responsible for this movement. Water potential, transpiration, and stomatal regulation influence how water and nutrients are transported in plants.

Plants are phenomenal hydraulic engineers. Using only the basic laws of physics and the simple manipulation of potential energy, plants can move water to the top of a 116-meter-tall tree (**Figure 1a**). Plants can also use hydraulics to generate enough force to split rocks and buckle sidewalks (**Figure 1b**). Plants achieve this because of **water potential**, a measure of the potential energy in water. The water potential in plant solutions is influenced by solute concentration, pressure, gravity, and factors called matrix effects. Water moves from an area of higher total water potential to an area of lower total water potential.

Figure 1. *With heights nearing 116 meters, (a) coastal redwoods (Sequoia sempervirens) are the tallest trees in the world. Plant roots can easily generate enough force to (b) buckle and break concrete sidewalks, much to the dismay of homeowners and city maintenance departments.*

Check out this cool animation that follows the path of water from roots to tips and beyond in a Douglas fir tree:

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Movement of Water and Minerals in the Xylem via Transpiration

Transpiration is the loss of water from the plant through evaporation at the leaf surface. It is the main driver of water movement in the xylem. Transpiration is caused by the evaporation of water at the leaf–atmosphere interface; it creates negative pressure (tension) equivalent to –2 MPa at the leaf surface. This value varies greatly depending on the vapor pressure deficit, which can be negligible at high relative humidity (RH) and substantial at low RH. This tension pulls water from the roots up. At night, when stomata shut and transpiration stops, the water is held in the stem and leaf by the adhesion of water to the cell walls of the xylem vessels and tracheids and the cohesion of water molecules to each other. This explanation is called the cohesion–tension theory of sap ascent.

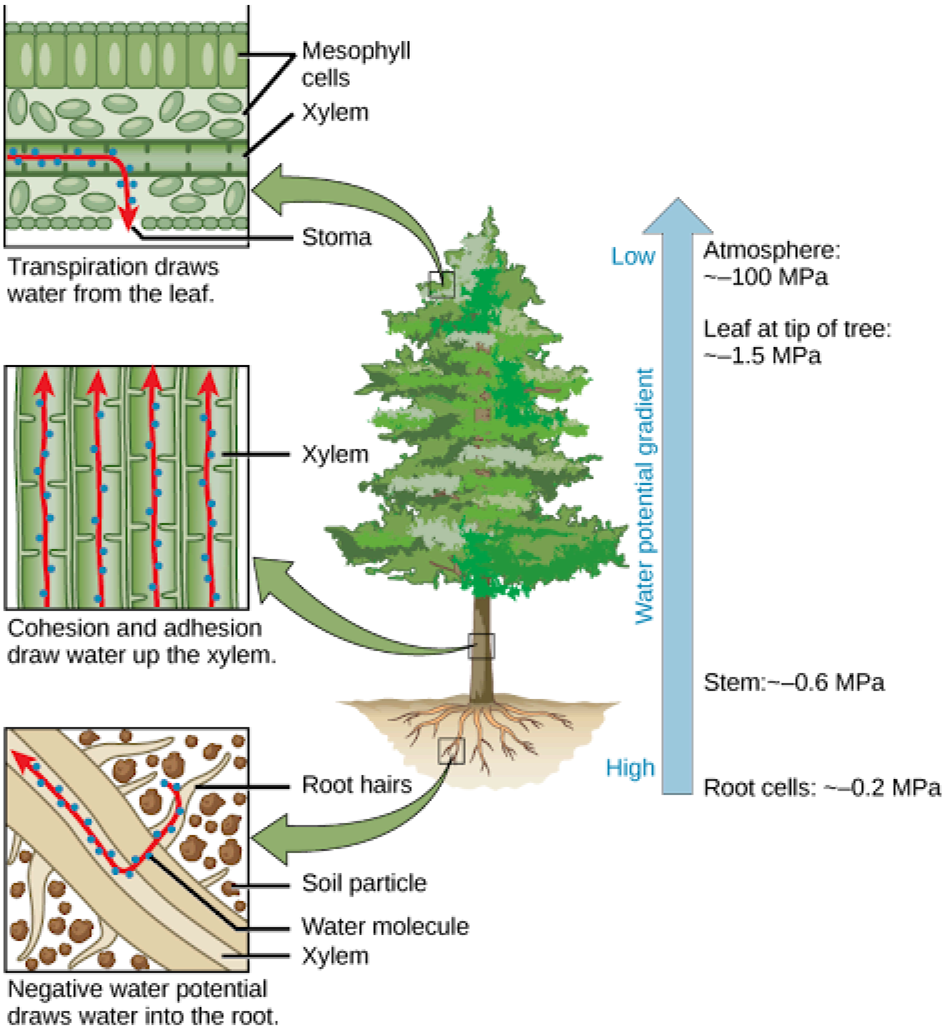

Figure 2. *The cohesion–tension theory of sap ascent is shown. Evaporation from the mesophyll cells produces a negative water potential gradient that causes water to move upwards from the roots through the xylem.*

Inside the leaf at the cellular level, water on the surface of mesophyll cells saturates the cellulose microfibrils of the primary cell wall. The leaf contains many large intercellular air spaces for the exchange of oxygen for carbon dioxide, which is required for photosynthesis. The wet cell wall is exposed to this leaf-internal air space, and the water on the surface of the cells evaporates into the air spaces, decreasing the thin film on the surface of the mesophyll cells.

This decrease creates a greater tension on the water in the mesophyll cells (**Figure 2**), thereby increasing the pull on the water in the xylem vessels. The xylem vessels and tracheids are structurally adapted to cope with large changes in pressure. Rings in the vessels maintain their tubular shape, much like the rings on a vacuum cleaner that keep the hose open while it is under pressure. Small perforations between vessel elements reduce the number and size of gas bubbles that can form via a process called cavitation. The formation of gas bubbles in the xylem interrupts the continuous stream of water from the base to the top of the plant, causing a break termed an embolism in the flow of xylem sap. The taller the tree, the greater the tension forces needed to pull water and the more cavitation events. In larger trees, the resulting embolisms can plug xylem vessels, making them non-functional.

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Transpiration—the loss of water vapor to the atmosphere through stomata—is a passive process, meaning that metabolic energy in the form of ATP is not required for water movement. The energy driving transpiration is the difference in energy between the water in the soil and the water in the atmosphere. However, transpiration is tightly controlled.

Control of Transpiration

The atmosphere to which the leaf is exposed drives transpiration but also causes massive water loss from the plant. Up to 90 percent of the water taken up by roots may be lost through transpiration.

Leaves are covered by a waxy **cuticle** on the outer surface that prevents the loss of water. Regulation of transpiration, therefore, is achieved primarily through the opening and closing of stomata on the leaf surface. Stomata are surrounded by two specialized cells called guard cells, which open and close in response to environmental cues such as light intensity and quality, leaf water status, and carbon dioxide concentrations. Stomata must open to allow air containing carbon dioxide and oxygen to diffuse into the leaf for photosynthesis and respiration. When stomata are open, however, water vapor is lost to the external environment, increasing the rate of transpiration. Therefore, plants must maintain a balance between efficient photosynthesis and water loss.

Over time, plants have evolved to adapt to their local environment and reduce transpiration (**Figure 3**). Desert plants (xerophytes) and plants that grow on other plants (epiphytes) have limited access to water. Such plants usually have a much thicker waxy cuticle than those growing in more moderate, well-watered environments (mesophytes). Aquatic plants (hydrophytes) also have their own set of anatomical and morphological leaf adaptations.

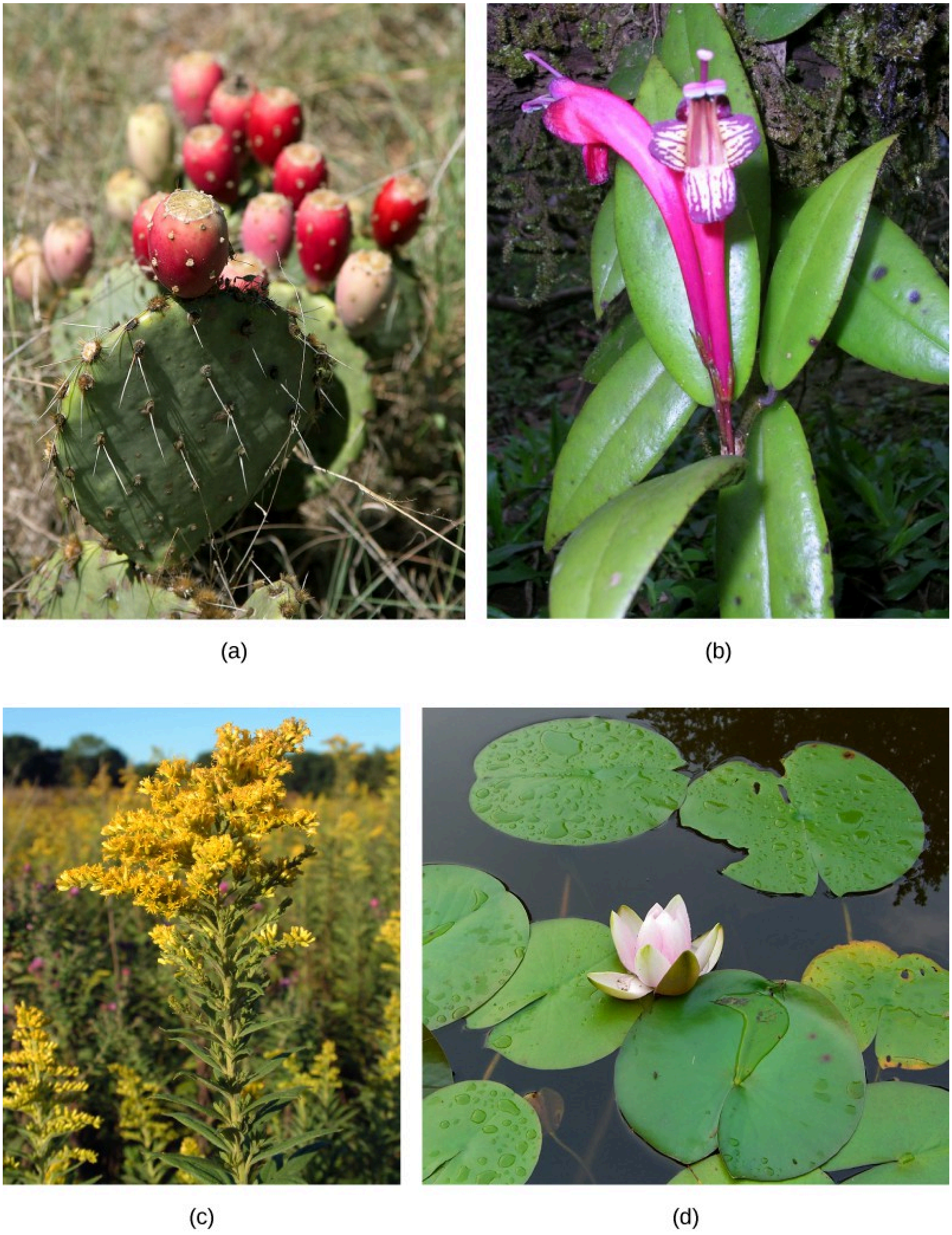

Figure 3. *Plants are suited to their local environment. (a) Xerophytes, like this prickly pear cactus (Opuntia sp.) and (b) epiphytes such as this tropical Aeschynanthus perrottetii have adapted to very limited water resources. The leaves of a prickly pear are modified into spines, which lowers the surface-to-volume ratio and reduces water loss. Photosynthesis takes place in the stem, which also stores water. (b) A. perrottetii leaves have a waxy cuticle that prevents water loss. (c) Goldenrod (Solidago sp.) is a mesophyte, well suited for moderate environments. (d) Hydrophytes, like this fragrant water lily (Nymphaea odorata),*

are adapted to thrive in aquatic environments.

Xerophytes and epiphytes often have a thick covering of trichomes or stomata that are sunken below the leaf's surface. Trichomes are specialized hair-like epidermal cells that secrete oils and substances. These adaptations impede airflow across the stomatal pore and reduce transpiration. Multiple epidermal layers are also commonly found in these types of plants.

Watch this video to review how transpiration works in plants and the factors that affect transpiration rate:

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Transport of Food in Plants

Section Goals

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

- Explain how photosynthates are transported in plants

Plants need an energy source to grow. Food is stored in polymers (such as starch) in seeds and bulbs, which are converted by metabolic processes into sucrose for newly developing plants. Once green shoots and leaves are growing, plants can produce their own food by photosynthesizing. The products of photosynthesis are called **photosynthates**, which are usually simple sugars such as sucrose.

Movement of Photosynthates in the Phloem via Translocation

Structures that produce photosynthates for the growing plant are referred to as **sources**. Sugars produced in sources, such as leaves, need to be delivered to growing parts of the plant via the phloem in a process called **translocation**. The points of sugar delivery, such as roots, young shoots, and developing seeds, are called **sinks**. Seeds, tubers, and bulbs can be either a source or a sink, depending on the plant's stage of development and the season.

The products from the source are usually translocated to the nearest sink through the phloem. For example, the highest leaves will send photosynthates upward to the growing shoot tip, whereas lower leaves will direct photosynthates downward to the roots. Intermediate leaves will send products in both directions, unlike the flow in the xylem, which is always unidirectional (soil to leaf to atmosphere). The pattern of photosynthate flow changes as the plant grows and develops. Photosynthates are directed primarily to the roots early on, to shoots and leaves during vegetative growth, and to seeds and fruits during reproductive development. They are also directed to tubers for storage.

Translocation: Transport from Source to Sink

Photosynthates, such as sucrose, are produced in the mesophyll cells of photosynthesizing leaves. From there, they are translocated through the phloem to where they are used or stored. Mesophyll cells are connected by cytoplasmic channels called plasmodesmata. Photosynthates move through these channels to reach phloem sieve-tube elements (STEs) in the vascular bundles. From the mesophyll cells, the photosynthates are loaded into the phloem STEs. The sucrose is actively transported against its concentration gradient (a process requiring ATP) into the phloem cells using the electrochemical potential of the proton gradient. This transport is coupled to the uptake of sucrose with a carrier protein called the sucrose-H^+ symporter.

Phloem STEs have reduced cytoplasmic contents and are connected by a sieve plate with pores that allow for pressure-driven bulk flow, or translocation, of phloem sap. Companion cells are associated with STEs. They assist with metabolic activities and produce energy for the STEs (**Figure 1**).

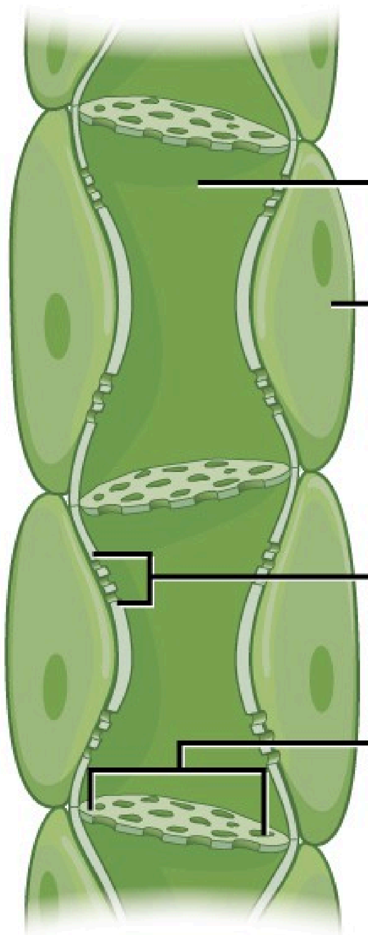

Figure 1. *Phloem is composed of cells called sieve-tube elements. Phloem sap travels through perforations called sieve tube plates. Neighboring companion cells carry out metabolic functions for the sieve-tube elements and provide them with energy. Lateral sieve areas connect the sieve-tube elements to the companion cells.*

Once in the phloem, the photosynthates are translocated to the closest sink. Phloem sap is an aqueous solution that contains up to 30 percent sugar, minerals, amino acids, and plant growth regulators. The high percentage of sugar decreases osmotic potential, causing water to move by osmosis from the adjacent xylem into the phloem tubes, thereby increasing pressure. This increase in total water potential causes the bulk flow of phloem from source to sink (**Figure 2**). Sucrose concentration in the sink cells is lower than in the phloem STEs because the sink sucrose has been metabolized for growth or converted to starch for storage or other polymers, such as cellulose, for structural integrity. Unloading at the sink end of the phloem tube occurs by either diffusion or active transport of sucrose molecules from an area of high concentration to one of low concentration. Water diffuses from the phloem by osmosis and is then transpired or recycled via the xylem back into the phloem sap.

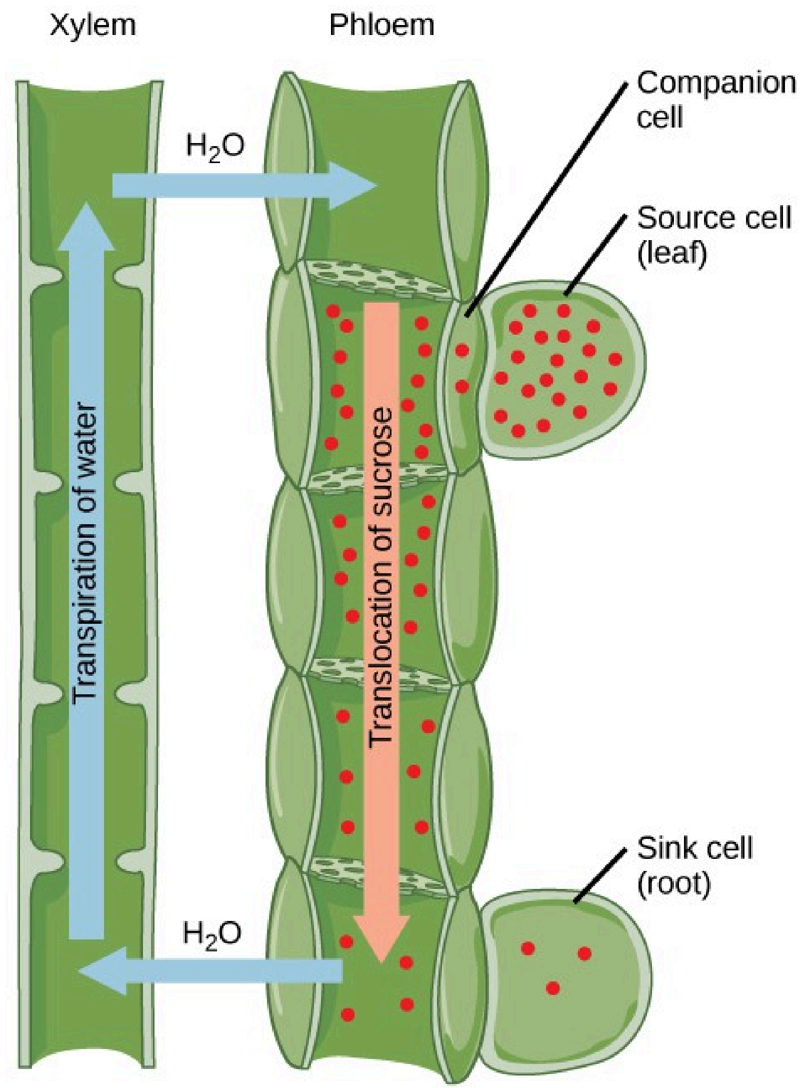

Figure 2. *Sucrose is actively transported from source cells into companion cells and then into the sieve-tube elements. This reduces the water potential, which causes water to enter the phloem from the xylem. The resulting positive pressure forces the sucrose-water mixture down toward the roots, where sucrose is unloaded. Transpiration causes water to return to the leaves through the xylem vessels.*

Watch the next two videos to review plant vascular tissues (xylem and phloem), transpiration (movement of water) and translocation (movement of food):

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IV

An Introduction to Animal Physiology

This module contains the following chapters:

Different Types of Respiratory Systems

Section Goals

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

- Discuss the respiratory processes used by animals without lungs
- Identify structures in mammalian respiratory systems and their functions
- Describe the passage of air from the outside environment to the lungs

The primary function of the respiratory system is to deliver oxygen to the cells of the body's tissues and remove carbon dioxide, a cell waste product.

All aerobic organisms require oxygen to carry out their metabolic functions. Along the evolutionary tree, different organisms have devised different means of obtaining oxygen from the surrounding atmosphere. The environment in which the animal lives greatly determines how an animal respires. The complexity of the respiratory system is correlated with the size of the organism. As animal size increases, diffusion distances increase and the ratio of surface area to volume drops. In unicellular organisms, diffusion across the cell membrane is sufficient for supplying oxygen to the cell (**Figure 1**).

Figure 1. *The cell of the unicellular alga Ventricaria ventricosa is one of the largest known, reaching one to five centimeters in diameter. Like all single-celled organisms, V. ventricosa exchanges gases across the cell membrane.*

Diffusion is a slow, passive transport process. In order for diffusion to be a feasible means of providing oxygen to the cell, the rate of oxygen uptake must match the rate of diffusion across the membrane. In other words, if the cell were very large or thick, diffusion would not be able to provide oxygen quickly enough to the inside of the cell. Therefore, dependence on diffusion as a means of obtaining oxygen and removing carbon dioxide remains feasible only for small organisms or those with highly-flattened bodies, such as many flatworms (Platyhelminthes). Larger organisms had to evolve specialized respiratory tissues, such as gills, lungs, and respiratory passages accompanied by complex circulatory systems, to transport oxygen throughout their entire body.

Direct Diffusion

For small multicellular organisms, diffusion across the outer membrane is sufficient to meet their oxygen needs. Gas exchange by direct diffusion across surface membranes is efficient for organisms less than 1 mm in diameter. In simple organisms, such as cnidarians and flatworms, every cell in the body is close to the external environment. Their cells are kept moist and gases diffuse quickly via direct diffusion. Flatworms are small, literally “flat” worms, which “breathe” through diffusion across the outer membrane (**Figure 2**).

Figure 2. *This flatworm’s process of respiration works by diffusion across the outer membrane. (credit: Stephen Childs)*

The flat shape of these organisms increases the surface area for diffusion, ensuring that each cell within the body is close to the outer membrane surface and has access to oxygen. If the flatworm had a cylindrical body, then the cells in the center would not be able to get oxygen.

Skin and Gills

Earthworms and amphibians use their skin (integument) as a respiratory organ. A dense network of capillaries lies just below the skin and facilitates gas exchange between the external environment and the circulatory system. The respiratory surface must be kept moist in order for the gases to dissolve and diffuse across cell membranes.

Organisms that live in water need to obtain oxygen from the water. Oxygen dissolves in water but at a lower concentration than in the atmosphere. The atmosphere has roughly 21 percent oxygen. In water, the oxygen concentration is much smaller than that. Fish and many other aquatic organisms have evolved gills to take up the dissolved oxygen from water (**Figure 3**).

Figure 3. *This common carp, like many other aquatic organisms, has gills that allow it to obtain oxygen from water.*

Gills are thin tissue filaments that are highly branched and folded. When water passes over the gills, the dissolved oxygen in water rapidly diffuses across the gills into the bloodstream. The circulatory system can then carry the oxygenated blood to the other parts of the body. In animals that contain coelomic fluid instead of blood, oxygen diffuses across the gill surfaces into the coelomic fluid. Gills are found in mollusks, annelids, and crustaceans.

The folded surfaces of the gills provide a large surface area to ensure that the fish gets sufficient oxygen. Diffusion is a process in which material travels from regions of high concentration to low concentration until equilibrium is reached. In this case, blood with a low concentration of oxygen molecules circulates through the gills. The concentration of oxygen molecules in water is higher than the concentration of oxygen molecules in gills. As a result, oxygen molecules diffuse from water (high concentration) to blood (low concentration), as shown in **Figure 4**. Similarly, carbon dioxide molecules in the blood diffuse from the blood (high concentration) to water (low concentration).

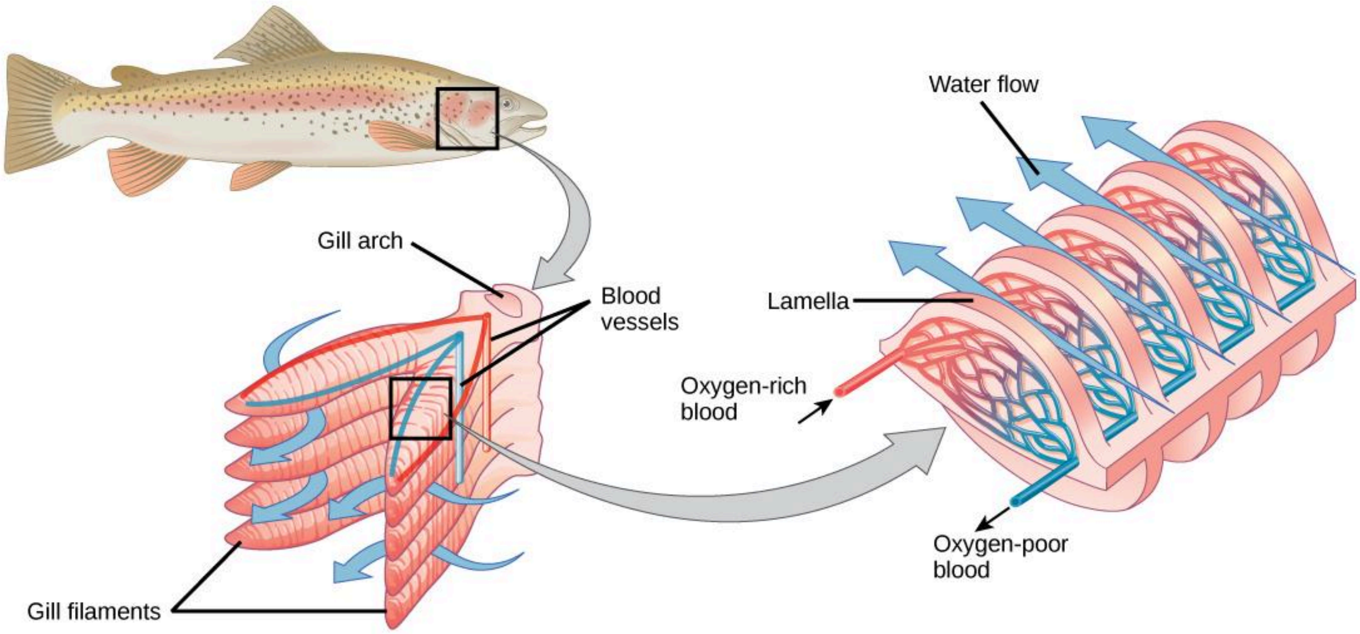

Figure 4. *As water flows over the gills, oxygen is transferred to blood via the veins.*

Tracheal Systems

Insect respiration is independent of its circulatory system; therefore, the blood does not play a direct role in oxygen transport. Insects have a highly specialized type of respiratory system called the tracheal system, which consists of a network of small tubes that carries oxygen to the entire body. The tracheal system is the most direct and efficient respiratory system in active animals. The tubes in the tracheal system are made of a polymeric material called chitin.

Insect bodies have openings, called spiracles, along the thorax and abdomen. These openings connect to the tubular network, allowing oxygen to pass into the body (**Figure 5**) and regulating the diffusion of CO2 and water vapor. Air enters and leaves the tracheal system through the spiracles. Some insects can ventilate the tracheal system with body movements.

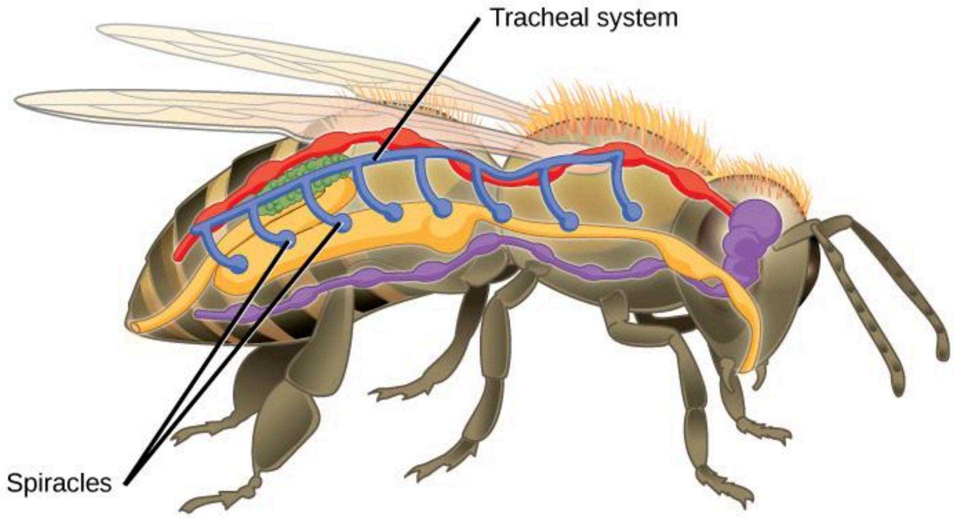

Figure 5. *Insects perform respiration via a tracheal system.*

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Mammalian Respiratory Systems

In mammals, pulmonary ventilation occurs via inhalation (breathing). During inhalation, air enters the body through the **nasal cavity** located just inside the nose (**Figure 6**). As air passes through the nasal cavity, the air is warmed to body temperature and humidified. The respiratory tract is coated with mucus to seal the tissues from direct contact with air. Mucus is high in water. As air crosses these surfaces of the mucous membranes, it picks up water. These processes help equilibrate the air to the body conditions, reducing any damage that cold, dry air can cause. Particulate matter that is floating in the air is removed in the nasal passages via mucus and cilia. The processes of warming, humidifying, and removing particles are important protective mechanisms that prevent damage to the trachea and lungs. Thus, inhalation serves several purposes in addition to bringing oxygen into the respiratory system.

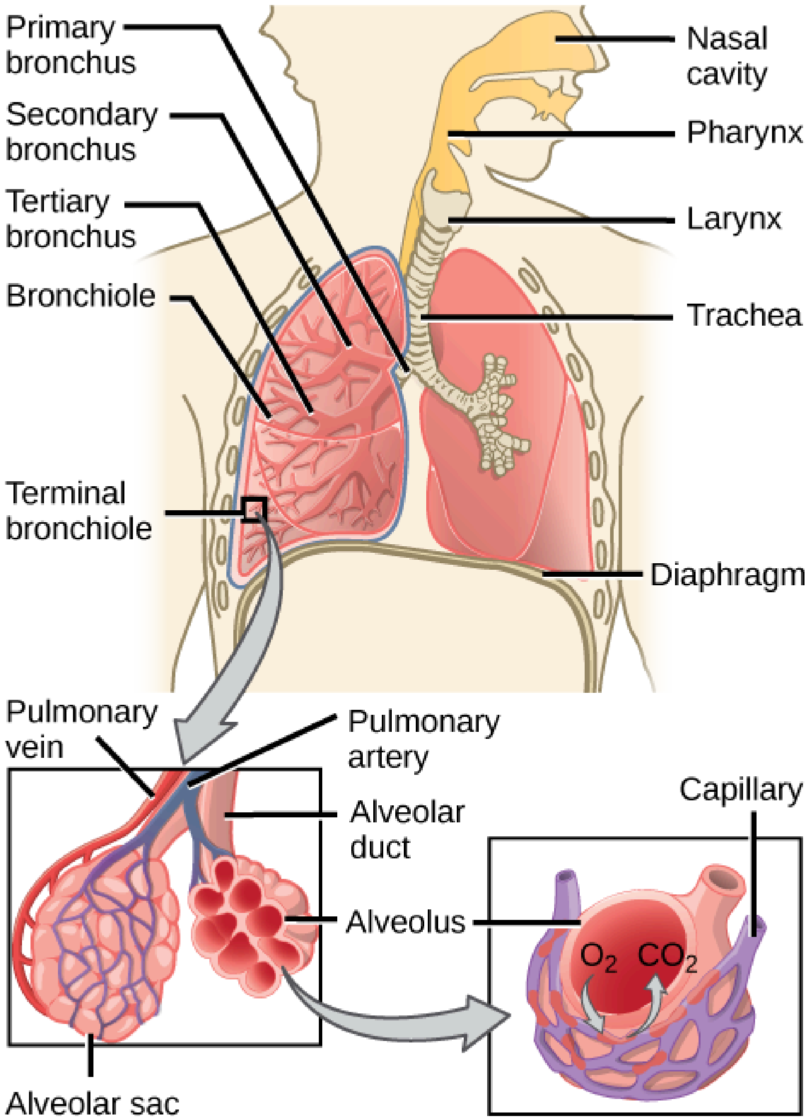

Figure 6. *Air enters the respiratory system through the nasal cavity and pharynx, and then passes through the trachea and into the bronchi, which bring air into the lungs.*

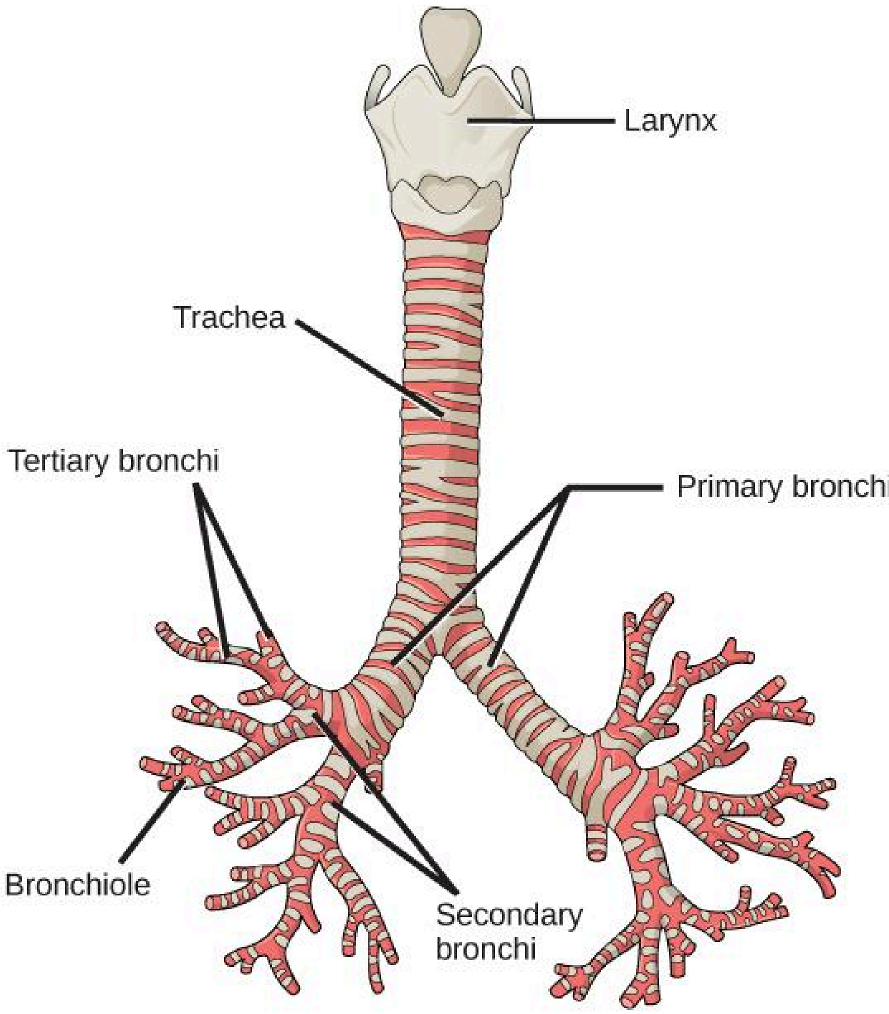

Figure 7. *The trachea and bronchi are made of incomplete rings of cartilage.*

From the nasal cavity, air passes through the **pharynx** (throat) and the **larynx** (voice box), as it makes its way to the **trachea** (**Figure 6**). The main function of the trachea is to funnel the inhaled air to the lungs and the exhaled air back out of the body. The human trachea is a cylinder about 10 to 12 cm long and 2 cm in diameter that sits in front of the esophagus and extends from the larynx into the chest cavity where it divides into the two primary bronchi at the midthorax. It is made of incomplete rings of hyaline cartilage and smooth muscle (**Figure 7**).

The trachea is lined with mucus-producing goblet cells and ciliated epithelia. The cilia propel foreign particles trapped in the mucus toward the pharynx. The cartilage provides strength and support to the trachea to keep the passage open. The smooth muscle can contract, decreasing the trachea's diameter, which causes expired air to rush upwards from the lungs at a great force. The forced exhalation helps expel mucus when we cough. Smooth muscle can contract or relax, depending on stimuli from the external environment or the body's nervous system.

Lungs: Bronchi and Alveoli

The end of the trachea bifurcates (divides) to the right and left lungs. The lungs are not identical. The right lung is larger and contains three lobes, whereas the smaller left lung contains two lobes (**Figure 8**). The muscular **diaphragm**, which facilitates breathing, is inferior (below) to the lungs and marks the end of the thoracic cavity.

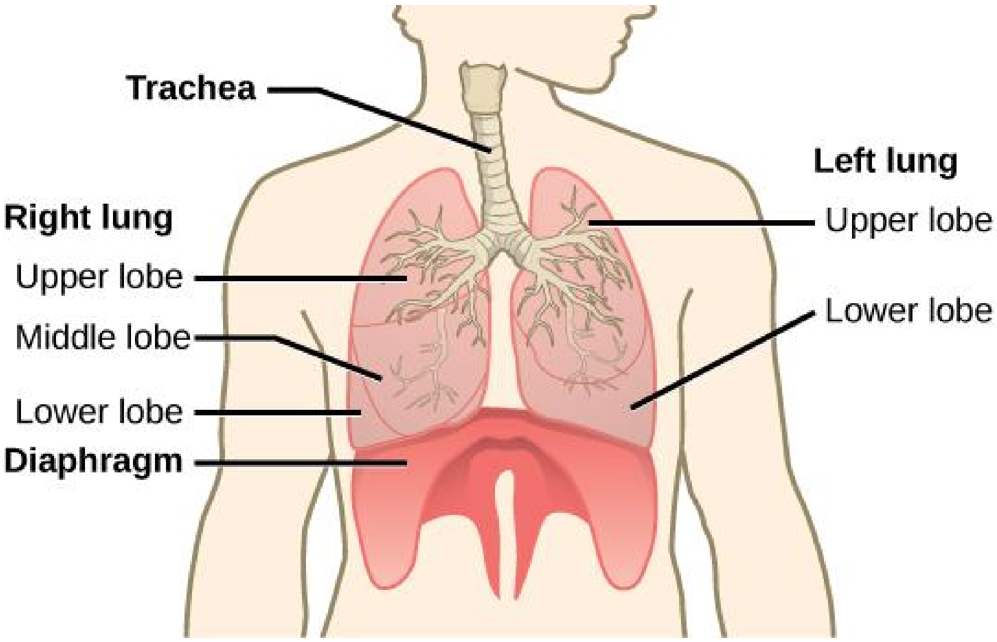

Figure 8. *The trachea bifurcates into the right and left bronchi in the lungs. The right lung is made of three lobes and is larger. To accommodate the heart, the left lung is smaller and has only two lobes.*

In the lungs, air is diverted into smaller and smaller passages, or **bronchi**. Air enters the lungs through the two **primary (main) bronchi** (singular: bronchus). Each bronchus divides into secondary bronchi, then into tertiary bronchi, which in turn divide, creating smaller and smaller diameter **bronchioles** as they split and spread through the lung. Like the trachea, the bronchi are made of cartilage and smooth muscle. At the bronchioles, the cartilage is replaced with elastic fibers. Bronchi are innervated by nerves of both the parasympathetic and sympathetic nervous systems that control muscle contraction (parasympathetic) or relaxation (sympathetic) in the bronchi and bronchioles, depending on the nervous system's cues. In humans, bronchioles with a diameter smaller than 0.5 mm are the **respiratory bronchioles**. They lack cartilage and therefore rely on inhaled air to support their shape. As the passageways decrease in diameter, the relative amount of smooth muscle increases.

The **terminal bronchioles** subdivide into microscopic branches called respiratory bronchioles. The respiratory bronchioles subdivide into several alveolar ducts. Numerous alveoli and alveolar sacs surround the alveolar ducts. The alveolar sacs resemble bunches of grapes tethered to the end of the bronchioles (**Figure 9**).

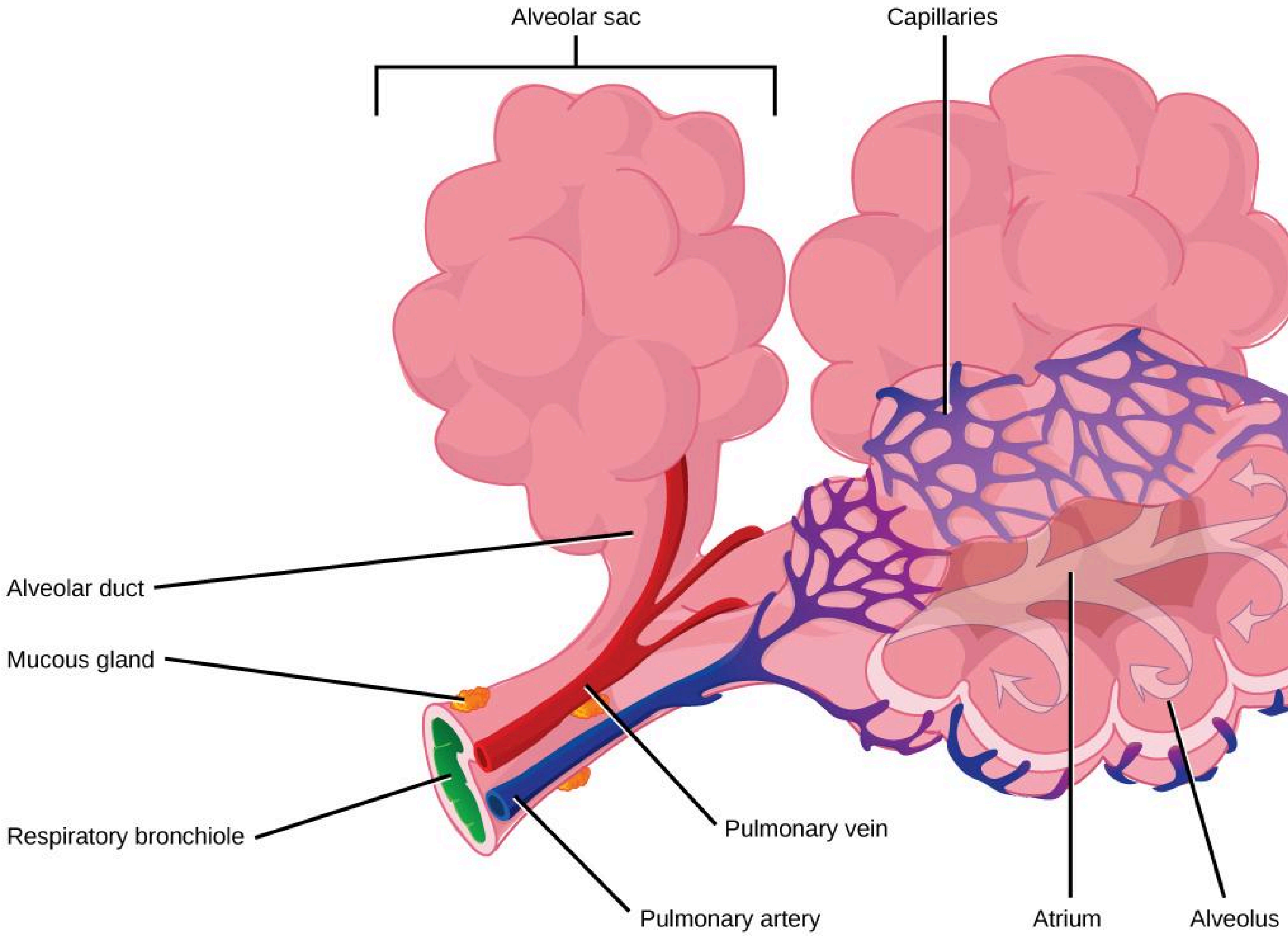

Figure 9. *Terminal bronchioles are connected by respiratory bronchioles to alveolar ducts and alveolar sacs. Each sac contains 20 to 30 spherical alveoli and has the appearance of a bunch of grapes. Air flows into the atrium of the alveolar sac, then circulates into alveoli where gas exchange occurs with the capillaries. Mucous glands secrete mu into the airways, keeping them moist and flexible.*

In the acinar region, the **alveolar ducts** are attached to the end of each bronchiole. At the end of each duct are approximately 100 **alveolar sacs**, each containing 20 to 30 **alveoli** that are 200 to 300 microns in diameter. Gas exchange occurs only in alveoli. Alveoli are made of thin-walled parenchymal cells, typically one-cell thick, that look like tiny bubbles within the sacs. Alveoli are in direct contact with capillaries (one-cell thick) of the circulatory system. Such intimate contact ensures that oxygen will diffuse from alveoli into the blood and be distributed to the cells of the body. In addition, the carbon dioxide that was produced by cells as a waste product will diffuse from the blood into alveoli to be exhaled. The anatomical arrangement of capillaries and alveoli emphasizes the structural and functional relationship of the respiratory and circulatory systems. Because there are so many alveoli (~300 million per lung) within each alveolar sac and so many sacs at the end of each alveolar duct, the lungs have a sponge-like consistency. This organization produces a very large surface area that is available for gas exchange. The surface area of alveoli in the lungs is approximately 75 m2. This large surface area, combined with the thin-walled nature of the alveolar parenchymal cells, allows gases to easily diffuse across the cells.

In the next video, watch as educator Sal Khan draws and explains the journey of our breath as it travels into the body, through the lungs, and ultimately delivers oxygen to our bloodstream.

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Types of Breathing

Section Goals

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

- Identify common types of breathing, including that of mammals and amphibians

Breathing is an involuntary event. How often a breath is taken and how much air is inhaled or exhaled are tightly regulated by the respiratory center in the brain. Humans, when they aren't exerting themselves, breathe approximately 15 times per minute on average. Canines, like the dog in **Figure 1**, have a respiratory rate of about 15–30 breaths per minute. With every inhalation, air fills the lungs, and with every exhalation, air rushes back out. That air is doing more than just inflating and deflating the lungs in the chest cavity. The air contains oxygen that crosses the lung tissue, enters the bloodstream, and travels to organs and tissues. Oxygen (O_2) enters the cells where it is used for metabolic reactions that produce ATP, a high-energy compound. At the same time, these reactions release carbon dioxide (CO_2) as a by-product. CO_2 is toxic and must be eliminated. Carbon dioxide exits the cells, enters the bloodstream, travels back to the lungs, and is expired out of the body during exhalation.

Figure 1. *Lungs, which appear as nearly transparent tissue surrounding the heart in this X-ray of a dog (left), are the central organs of the respiratory system. The left lung is smaller than the right lung to accommodate space for the heart. A dog's nose (right) has a slit on the side of each nostril. When tracking a scent, the slits open, blocking the front of the nostrils. This allows the dog to exhale though the now-open area on the side of the nostrils without losing the scent that is being followed.*

Amphibian Respiration

Amphibians have evolved multiple ways of breathing. Young amphibians, like tadpoles, use gills to breathe, and they don't leave the water. Some amphibians retain gills for life. As the tadpole grows, the gills disappear and lungs grow. These lungs are primitive and not as evolved as mammalian lungs. Adult amphibians are lacking or have a reduced diaphragm, so breathing via lungs is forced. The other means of breathing for amphibians is diffusion across the skin. To aid this diffusion, amphibian skin must remain moist.

Avian Respiration

Birds face a unique challenge with respect to breathing: They fly. Flying consumes a great amount of energy; therefore, birds require a lot of oxygen to aid their metabolic processes. Birds have evolved a respiratory system that supplies them with the oxygen needed to enable flying. Similar to mammals, birds have lungs, which are organs specialized for gas exchange. Oxygenated air, taken in during inhalation, diffuses across the surface of the lungs into the bloodstream, and carbon dioxide diffuses from the blood into the lungs and expelled during exhalation. The details of breathing between birds and mammals differ substantially.

In addition to lungs, birds have air sacs inside their body. Air flows in one direction from the posterior air sacs to the lungs and out of the anterior air sacs. The flow of air is in the opposite direction from blood flow, and gas exchange takes place much more efficiently. This type of breathing enables birds to obtain the requisite oxygen, even at higher altitudes where the oxygen concentration is low. This directionality of airflow requires two cycles of air intake and exhalation to completely get the air out of the lungs.

Birds: Breathing And Flight

Birds have evolved a respiratory system that enables them to fly. Flying is a high-energy process and requires a lot of oxygen. Furthermore, many birds fly in high altitudes where the concentration of oxygen in low. How did birds evolve a respiratory system that is so unique?

Decades of research by paleontologists have shown that birds evolved from therapods, meat-eating dinosaurs (**Figure 2**). In fact, fossil evidence shows that meat-eating dinosaurs that lived more than 100 million years ago had a similar flow-through respiratory system with lungs and air sacs. *Archaeopteryx*and *Xiaotingia*, for example, were flying dinosaurs and are believed to be early precursors of birds.

Most of us consider that dinosaurs are extinct. However, modern birds are descendants of avian dinosaurs. The respiratory system of modern birds has been evolving for hundreds of millions of years.

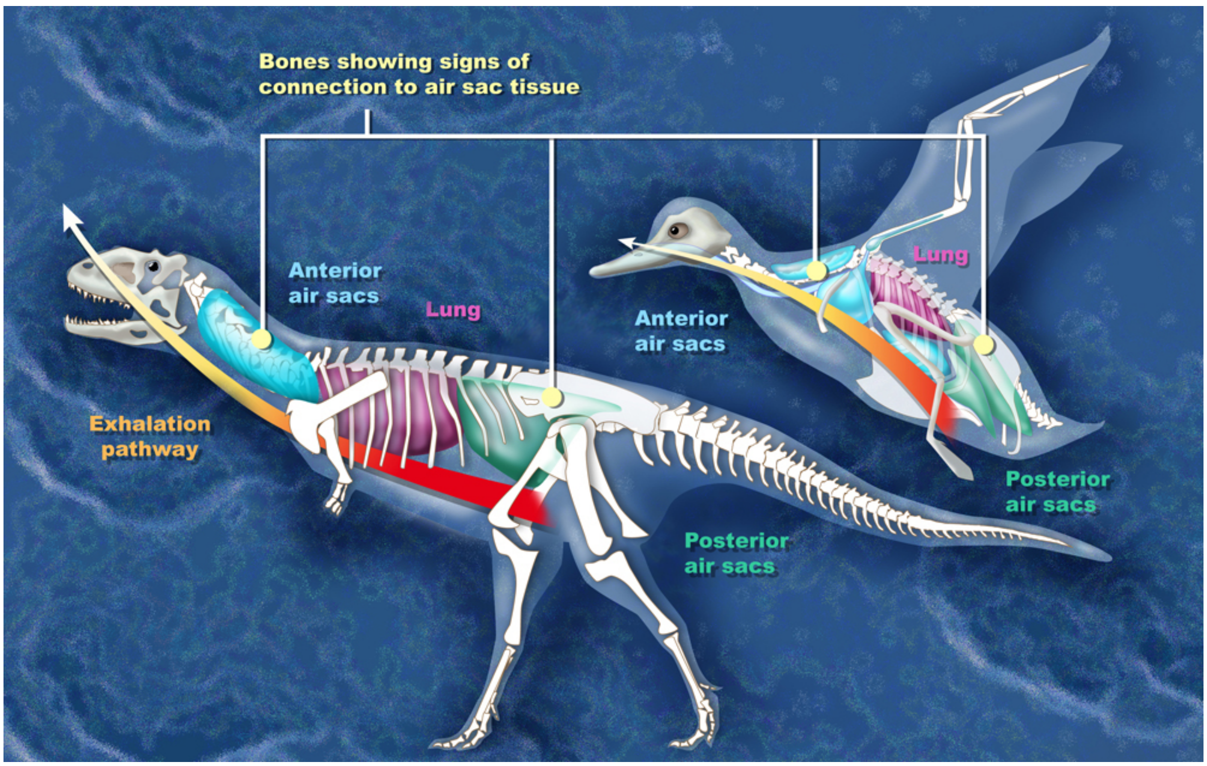

Figure 2. *Dinosaurs, from which birds descended, have similar hollow bones and are believed to have had a similar respiratory system.*

Mammalian Respiration

All mammals have lungs that are the main organs for breathing. Lung capacity has evolved to support the animal's activities. During inhalation, the lungs expand with air, and oxygen diffuses across the lung's surface and enters the bloodstream. During exhalation, the lungs expel air and lung volume decreases.

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Animal Circulatory Systems

Section Goals

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

- Describe a closed circulatory system
- Describe an open circulatory system
- Compare and contrast the organization and evolution of vertebrate circulatory systems

The circulatory system is effectively a network of cylindrical vessels: the arteries, veins, and capillaries that emanate from a pump, the heart. In all vertebrate organisms, as well as some invertebrates, this is a closed-loop system in which the blood is not free in a cavity. Circulatory systems may be open (mixed with the interstitial fluid) or closed (separated from the interstitial fluid).

Closed Circulatory Systems

In a **closed circulatory system**, blood is contained inside blood vessels and circulates **unidirectionally** from the heart around the systemic circulatory route, then returns to the heart again, as illustrated in **Figure 1a**.

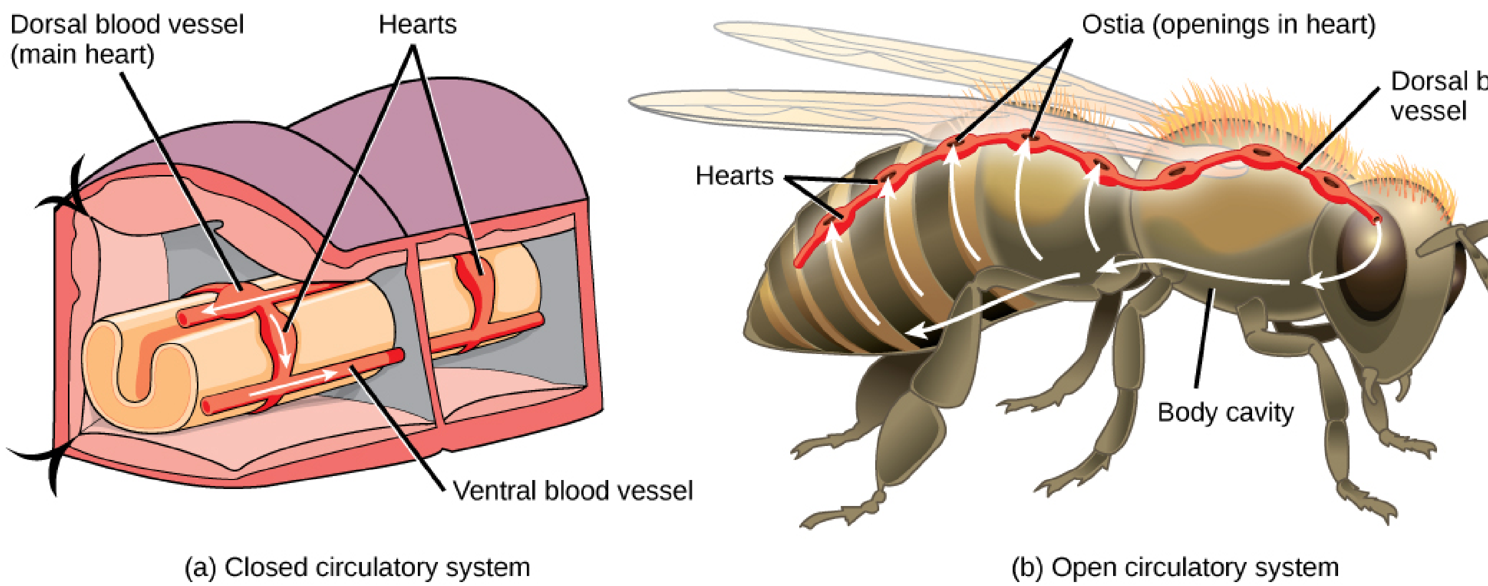

Figure 1. *In (a) closed circulatory systems, the heart pumps blood through vessels that are separate from the interst fluid of the body. Most vertebrates and some invertebrates, like this annelid earthworm, have a closed circulatory sy (b) open circulatory systems, a fluid called hemolymph is pumped through a blood vessel that empties into the body Hemolymph returns to the blood vessel through openings called ostia. Arthropods like this bee and most mollusks ha circulatory systems.*

Open Circulatory Systems

As opposed to a closed system, arthropods—including insects, crustaceans, and most mollusks—have an open circulatory system, as illustrated in **Figure 1b**. In an **open circulatory system**, the blood is not enclosed in the blood vessels but is pumped into a cavity called a **hemocoel** and is called **hemolymph** because the blood mixes with the **interstitial fluid**. As the heart beats and the animal moves, the hemolymph circulates around the organs within the body cavity and then reenters the hearts through openings called **ostia**. This movement allows for gas and nutrient exchange. An open circulatory system does not use as much energy as a closed system to operate or to maintain; however, there is a trade-off with the amount of blood that can be moved to metabolically active organs and tissues that require high levels of oxygen. In fact, one reason that insects with wing spans of up to two feet wide (70 cm) are not around today is probably because they were outcompeted by the arrival of birds 150 million years ago. Birds, having a closed circulatory system, are thought to have moved more agilely, allowing them to get food faster and possibly to prey on the insects.

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Circulatory System Variation in Animals

The circulatory system varies from simple systems in invertebrates to more complex systems in vertebrates. The simplest animals, such as the sponges (Porifera) and rotifers (Rotifera), do not need a circulatory system because diffusion allows adequate exchange of water, nutrients, and waste, as well as dissolved gases, as shown in **Figure 2a**. Organisms that are more complex but still only have two layers of cells in their body plan, such as jellies (Cnidaria) and comb jellies (Ctenophora) also use diffusion through their epidermis and internally through the gastrovascular compartment. Both their internal and external tissues are bathed in an aqueous environment and exchange fluids by diffusion on both sides, as illustrated in **Figure 2b**. Exchange of fluids is assisted by the pulsing of the jellyfish body.

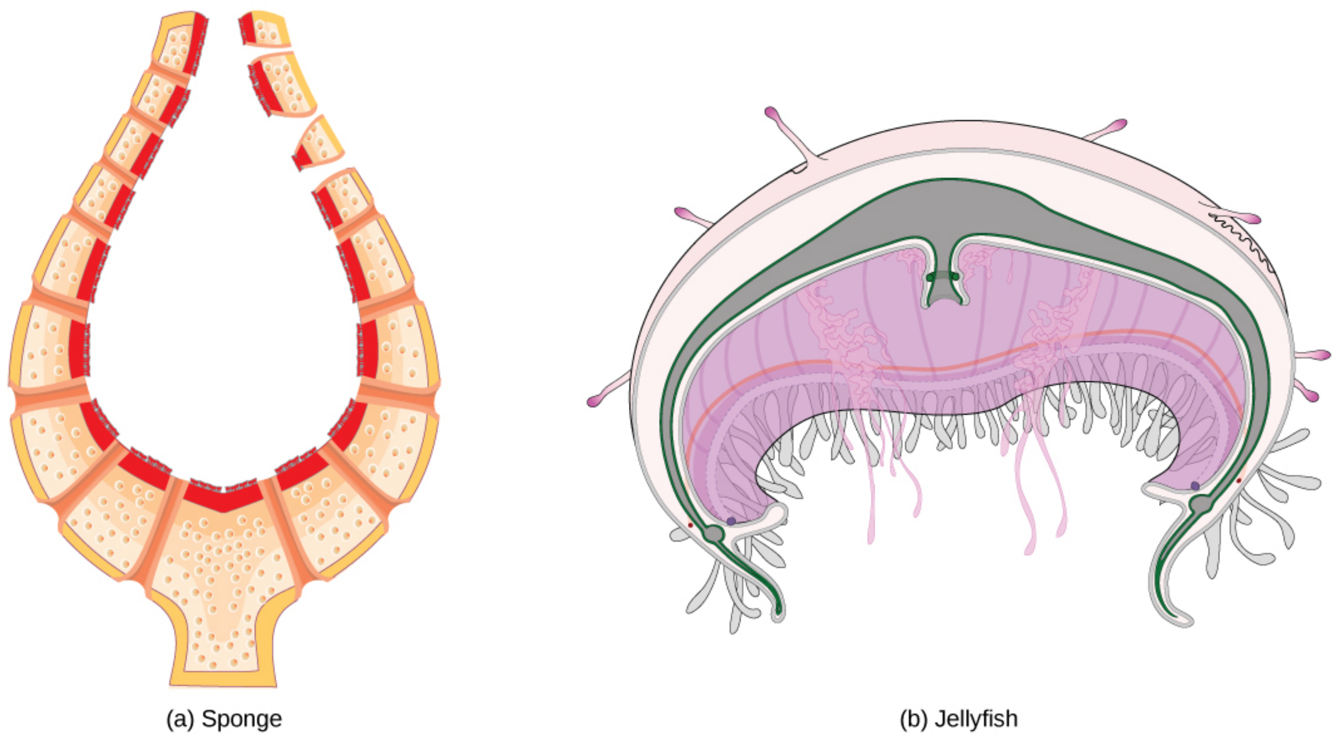

Figure 2. Simple animals consisting of a single cell layer such as the (a) sponge or only a few cell layers such as the (b) jellyfish do not have a circulatory system. Instead, gasses, nutrients, and wastes are exchanged by diffusion.

For more complex organisms, diffusion is not efficient for cycling gasses, nutrients, and waste effectively through the body; therefore, more complex circulatory systems evolved. Most arthropods and many mollusks have open circulatory systems. In an open system, an elongated beating heart pushes the hemolymph through the body and muscle contractions help to move fluids. The larger more complex crustaceans, including lobsters, have developed arterial-like vessels to push blood through their bodies, and the most active mollusks, such as squids, have evolved a closed circulatory system and are able to move rapidly to catch prey. Closed circulatory systems are a characteristic of vertebrates; however, there are significant differences in the structure of the heart and the circulation of blood between the different vertebrate groups due to adaptation during evolution and associated differences in anatomy. **Figures 3 and 4** illustrate the basic circulatory systems of some vertebrates: fish, amphibians, reptiles, and mammals.

Fish

As illustrated in **Figure 3a**, fish have a single circuit for blood flow and a two-chambered heart that has only a single atrium and a single ventricle. The atrium collects blood that has returned from the body and the ventricle pumps the blood to the gills where gas exchange occurs and the blood is reoxygenated; this is called **gill circulation**. The blood then continues through the rest of the body before arriving back at the atrium; this is called **systemic circulation**. This unidirectional flow of blood produces a gradient of oxygenated to deoxygenated blood around the fish's systemic circuit. The result is a limit in the amount of oxygen that can reach some of the organs and tissues of the body, reducing the overall metabolic capacity of fish.

In amphibians, reptiles, birds, and mammals, blood flow is directed in two circuits: one through the lungs and back to the heart, which is called **pulmonary circulation**, and the other throughout the rest of the body and its organs including the brain (systemic circulation). In amphibians, gas exchange also occurs through the skin during pulmonary circulation and is referred to as **pulmocutaneous circulation**.

Amphibians

As shown in **Figure 3b**, amphibians have a three-chambered heart that has two atria and one ventricle rather than the two-chambered heart of fish. The two **atria** (superior heart chambers) receive blood from the two different circuits (the lungs and the systems), and then there is some mixing of the blood in the heart's **ventricle** (inferior heart chamber), which reduces the efficiency of oxygenation. The advantage to this arrangement is that high pressure in the vessels pushes blood to the lungs and body. The mixing is mitigated by a ridge within the ventricle that diverts oxygen-rich blood through the systemic circulatory system and deoxygenated blood to the pulmocutaneous circuit. For this reason, amphibians are often described as having **double circulation**.

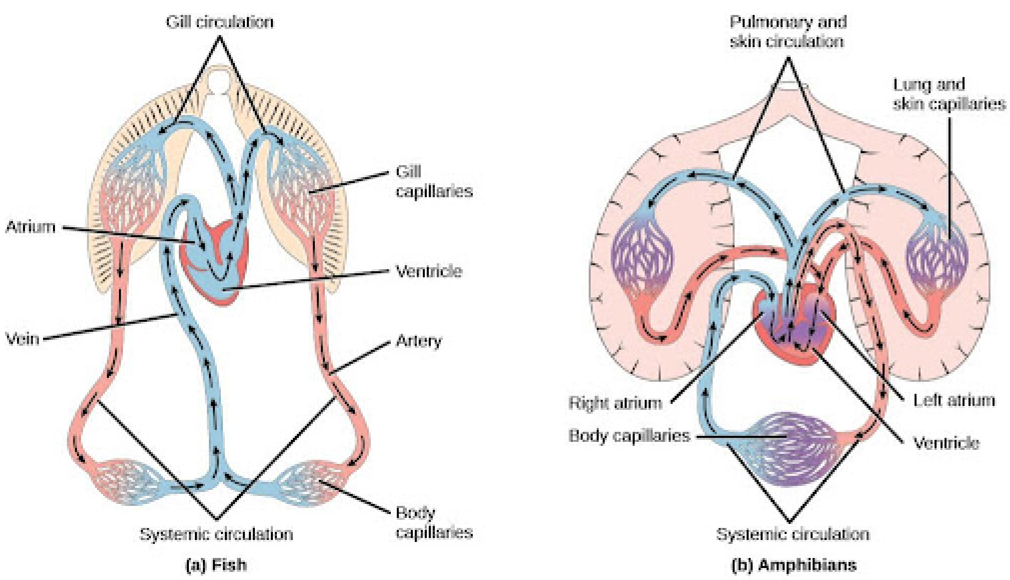

Figure 3. (a) Fish have the simplest circulatory systems of the vertebrates: blood flows unidirectionally from the two-chambered heart through the gills and then the rest of the body. (b) Amphibians have two circulatory routes: one

for oxygenation of the blood through the lungs and skin, and the other to take oxygen to the rest of the body. The blood is pumped from a three-chambered heart with two atria and a single ventricle.

Reptiles

Most reptiles also have a three-chambered heart similar to the amphibian heart that directs blood to the pulmonary and systemic circuits, as shown in **Figure 4a**. The ventricle is divided more effectively by a partial septum, which results in less mixing of oxygenated and deoxygenated blood. Some reptiles (alligators and crocodiles) are the most primitive animals to exhibit a four-chambered heart. Crocodilians have a unique circulatory mechanism where the heart shunts blood from the lungs toward the stomach and other organs during long periods of submergence, for instance, while the animal waits for prey or stays underwater waiting for prey to rot. One adaptation includes two main arteries that leave the same part of the heart: one takes blood to the lungs and the other provides an alternate route to the stomach and other parts of the body. Two other adaptations include a hole in the heart between the two ventricles, called the foramen of Panizza, which allows blood to move from one side of the heart to the other, and specialized connective tissue that slows the blood flow to the lungs. Together these adaptations have made crocodiles and alligators one of the most evolutionarily successful animal groups on earth.

Mammals and Birds

In mammals and birds, the heart is also divided into four chambers: two atria and two ventricles, as illustrated in **Figure 4b**. The oxygenated blood is separated from the deoxygenated blood, which improves the efficiency of double circulation and is probably required for the warm-blooded lifestyle of mammals and birds. The four-chambered heart of birds and mammals evolved independently from a three-chambered heart. The independent evolution of the same or a similar biological trait is referred to as convergent evolution.

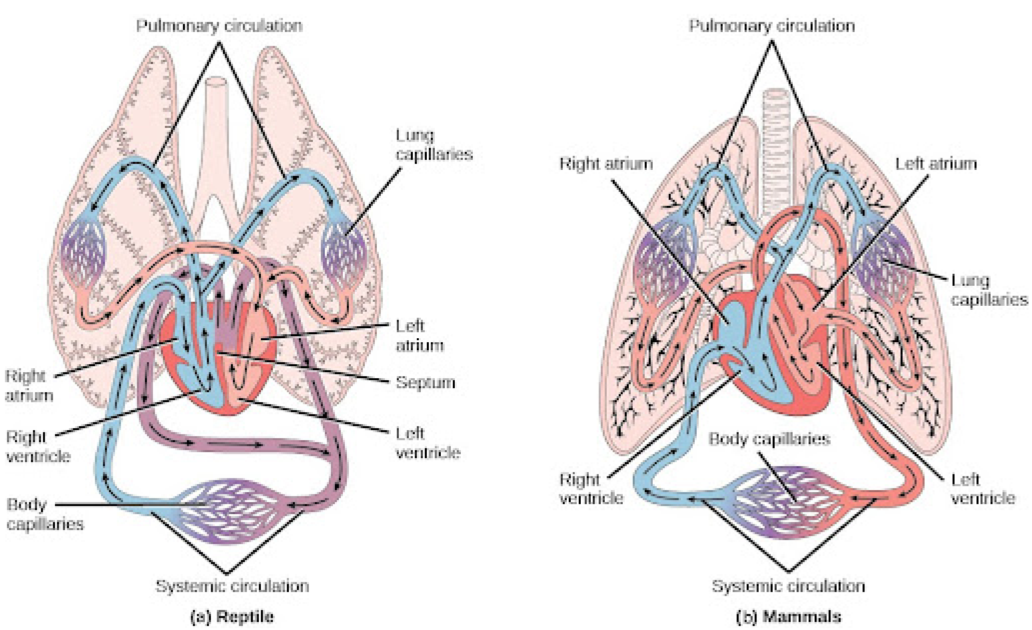

Figure 4. (a) Reptiles also have two circulatory routes; however, blood is only oxygenated through the lungs. The heart is three chambered, but the ventricles are partially separated so some mixing of oxygenated and deoxygenated blood occurs except in crocodilians and birds. (b) Mammals and birds have the most efficient heart with four chambers that completely separate the oxygenated and deoxygenated blood; it pumps only oxygenated blood through the body and deoxygenated blood to the lungs.

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The Mammalian Heart

Section Goals

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

- Describe the structure of the heart and explain how cardiac muscle is different from other muscles

The heart is a complex muscle that pumps blood through the three divisions of the circulatory system: the coronary (vessels that serve the heart), pulmonary (heart and lungs), and systemic (systems of the body), as shown in **Figure 1**. Coronary circulation intrinsic to the heart takes blood directly from the main artery (aorta) coming from the heart. For pulmonary and systemic circulation, the heart has to pump blood to the lungs or the rest of the body, respectively. In vertebrates, the lungs are relatively close to the heart in the thoracic cavity. The shorter distance to pump means that the muscle wall on the right side of the heart is not as thick as the left side which must have enough pressure to pump blood all the way to your big toe.

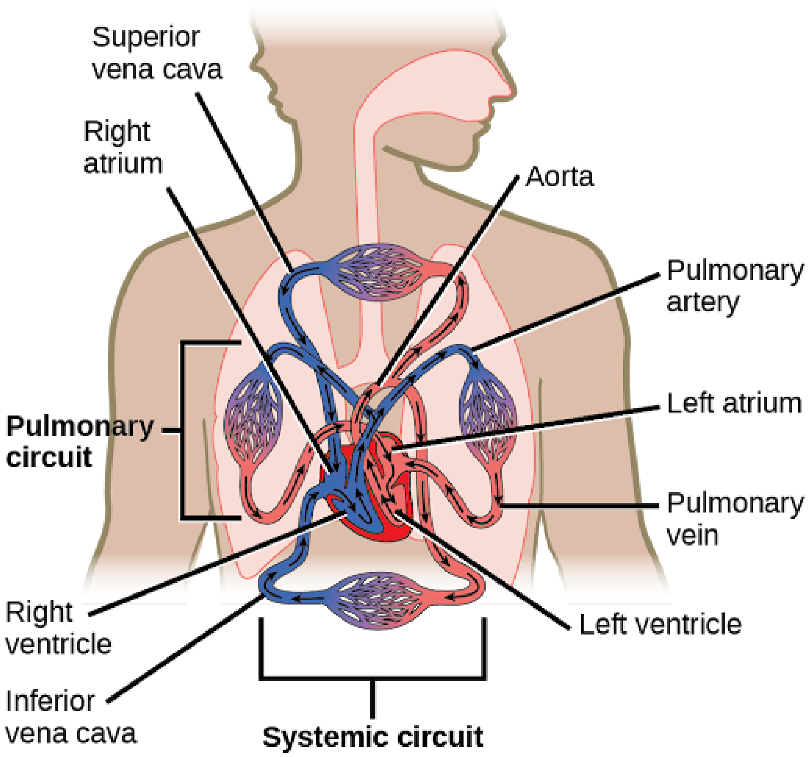

Figure 1. *The mammalian circulatory system is divided into three circuits: the systemic circuit, the pulmonary circuit, and the coronary circuit. Blood is pumped from veins of the systemic circuit into the right atrium of the heart, then into the right ventricle. Blood then enters the pulmonary circuit, and is oxygenated by the lungs. From the pulmonary circuit, blood re-enters the heart through the left atrium. From the left ventricle, blood re-enters the systemic circuit through the aorta and is distributed to the rest of the body. The coronary circuit, which provides blood to the heart, is not shown.*

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Structure of the Heart

The heart muscle is asymmetrical as a result of the distance blood must travel in the pulmonary and systemic circuits. Since the right side of the heart sends blood to the pulmonary circuit, it is smaller than the left side, which must send blood out to the whole body in the systemic circuit, as shown in **Figure 2**. In humans, the heart is about the size of a clenched fist; it is divided into four chambers: two atria and two ventricles. There is one atrium and one ventricle on the right side and one atrium and one ventricle on the left side. The atria are the chambers that receive blood, and the ventricles are the chambers that pump blood. The right atrium receives deoxygenated blood from the **superior vena cava**, which drains blood from the jugular vein that comes from the brain and from the veins that come from the arms, as well as from the **inferior vena cava** which drains blood from the veins that come from the lower organs and the legs. In addition, the right atrium receives blood from the coronary sinus which drains deoxygenated blood from the heart itself. This deoxygenated blood then passes to the right ventricle through the **atrioventricular valve** or the **tricuspid valve**, a flap of connective tissue that opens in only one direction to prevent the backflow of blood. The valve separating the chambers on the left side of the heart valve is called the bicuspid or mitral valve. After it is filled, the right ventricle pumps the blood through the pulmonary arteries, bypassing the **semilunar valve** (or pulmonic valve) to the lungs for re-oxygenation. After blood passes through the pulmonary arteries, the right semilunar valves close, preventing the blood from flowing backward into the right ventricle. The left atrium then receives the oxygen-rich blood from the lungs via the pulmonary veins. This blood passes through the **bicuspid valve** or mitral valve (the atrioventricular valve on the left side of the heart) to the left ventricle where the blood is pumped out through the **aorta**, the major artery of the body, taking oxygenated blood to the organs and muscles of the body. Once blood is pumped out of the left ventricle and into the aorta, the aortic semilunar valve (or aortic valve) closes, preventing blood from flowing backward into the left ventricle, this overall pattern of pumping is referred to as double circulation and is found in all mammals.

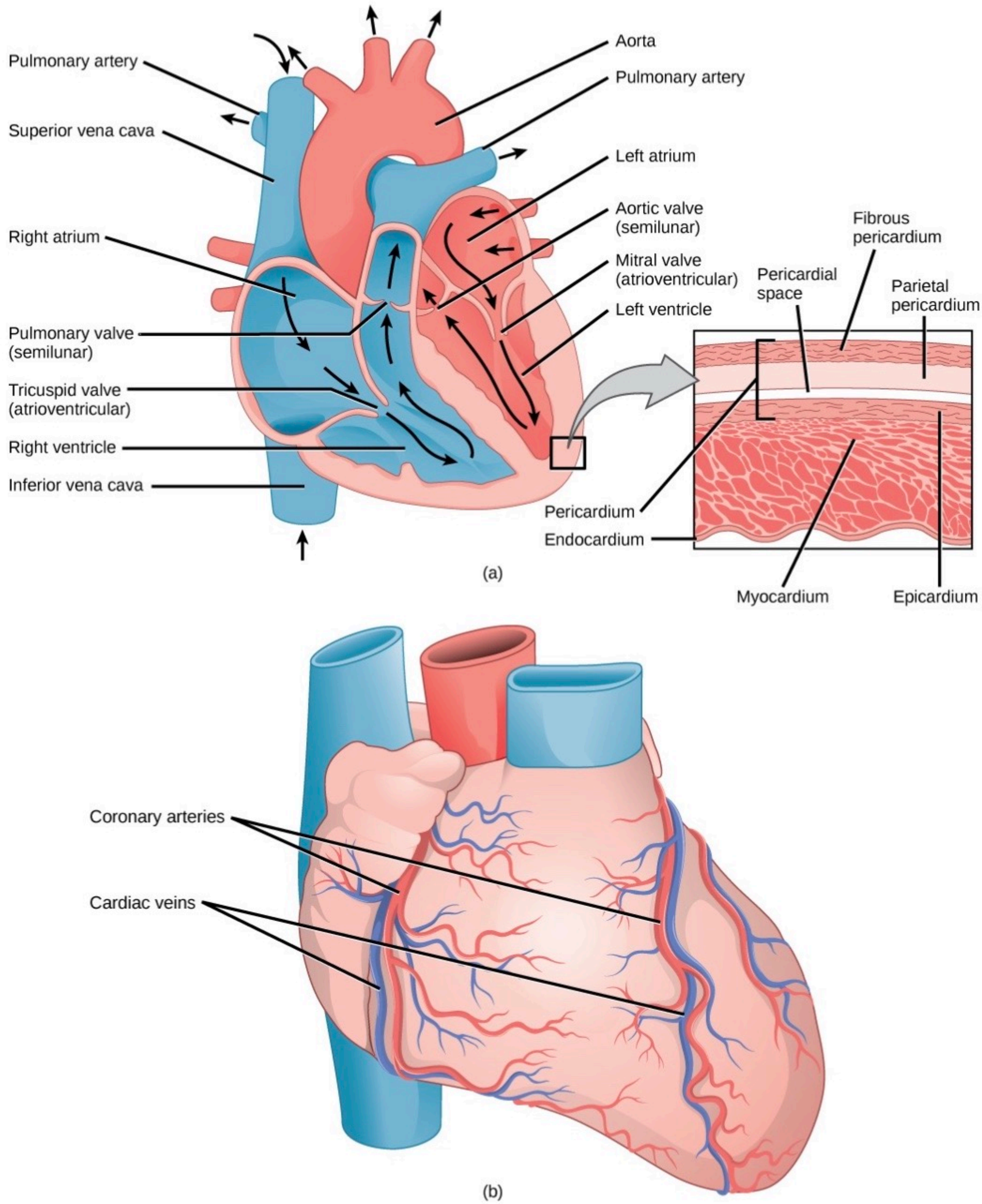

Figure 2. *(a) The heart is primarily made of a thick muscle layer, called the myocardium, surrounded by membranes. One-way valves separate the four chambers. (b) Blood vessels of the coronary system, including*

the coronary arteries and veins, keep the heart musculature oxygenated.

The heart is composed of three layers; the epicardium, the myocardium, and the endocardium, illustrated in **Figure 2**. The inner wall of the heart has a lining called the **endocardium**. The **myocardium** consists of the heart muscle cells that make up the middle layer and the bulk of the heart wall. The outer layer of cells is called the **epicardium**, of which the second layer is a membranous layered structure called the **pericardium** that surrounds and protects the heart; it allows enough room for vigorous pumping but also keeps the heart in place to reduce friction between the heart and other structures.

The heart has its own blood vessels that supply the heart muscle with blood. The **coronary arteries** branch from the aorta and surround the outer surface of the heart like a crown. They diverge into capillaries, where the heart muscle is supplied with oxygen before converging again into the **coronary veins** to take the deoxygenated blood back to the right atrium, where the blood will be re-oxygenated through the pulmonary circuit.

To learn more about what the heart looks like, how blood flows through the heart, and how the heart beats, visit the site How the Heart Works from the National Heart, Lung and Blood Institute.

The heart muscle will die without a steady supply of blood. **Atherosclerosis** is the blockage of an artery by the buildup of fatty plaques. Because of the size (narrow) of the coronary arteries and their function in serving the heart itself, atherosclerosis can be deadly in these arteries. The slowdown of blood flow and subsequent oxygen deprivation that results from atherosclerosis causes severe pain, known as **angina**, and complete blockage of the arteries will cause **myocardial infarction**: the death of cardiac muscle tissue, commonly known as a heart attack.

Scientist Spotlight

Marie M. Daly was the first black woman to receive a Ph.D. in Chemistry. She conducted groundbreaking research that associated cholesterol, high blood pressure, and the causes of atherosclerosis, which led to a deeper understanding of ways to prevent heart attack and treat heart disease. She has been honored by the American Chemical Society (ACS) on their National Historic Chemical Landmarks site dedicated to chemists and chemistry that has transformed our lives. You can also read more about her life and work from the Science History Institute's Scientific Biographies pages!

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Animal Digestive Systems

Section Goals

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

- Compare and contrast different types of digestive systems in animals
- Explain the specialized functions of the organs involved in processing food in the vertebrate body

Animals obtain their nutrition from the consumption of other organisms. Depending on their diet, animals can be classified into the following categories: plant eaters (herbivores), meat eaters (carnivores), and those that eat both plants and animals (omnivores). The nutrients and macromolecules present in food are not immediately accessible to the cells. There are a number of processes that modify food within the animal body in order to make the nutrients and organic molecules accessible for cellular function. As animals evolved in complexity of form and function, their digestive systems have also evolved to accommodate their various dietary needs.

Invertebrate Digestive Systems

Animals have evolved different types of digestive systems to aid in the digestion of the different foods they consume. The simplest example is that of a **gastrovascular cavity,** found in organisms with only one opening for digestion. Platyhelminthes (flatworms), Ctenophora (comb jellies), and Cnidaria (coral, jellyfish, and sea anemones) use this type of digestion. Gastrovascular cavities, as shown in **Figure 1a**, are typically a blind tube or cavity with only one opening, the "mouth," which also serves as an "anus." Ingested material enters the mouth and passes through a hollow, tubular cavity. Cells within the cavity secrete digestive enzymes that break down the food. The food particles are engulfed by the cells lining the gastrovascular cavity.

The **alimentary canal**, shown in **Figure 1b**, is a more advanced system: it consists of one tube with a mouth at one end and an anus at the other. Earthworms are an example of an animal with an alimentary canal. Once the food is ingested through the mouth, it passes through the esophagus and is stored in an organ called the crop; then, it passes into the gizzard where it is churned and digested. From the gizzard, the food passes through the intestine, the nutrients are absorbed, and the waste is eliminated as feces, called castings, through the anus.

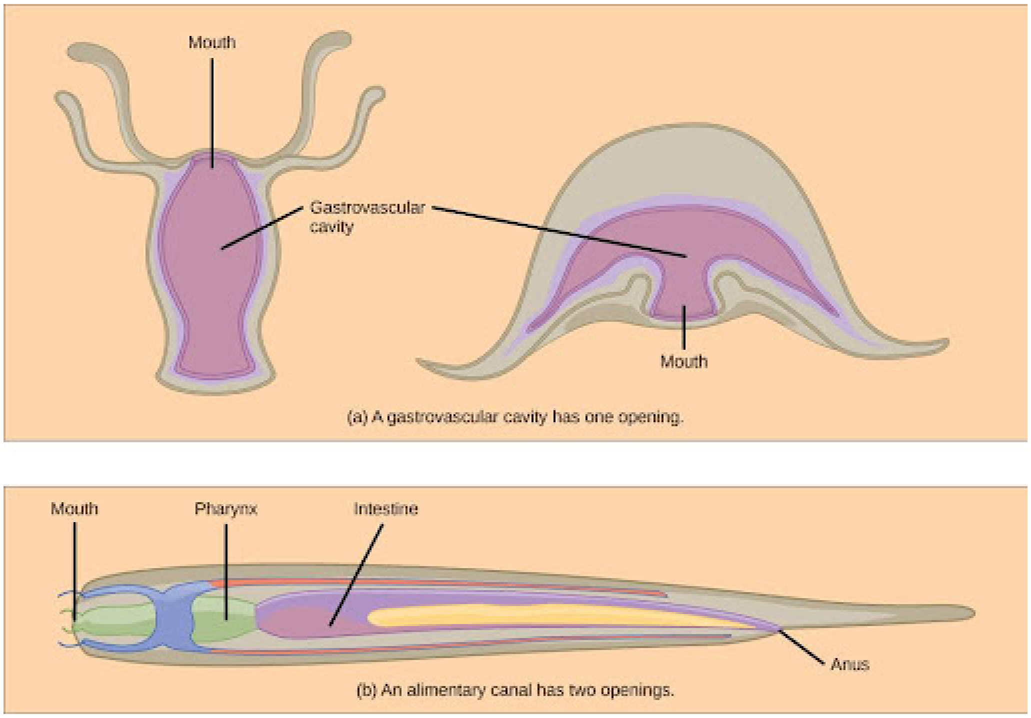

Figure 1. *(a) A gastrovascular cavity has a single opening through which food is ingested and waste is excreted, as shown in this hydra and in this jellyfish medusa. (b) An alimentary canal has two openings: a mouth for ingesting food, and an anus for eliminating waste, as shown in this nematode.*

Vertebrate Digestive Systems

Vertebrates have evolved more complex digestive systems to adapt to their dietary needs. Some animals have a single stomach, while others have multi-chambered stomachs. Birds have developed a digestive system adapted to eating unmasticated (not chewed up) food.

Monogastric: Single-chambered Stomach

As the word **monogastric** suggests, this type of digestive system consists of one ("mono") stomach chamber ("gastric"). Humans and many animals have a monogastric digestive system as illustrated in **Figure 2a and 2b**. The process of digestion begins with the mouth and the intake of food. The teeth play an important role in masticating (chewing) or physically breaking down food into smaller particles. The enzymes present in saliva also begin to chemically break down food. The esophagus is a long tube that connects the mouth to the stomach. Using peristalsis, or wave-like smooth muscle contractions, the muscles of the esophagus push the food towards the stomach. In order to speed up the actions of enzymes in the stomach, the stomach is an extremely acidic environment, with a pH between 1.5 and 2.5. The gastric juices, which include enzymes in the stomach, act on the food particles and continue the process of digestion. Further breakdown of food takes place in the small intestine where enzymes produced by the liver, the small intestine, and the pancreas continue the process of digestion. The nutrients are absorbed into the bloodstream across the epithelial cells lining the walls of the small intestines. The waste material travels on to the large intestine where water is absorbed and the drier waste material is compacted into feces; it is stored until it is excreted through the rectum.

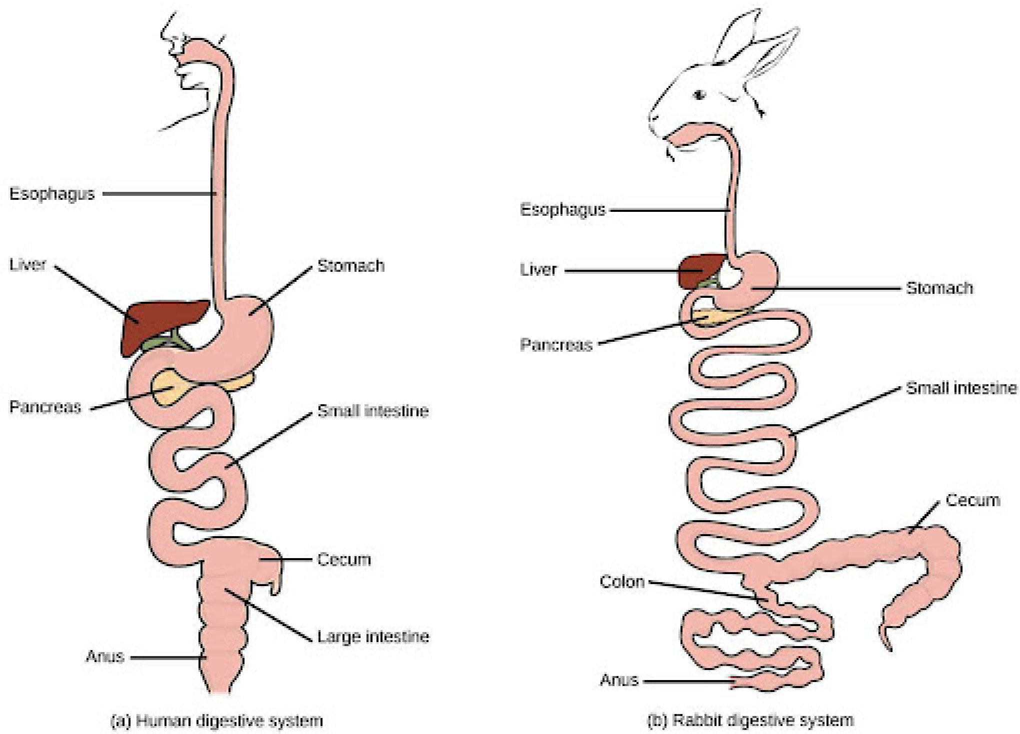

Figure 2. *(a) Humans and herbivores, such as the (b) rabbit, have a monogastric digestive system. However, in the rabbit the small intestine and cecum are enlarged to allow more time to digest plant material. The enlarged organ provides more surface area for absorption of nutrients. Rabbits digest their food twice: the first time food passes through the digestive system, it collects in the cecum, and then it passes as soft feces called cecotrophes. The rabbit re-ingests these cecotrophes to further digest them.*

Avian

Birds face special challenges when it comes to obtaining nutrition from food. They do not have teeth and, so their digestive system, shown in **Figure 3**, must be able to process un-masticated food. Birds have evolved a variety of beak types that reflect the vast variety in their diet, ranging from seeds and insects to fruits and nuts. Because most birds fly, their metabolic rates are high in order to efficiently process food and keep their body weight low. The stomach of birds has two chambers: the **proventriculus**, where gastric juices are produced to digest the food before it enters the stomach, and the **gizzard**, where the food is stored, soaked, and mechanically ground. The undigested material forms food pellets that are sometimes regurgitated. Most of the chemical digestion and absorption happens in the intestine and the waste is excreted through the cloaca.

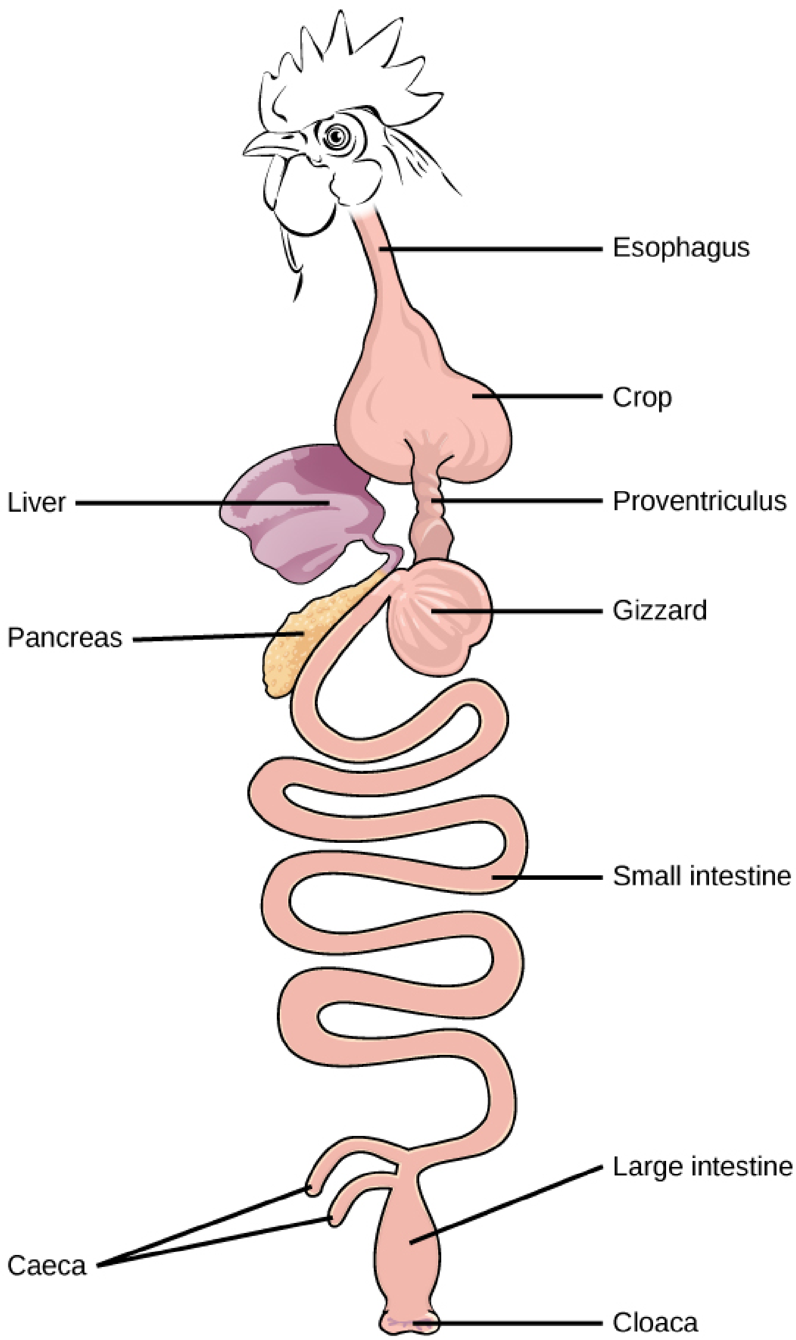

Figure 3. *The avian esophagus has a pouch, called a crop, which stores food.*

In the avian digestive system, food passes from the crop to the first of two stomachs, called the proventriculus, which contains digestive juices that break down food. From the proventriculus, the food enters the second stomach, called the gizzard, which grinds food. Some birds swallow stones or grit, which are stored in the gizzard, to aid the grinding process. Birds do not have separate openings to excrete urine and feces. Instead, uric acid from the kidneys is secreted into the large intestine and combined with waste from the digestive process. This waste is excreted through an opening called the cloaca.

Avian Digestive Adaptations

Birds have a highly efficient, simplified digestive system. Recent fossil evidence has shown that the evolutionary divergence of birds from other land animals was characterized by streamlining and simplifying the digestive system. Unlike many other animals, birds do not have teeth to chew their food. In place of lips, they have sharp pointy beaks. The horny beak, lack of jaws, and the smaller tongue of the birds can be traced back to their dinosaur ancestors. The emergence of these changes seems to coincide with the inclusion of seeds in the bird diet. Seed-eating birds have beaks that are shaped for grabbing seeds, and the two-compartment stomach allows for delegation of tasks. Since birds need to remain light in order to fly, their metabolic rates are very high, which means they digest their food very quickly and need to eat often. Contrast this with the ruminants, where the digestion of plant matter takes a very long time.

Ruminants

Ruminants are mainly herbivores like cows, sheep, and goats, whose entire diet consists of eating large amounts of **roughage** or fiber. They have evolved digestive systems that help them digest vast amounts of cellulose. An interesting feature of the ruminants' mouth is that they do not have upper incisor teeth. They use their lower teeth, tongue, and lips to tear and chew their food. From the mouth, the food travels to the esophagus and on to the stomach.

To help digest the large amount of plant material, the stomach of the ruminants is a multi-chambered organ, as illustrated in **Figure 4**. The four compartments of the stomach are called the rumen, reticulum, omasum, and abomasum. These chambers contain many microbes that break down cellulose and ferment ingested food. The abomasum is the "true" stomach and is the equivalent of the monogastric stomach chamber where gastric juices are secreted. The four-compartment gastric chamber provides larger space and the microbial support necessary to digest plant material in ruminants. The fermentation process produces large amounts of gas in the stomach chamber, which must be eliminated. As in other animals, the small intestine plays an important role in nutrient absorption, and the large intestine helps in the elimination of waste.

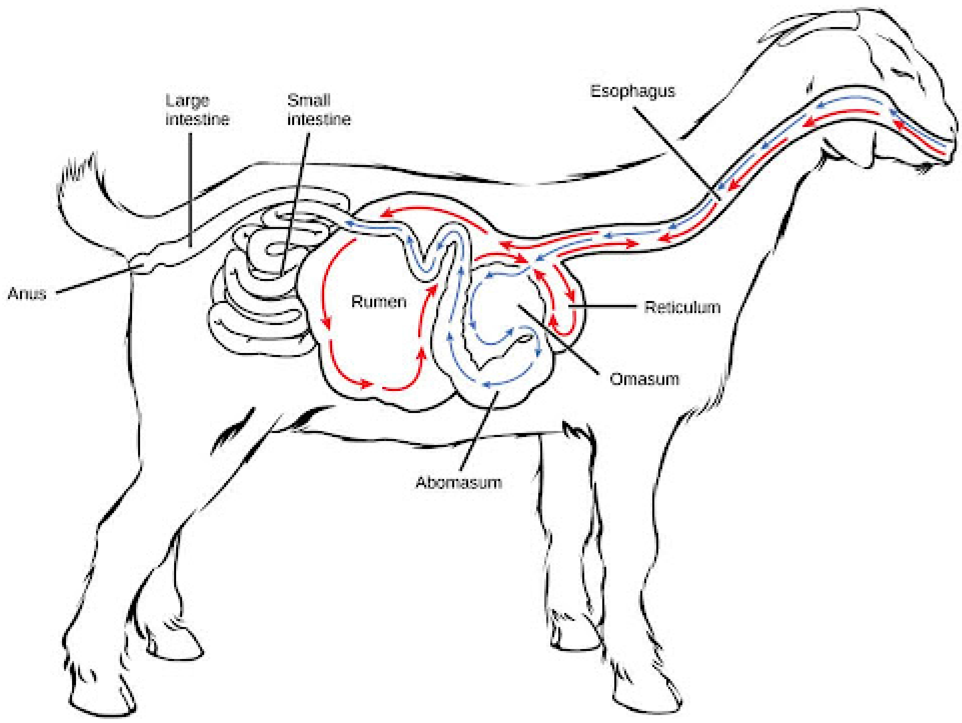

Figure 4. *Ruminant animals, such as goats and cows, have four stomachs. The first two stomachs, the rumen and the reticulum, contain prokaryotes and protists that are able to digest cellulose fiber. The ruminant regurgitates cud from the reticulum, chews it, and swallows it into a third stomach, the omasum, which removes water. The cud then passes onto the fourth stomach, the abomasum, where it is digested by enzymes produced by the ruminant.*

Pseudo-ruminants

Some animals, such as camels and alpacas, are pseudo-ruminants. They eat a lot of plant material and roughage. Digesting plant material is not easy because plant cell walls contain the polymeric sugar molecule cellulose. The digestive enzymes of these animals cannot break down cellulose, but microorganisms present in the digestive system can. Therefore, the digestive system must be able to handle large amounts of roughage and break down the cellulose. Pseudo-ruminants have a three-chamber stomach in the digestive system. However, their cecum—a pouched organ at the beginning of the large intestine containing many microorganisms that are necessary for the digestion of plant materials—is large and is the site where the roughage is fermented and digested. These animals do not have a rumen but have an omasum, abomasum, and reticulum.

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Parts of the Digestive System

The vertebrate digestive system is designed to facilitate the transformation of food matter into the nutrient components that sustain organisms.

Oral Cavity

The oral cavity, or mouth, is the point of entry of food into the digestive system, illustrated in **Figure 5**. The food consumed is broken into smaller particles by mastication, the chewing action of the teeth. All mammals have teeth and can chew their food.

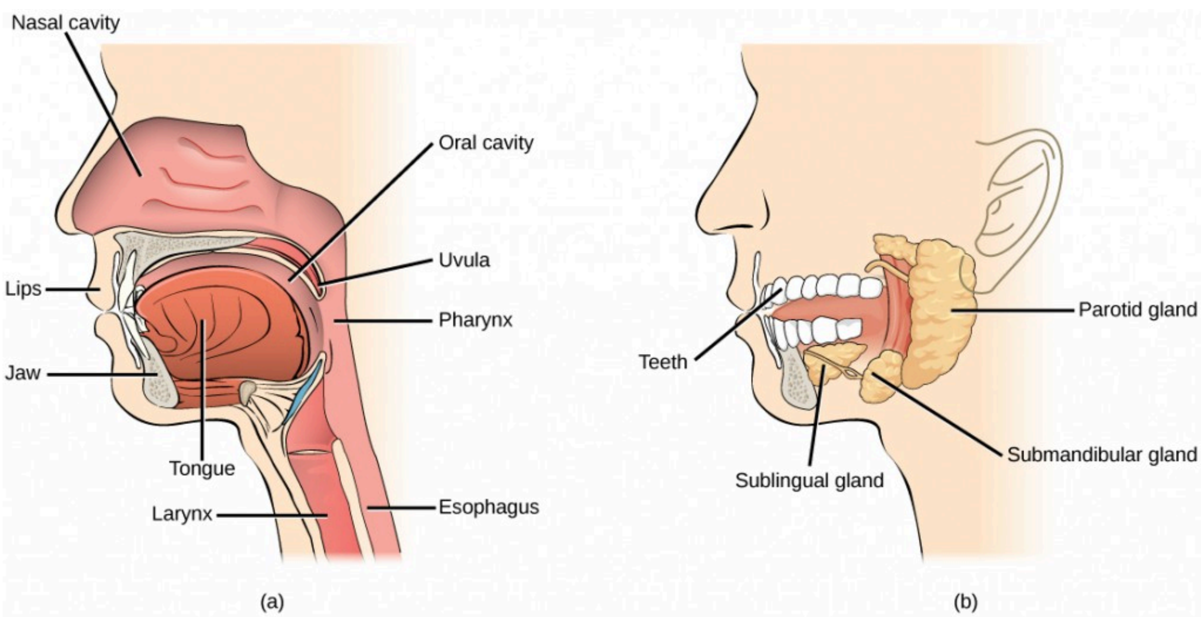

Figure 5. *Digestion of food begins in the (a) oral cavity. Food is masticated by teeth and moistened by saliva secreted from the (b) salivary glands. Enzymes in the saliva begin to digest starches and fats. With the help of the tongue, the resulting bolus is moved into the esophagus by swallowing. (credit: modification of work by the National Cancer Institute)*

The extensive chemical process of digestion begins in the mouth. As food is being chewed, saliva, produced by the salivary glands, mixes with the food. Saliva is a watery substance produced in the mouths of many animals. There are three major glands that secrete saliva—the parotid, the submandibular, and the sublingual. Saliva contains mucus that moistens food and buffers the pH of the food. Saliva also contains immunoglobulins and lysozymes, which have antibacterial action to reduce tooth decay by inhibiting growth of some bacteria.

Saliva also contains an enzyme called **salivary amylase** that begins the process of converting starches in the food into a disaccharide called maltose. Another enzyme called **lipase** is produced by the cells in the tongue. Lipases are a class of enzymes that can break down triglycerides. The lingual lipase begins the breakdown of fat components in the food.

The chewing and wetting action provided by the teeth and saliva prepare the food into a mass called the

bolus for swallowing. The tongue helps in swallowing—moving the bolus from the mouth into the pharynx. The pharynx opens to two passageways: the trachea, which leads to the lungs, and the esophagus, which leads to the stomach. The trachea has an opening called the glottis, which is covered by a cartilaginous flap called the epiglottis. When swallowing, the epiglottis closes the glottis and food passes into the esophagus and not the trachea. This arrangement allows food to be kept out of the trachea.

Esophagus

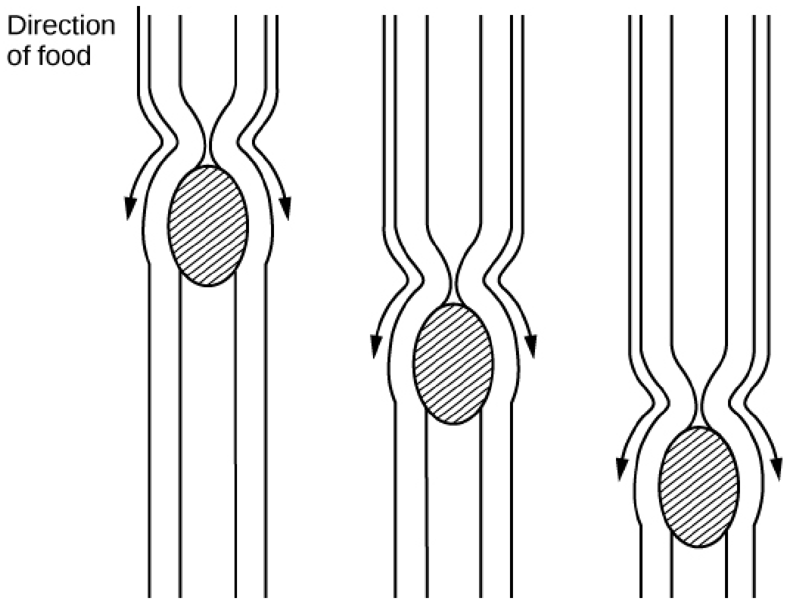

Figure 6. *The esophagus transfers food from the mouth to the stomach through peristaltic movements.*

The **esophagus** is a tubular organ that connects the mouth to the stomach. The chewed and softened food passes through the esophagus after being swallowed. The smooth muscles of the esophagus undergo a series of wave-like movements called **peristalsis** that push the food toward the stomach, as illustrated in **Figure 6**. The peristalsis wave is unidirectional—it moves food from the mouth to the stomach, and reverse movement is not possible. The peristaltic movement of the esophagus is an involuntary reflex; it takes place in response to the act of swallowing.

A ring-like muscle called a **sphincter** forms valves in the digestive system. The gastro-esophageal sphincter is located at the stomach end of the esophagus. In response to swallowing and the pressure exerted by the bolus of food, this sphincter opens, and the bolus enters the stomach. When there is no swallowing action, this sphincter is shut and prevents the contents of the stomach from traveling up the esophagus. Many animals have a true sphincter; however, in humans, there is no true sphincter, but the esophagus remains closed when there is no swallowing action. Acid reflux or "heartburn" occurs when the acidic digestive juices escape into the esophagus.

Stomach

A large part of digestion occurs in the stomach, shown in **Figure 7**. The **stomach** is a saclike organ that secretes gastric digestive juices. The pH in the stomach is between 1.5 and 2.5. This highly acidic environment is required for the chemical breakdown of food and the extraction of nutrients. When empty, the stomach is a rather small organ; however, it can expand to up to 20 times its resting size when filled with food. This characteristic is particularly useful for animals that need to eat when food is available.

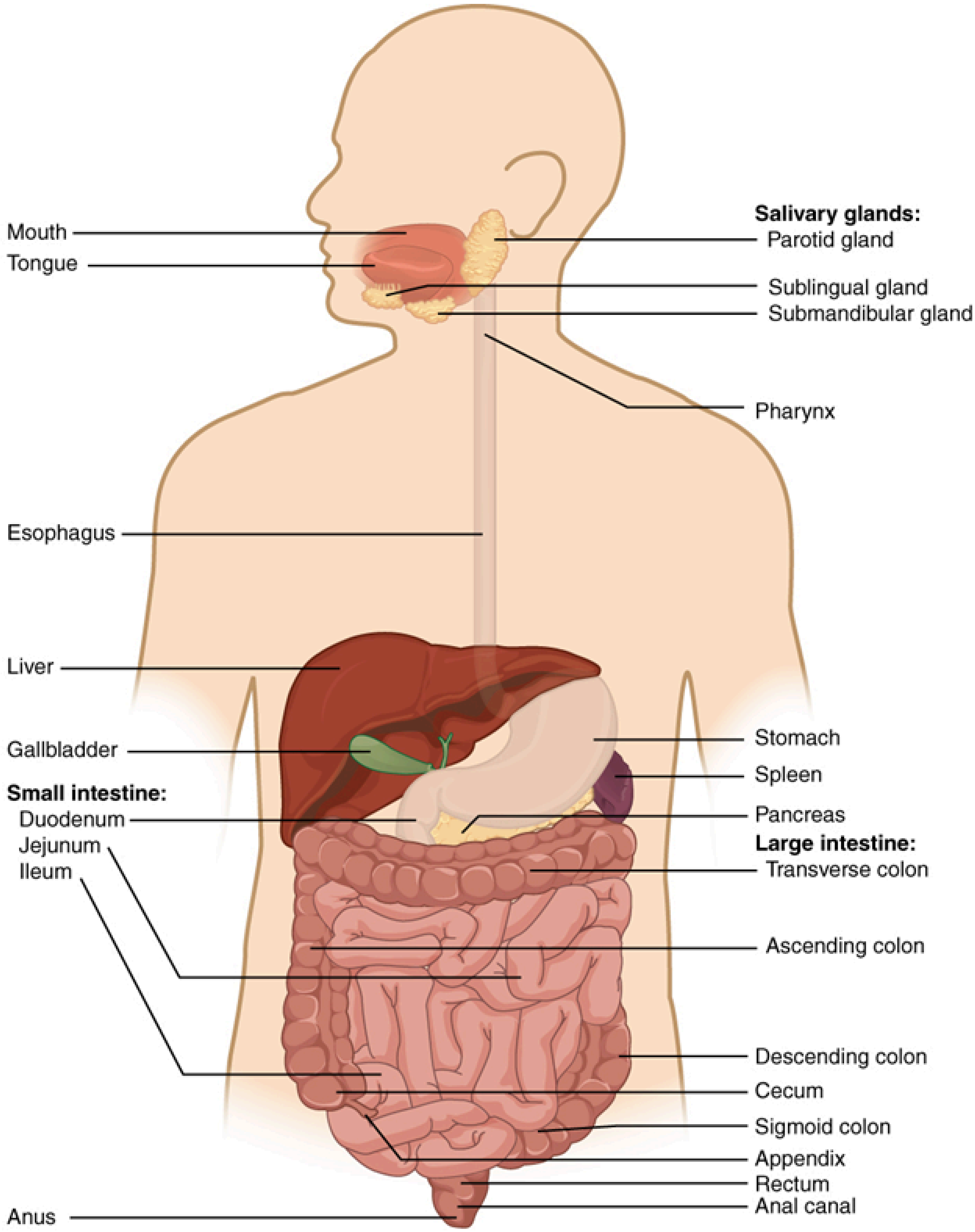

Figure 7. *The human stomach has an extremely acidic environment where most of the protein gets digested. (credit: modification of work by Mariana Ruiz Villareal)*

The stomach is also the major site for protein digestion in animals other than ruminants. Protein digestion is mediated by an enzyme called pepsin in the stomach chamber. **Pepsin** is secreted by the chief cells in the stomach in an inactive form called **pepsinogen**. Pepsin breaks peptide bonds and cleaves proteins into smaller polypeptides; it also helps activate more pepsinogen, starting a positive feedback mechanism that generates more pepsin. Another cell type—parietal cells—secrete hydrogen and chloride ions, which combine in the lumen to form hydrochloric acid, the primary acidic component of the stomach juices. Hydrochloric acid helps to convert the inactive pepsinogen to pepsin. The highly acidic environment also kills many microorganisms in the food and, combined with the action of the enzyme pepsin, results in the hydrolysis of protein in the food. Chemical digestion is facilitated by the churning action of the stomach. Contraction and relaxation of smooth muscles mixes the stomach contents about every 20 minutes. The partially digested food and gastric juice mixture is called **chyme**. Chyme passes from the stomach to the small intestine. Further protein digestion takes place in the small intestine. Gastric emptying occurs within two to six hours after a meal. Only a small amount of chyme is released into the small intestine at a time. The movement of chyme from the stomach into the small intestine is regulated by the pyloric sphincter.

When digesting protein and some fats, the stomach lining must be protected from getting digested by pepsin. There are two points to consider when describing how the stomach lining is protected. First, as previously mentioned, the enzyme pepsin is synthesized in the inactive form. This protects the chief cells, because pepsinogen does not have the same enzyme functionality of pepsin. Second, the stomach has a thick mucus lining that protects the underlying tissue from the action of the digestive juices. When this mucus lining is ruptured, ulcers can form in the stomach. Ulcers are open wounds in or on an organ caused by bacteria (*Helicobacter pylori*) when the mucus lining is ruptured and fails to reform.

Small Intestine

Chyme moves from the stomach to the small intestine. The **small intestine** is the organ where the digestion of protein, fats, and carbohydrates is completed. The small intestine is a long tube-like organ with a highly folded surface containing finger-like projections called the **villi**. The apical surface of each villus has many microscopic projections called microvilli. These structures, illustrated in **Figure 8**, are lined with epithelial cells on the luminal side and allow for the nutrients to be absorbed from the digested food and absorbed into the bloodstream on the other side. The villi and microvilli, with their many folds, increase the surface area of the intestine and increase absorption efficiency of the nutrients. Absorbed nutrients in the blood are carried into the hepatic portal vein, which leads to the liver. There, the liver regulates the distribution of nutrients to the rest of the body and removes toxic substances, including drugs, alcohol, and some pathogens.

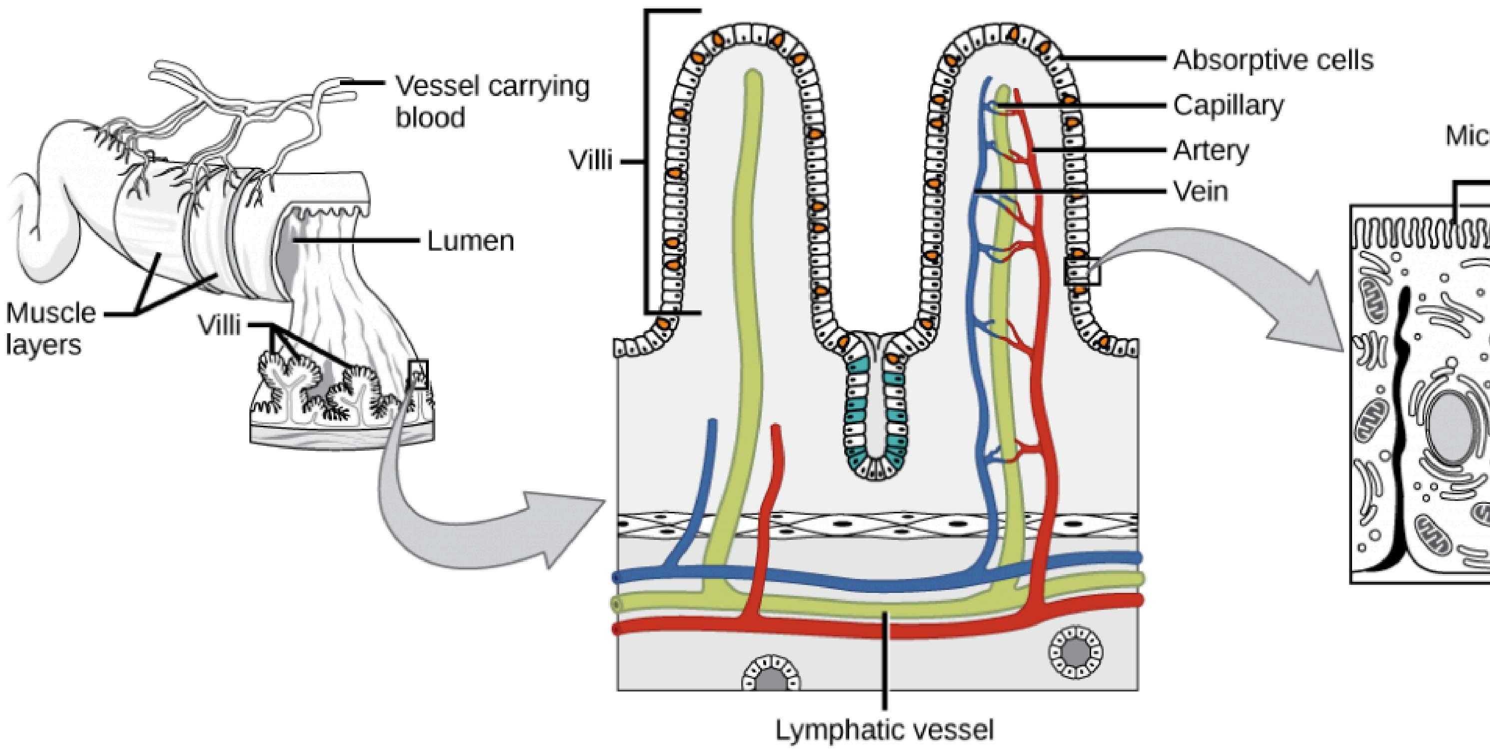

Figure 8. *Villi are folds on the small intestine lining that increase the surface area to facilitate the absorption of nut*

The human small intestine is over 6m long and is divided into three parts: the duodenum, the jejunum, and the ileum. The "C-shaped," fixed part of the small intestine is called the **duodenum** and is shown in **Figure 8**. The duodenum is separated from the stomach by the pyloric sphincter which opens to allow chyme to move from the stomach to the duodenum. In the duodenum, chyme is mixed with pancreatic juices in an alkaline solution rich in bicarbonate that neutralizes the acidity of chyme and acts as a buffer. Pancreatic juices also contain several digestive enzymes. Digestive juices from the pancreas, liver, and gallbladder, as well as from gland cells of the intestinal wall itself, enter the duodenum. **Bile** is produced in the liver and stored and concentrated in the gallbladder. Bile contains bile salts which emulsify lipids while the pancreas produces enzymes that catabolize starches, disaccharides, proteins, and fats. These digestive juices break down the food particles in the chyme into glucose, triglycerides, and amino acids. Some chemical digestion of food takes place in the duodenum. Absorption of fatty acids also takes place in the duodenum.

The second part of the small intestine is called the **jejunum**, shown in **Figure 8**. Here, hydrolysis of nutrients is continued while most of the carbohydrates and amino acids are absorbed through the intestinal lining. The bulk of chemical digestion and nutrient absorption occurs in the jejunum.

The **ileum**, also illustrated in **Figure 8** is the last part of the small intestine and here the bile salts and vitamins are absorbed into blood stream. The undigested food is sent to the colon from the ileum via peristaltic movements of the muscle. The ileum ends and the large intestine begins at the ileocecal valve. The vermiform, "worm-like," appendix is located at the ileocecal valve. The appendix of humans secretes no enzymes and has an insignificant role in immunity.

Large Intestine

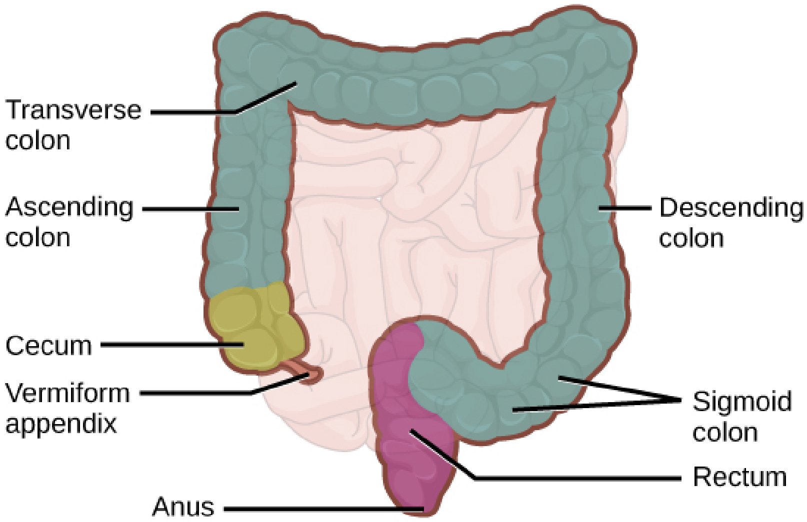

Figure 9. *The large intestine reabsorbs water from undigested food and stores waste material until it is eliminated.*

The **large intestine**, illustrated in **Figure 9**, reabsorbs the water from the undigested food material and processes the waste material. The human large intestine is much smaller in length compared to the small intestine but larger in diameter. It has three parts: the cecum, the colon, and the rectum. The cecum joins the ileum to the colon and is the receiving pouch for the waste matter. The colon is home to many bacteria or "intestinal flora" that aid in the digestive processes. The colon can be divided into four regions, the ascending colon, the transverse colon, the descending colon and the sigmoid colon. The main functions of the colon are to extract the water and mineral salts from undigested food, and to store waste material. Carnivorous mammals have a shorter large intestine compared to herbivorous mammals due to their diet.

Rectum and Anus

The **rectum** is the terminal end of the large intestine, as shown in **Figure 9**. The primary role of the rectum is to store the feces until defecation. The feces are propelled using peristaltic movements during elimination. The **anus** is an opening at the far-end of the digestive tract and is the exit point for the waste material. Two sphincters between the rectum and anus control elimination: the inner sphincter is involuntary and the outer sphincter is voluntary.

Accessory Organs

The organs discussed above are the organs of the digestive tract through which food passes. Accessory organs are organs that add secretions (enzymes) that catabolize food into nutrients. Accessory organs include salivary glands, the liver, the pancreas, and the gallbladder. The liver, pancreas, and gallbladder are regulated by hormones in response to the food consumed.

The **liver** is the largest internal organ in humans and it plays a very important role in digestion of fats and detoxifying blood. The liver produces bile, a digestive juice that is required for the breakdown of fatty components of the food in the duodenum. The liver also processes the vitamins and fats and synthesizes many plasma proteins.

The **pancreas** is another important gland that secretes digestive juices. The chyme produced from the stomach is highly acidic in nature; the pancreatic juices contain high levels of bicarbonate, an alkali that neutralizes the acidic chyme. Additionally, the pancreatic juices contain a large variety of enzymes that are required for the digestion of protein and carbohydrates.

The **gallbladder** is a small organ that aids the liver by storing bile and concentrating bile salts. When chyme containing fatty acids enters the duodenum, the bile is secreted from the gallbladder into the duodenum.

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In Summary: Parts Of The Digestive System

Many organs work together to digest food and absorb nutrients. The mouth is the point of ingestion and the location where both mechanical and chemical breakdown of food begins. Saliva contains an enzyme called amylase that breaks down carbohydrates. The food bolus travels through the esophagus by peristaltic movements to the stomach. The stomach has an extremely acidic environment. An enzyme called pepsin digests protein in the stomach. Further digestion and absorption take place in the small intestine. The large intestine reabsorbs water from the undigested food and stores waste until elimination.

Animal Bioenergetics

Section Goals

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

- Explain the difference between endotherms and ectotherms.
- Interpret graphs related to endotherms and ectotherms.
- Relate bioenergetics to body size, levels of activity, and the environment
- Describe thermoregulation of endothermic and ectothermic animals

Endotherms and Ectotherms

What's it like outside today? If it's winter where you are, it might be pretty cold. If it's summer, it might be pretty hot. Either way, odds are that your core body temperature is right around 98.6℉/37℃. Mechanisms like shivering and sweating kick in when your body gets too cold or too hot, keeping your internal temperature steady.

Not all organisms keep their body temperature in as narrow a range as we humans do, but virtually every animal on the planet has to regulate body temperature to some degree—if only to keep the water in its cells from turning to ice or to avoid denaturing its metabolic enzymes with heat.

Broadly speaking, animals can be divided into two groups based on how they regulate body temperature: endotherms and ectotherms. Let's take a closer look at the difference between these two groups.

People, polar bears, penguins, and prairie dogs, like most other birds and mammals, are endotherms. Iguanas and rattlesnakes, like most other reptiles—along with most fishes, amphibians, and invertebrates—are ectotherms.

Endotherms generate most of the heat they need internally. When it's cold out, they increase metabolic heat production to keep their body temperature constant. Because of this, the internal body temperature of an endotherm is more or less independent of the temperature of the environment.

The sum total of the biochemical reactions that take place in an organism are called its **metabolism**. Metabolic reactions involve breaking down fuel molecules, such as sugars, and using the energy stored in them to do work. The processes that convert energy stored in food molecules into biological work are not very efficient, so heat is generated as a byproduct. The higher an organism's metabolic rate—the amount of chemical fuel it burns in a given period of time—the more heat it will produce.

So, as an endotherm is exposed to colder external temperatures, it will increase its metabolic rate, burn more fuel, and produce extra heat to keep its body temperature constant. This pattern is shown in **Figure 1** below: the mouse maintains a steady body temperature close to 37℃ across a wide range of external temperatures.

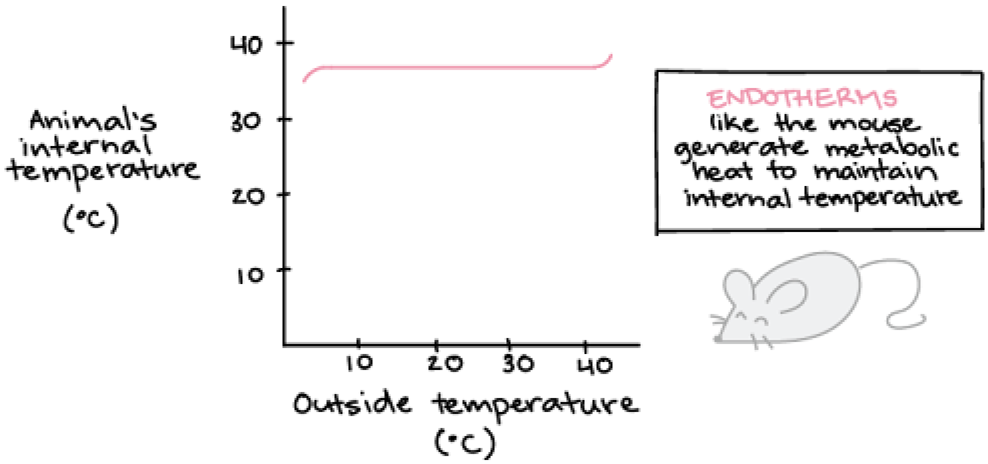


Figure 1. *Diagram based on data from Cannon and Nedergaard1, Figure 2, and on a similar figure in Purves et al.*

For **ectotherms**, on the other hand, body temperature mainly depends on external heat sources. That is, ectotherm body temperature rises and falls along with the temperature of the surrounding environment (**Figure 2**). Although ectotherms do generate some metabolic heat—like all living things—ectotherms can't increase this heat production to maintain a specific internal temperature.

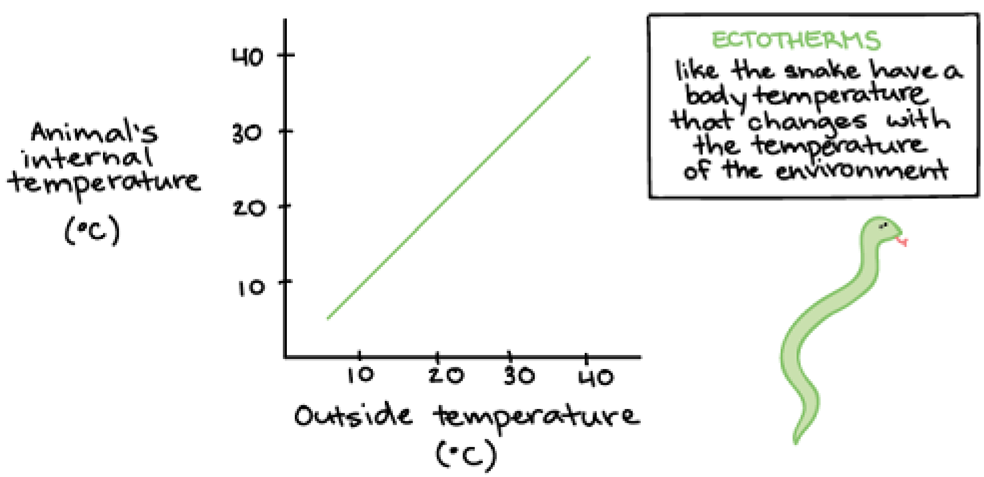


Figure 2. *Diagram based on theoretical graph from Meek, Figure 1 and on Akin, Figure 1.*

Most ectotherms *do* regulate their body temperature to some degree, though. They just don't do it by producing heat. Instead, they use other strategies, such as behavior—seeking sun, shade, etc.—to find environments whose temperature meets their needs.

Some species blur the line between endotherms and ectotherms. Animals that hibernate, for instance, are endothermic when they are active but resemble ectotherms when they are hibernating. Large fish like tuna and sharks generate and conserve enough heat to raise their body temperature above that of the surrounding water. Still, unlike a true endotherm, they don't maintain a specific body temperature. Even some insects can use metabolic heat to increase body temperature by contracting their flight muscles!

One other important point: as a general rule, endotherms have considerably higher metabolic rates than ectotherms. That's because they have to burn large quantities of fuel—food—to maintain their internal body temperature.

Why regulate temperature?

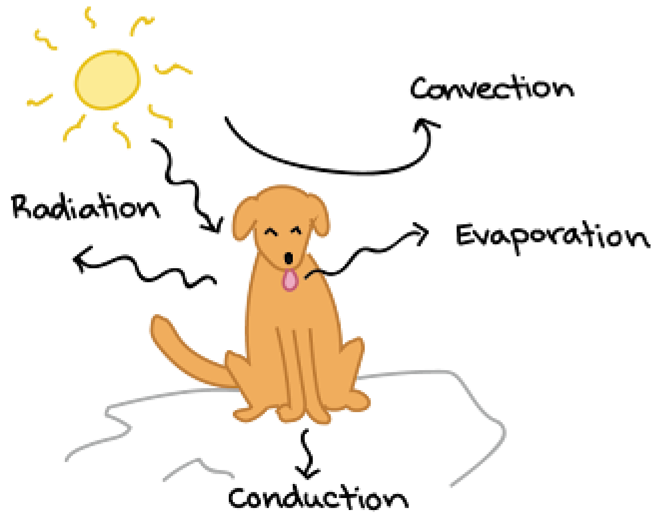
There are some basic limits on survivable body temperature for most animals. At one end of the spectrum, water freezes at 32℉/0℃ to form ice. If ice crystals form inside a cell, they'll generally rupture its membranes. At the other end of the spectrum, enzymes and other proteins in cells often start to lose shape and function, or **denature**, at temperatures above 104℉/40℃.

Why do many organisms—including you and me—keep their body temperature in a narrower range than this? The rate of chemical reactions changes with temperature, both because temperature affects the rate of collisions between molecules and because the enzymes that control the reactions may be temperature-sensitive. Reactions tend to go faster with higher temperatures, up to a point beyond which their rate drops sharply as their enzymes denature.

Each species has its network of metabolic reactions and set of enzymes optimized for a particular temperature range. By keeping body temperature in that target range, organisms ensure that their metabolic reactions run properly.

Temperature balance

For both endotherms and ectotherms, body temperature depends on the balance between heat generated by the organism and heat exchanged with—lost to or gained from—the environment. Heat always moves from warmer to cooler objects, as described in the Second Law of Thermodynamics. There are three main ways that an organism can exchange heat with its environment: radiation, conduction—along with convection—and evaporation.



- **Radiation:** Radiation is the transfer of heat from a warmer object to a cooler one by infrared radiation, that is, without direct contact. You've experienced radiation if you've been warmed by heat from the sun, a fire, or a radiator in a building.
- **Conduction:** Heat can be transferred between two objects in direct contact by means of conduction. If you pick up an ice cube, you'll lose heat to the ice by means of conduction. If you walk barefoot on stone on a sunny day, on the other hand, you'll absorb heat from the stone by conduction.
- **Evaporation:** Vaporization of water from a surface leads to loss of heat—for example, when sweat evaporates from your skin.

Did I Get It?

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Hint/Explanation

We can use what we know about how endotherms and ectotherms maintain body temperature to figure out which line corresponds to which animal.

To start with, let's "translate" the Y axis of the graph. Oxygen consumption is a common measure of metabolic rate because O_2 gas is used up when fuel molecules are broken down during cellular respiration. The faster an organism is using up oxygen, the higher its metabolic rate. We could measure CO_2 production or heat production to determine metabolic rate.

So, which curve represents the endotherm? Endotherms increase their metabolic rate as temperature drops, producing more heat and thus keeping their internal temperature up. The only curve that goes up as temperature goes down is the upper curve— the blue curve A— so this must be the endotherm (**Figure 4**).

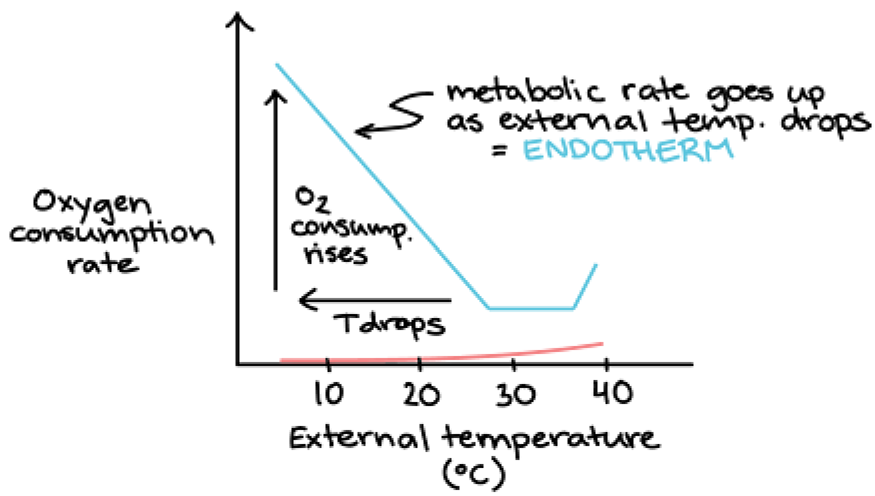

Figure 4. Diagram based on Hiebert and Noveral, Figure 1, and Purves et al.2

The flat part of the curve corresponds to the thermoneutral zone—the range of external temperatures over which the endotherm doesn't have to expend extra energy above its basal, or resting, metabolic rate to maintain body temperature. The increase in metabolic rate at higher temperatures represents the expenditure of energy to try to cool the body and/or the heating of tissue as cooling systems fail.

The remaining curve— the red curve B— must be our ectotherm (**Figure 5**). Not only is the ectotherm's metabolic rate consistently lower than that of the endotherm, but it also drops as external temperature decreases—the opposite pattern from the endotherm. That's because biochemical reactions tend to slow down at low temperatures, such as those of an ectotherm's body when external temperature decreases.

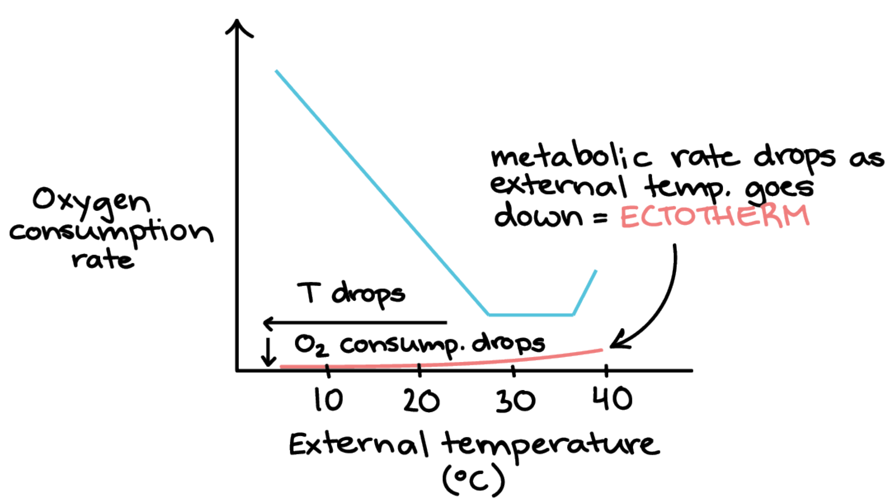

Figure 5. Diagram based on Hiebert and Noveral, Figure 1, and Purves et al.

Metabolic Rate

You may be used to thinking about metabolism in terms of human eating patterns. For instance, a person who has to eat constantly to keep from losing weight may say they have a “fast metabolism,” while a person who eats only a little and still gains weight may say they have a “slow metabolism.”

However, metabolism isn’t unique to humans. In fact, when you get right down to it, **metabolism** just refers to the sum total of the biochemical reactions that take place in an organism’s body. So, every living thing has a metabolism, from a bacterium to a plant to you!

What, exactly, is the rate of an organism’s metabolism? Broadly speaking, **metabolic rate** refers to how quickly fuels (such as sugars) are broken down to keep the organism’s cells running. There are general differences in metabolic rate among species, and the environmental conditions and activity level of an individual organism will also affect its metabolic rate.

Metabolism and heat production

It’s probably not news to you that animals (such as humans) need food as a source of energy. But why is this the case?

The molecules in your breakfast, lunch, or dinner have energy stored in their chemical bonds. Some of your body’s metabolic reactions, like the ones that make up cellular respiration, extract this energy and capture part of it as adenosine triphosphate (ATP) (**Figure 6**). This energy-carrying molecule can, in turn, be used to power other metabolic reactions that keep your cells running.

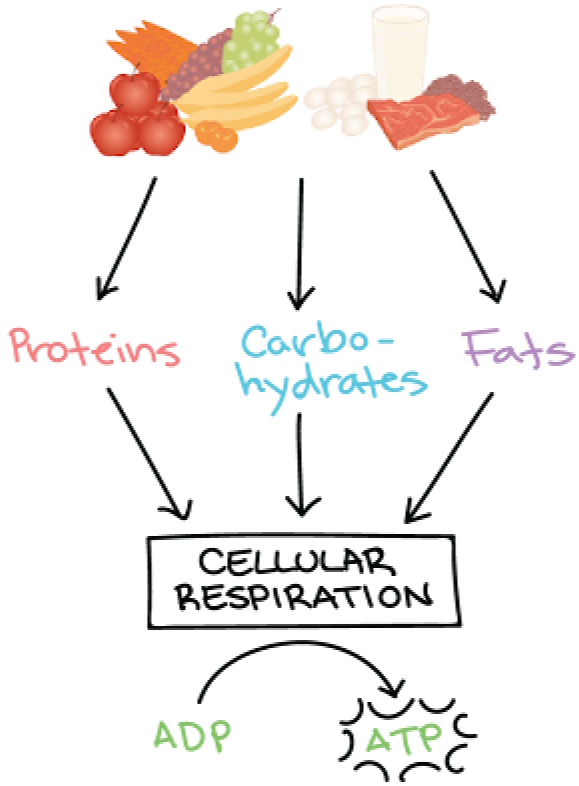

Figure 6. *Sources of ATP. Modified from Overview of metabolic reactions: Figure 2 by OpenStax College, Anatomy & Physiology, CC BY 4.0*

Molecules from food are also used as building blocks for the structures of your body. For instance, proteins from your food are broken down into their parts (amino acids) and may be used to build new proteins in your cells. If you eat more than enough food to replenish the energy you use, food energy may also be stored as glycogen (a chain of linked glucose molecules) or as triglycerides (fat molecules) for later use.

The business of extracting energy from fuel molecules and using it to power cellular reactions is a process that could be more efficient. In fact, no energy transfer can be perfectly efficient – that's a basic law of physics. Instead, each time energy changes forms, some amount of it is converted into a non-usable form. In the reactions of an animal's metabolism, much of the energy stored in fuel molecules is released as heat.

This release of heat is a good thing! Some animals can use (and regulate) their metabolic heat production to maintain a relatively constant body temperature. These animals, called **endotherms**, include mammals, such as humans, as well as birds. **Ectotherms**, on the other hand, are animals that don't use metabolic heat production to maintain a constant body temperature. Instead, their body temperature changes with the temperature of the environment. Lizards and snakes are examples of ectotherms (**Figure 7**).

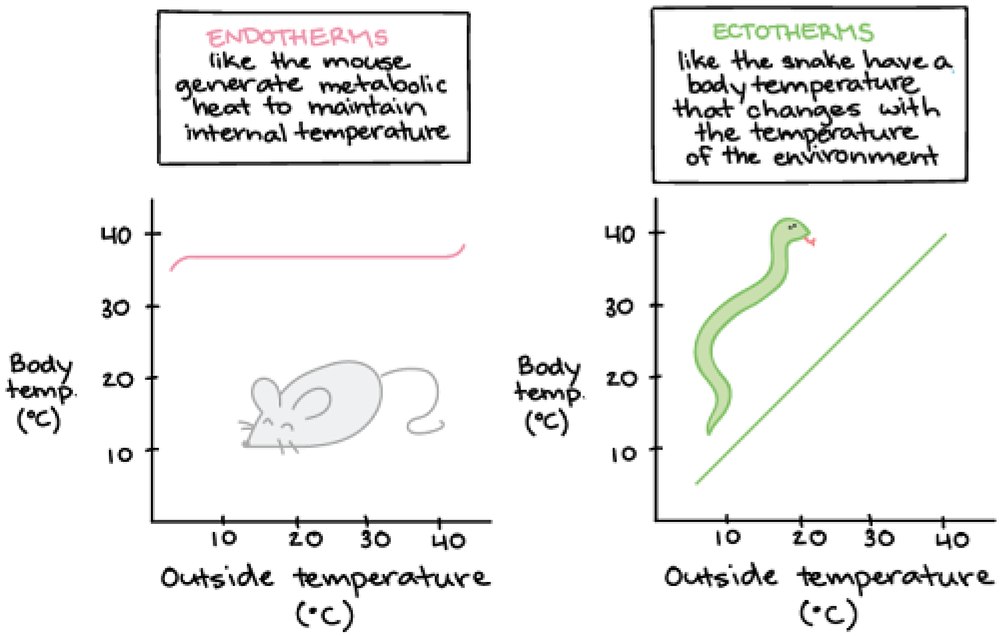

Figure 7. *Left panel diagram based on data from Cannon and Nedergaard, Figure 2, and on similar figure in Purves et al. Right panel diagram based on theoretical graph from Meek, Figure 1 and on Akin, Figure 1.*

Metabolic rate

The amount of energy expended by an animal over a specific period of time is called its **metabolic rate**. Metabolic rate may be measured in joules, calories, or kilocalories per unit of time. You may also see metabolic rate given as oxygen consumed (or carbon dioxide produced) per unit time. Oxygen is used up in cellular respiration, and carbon dioxide is produced as a by-product, so both of these measurements indicate how much fuel is being burned.

In some cases, metabolic rate is given for the entire animal. In other cases, metabolic rate is given on a per-mass basis – for example, how much energy one gram of the animal's tissues uses per unit of time. Per-mass metabolic rates help us make meaningful comparisons between organisms of different sizes.

The "baseline" metabolic rate of an animal is measured as the **basal metabolic rate** (**BMR**) for an endotherm or as the **standard metabolic rate** (**SMR**) for an ectotherm. Both the BMR and SMR are measures of metabolic rate in animals that are at rest, calm/unstressed, and not actively digesting food (fasting).

- For an endotherm, the BMR is also measured when the animal is in a thermoneutral environment, that is, one where the organism does not expend extra energy (above baseline) to maintain temperature.
- For an ectotherm, SMR will vary with temperature, so any SMR measurement is specific to the temperature at which it's taken.

Endotherms tend to have basal high metabolic rates and high energy needs, thanks to their maintenance of a constant body temperature. Ectotherms of similar size tend to have much lower standard metabolic rates and energy requirements, sometimes 10% or less of those of comparable endotherms. What about humans? Human adult males typically have a BMR of 1600 to 1800 kcal/day, and human adult females typically have a BMR of 1300 to 1500 kcal/day. That doesn't mean that's all the calories you should eat, though! Most people have a higher metabolic rate than this just from carrying out daily activities like standing up, walking around, and working or studying.

Energy requirements related to body size

Which one has a higher basal metabolic rate: a mouse or an elephant? If we look at the metabolic rate of the entire organism, the elephant is going to win – there is way more metabolizing tissue in an elephant than in a mouse. If we look at the per-mass metabolic rate, however, the situation flips. A gram of mouse tissue metabolizes more than ten times faster than a gram of elephant tissue (**Figure 8**)!

Species		
Mass	35 g	4,500,000 g
Metabolic rate	890 mm^3 0_2/g body mass/hr	75 mm^3 0_2/g body mass/hr

Figure 8. *"Animal form and function: Figure 3," by OpenStax College, Biology, CC BY 4.0. "Mouse": modificatior work by Magnus Kjaergaard; "Elephant": modification of work by "TheLizardQueen"/Flickr.*

Curiously enough, this is a very general relationship in nature. Among endotherms (animals that use body heat to maintain a constant internal temperature), the smaller the organism's mass, the higher its basal metabolic rate is likely to be. The relationship between mass and metabolic rate holds true across many species, and even follows a specific mathematical equation.

Why is this the case? The short answer is that we don't know for sure! Part of the explanation may relate to animals' surface area-to-volume ratio and how it varies with size. Just as a small cell has more surface area relative to its volume than a large cell, so a small animal has more body surface relative to its volume of metabolizing tissue.

Since animals exchange heat with their environment across their body surfaces, small animals will tend to lose heat to a cooler environment faster than large animals. Because of this, a smaller animal would need more energy and a higher metabolic rate to maintain a constant internal temperature (in an environment below its body temperature).

However, this probably isn't the full explanation for the relationship between body mass and metabolic rate. Why not? For one thing, the metabolic rates of ectotherms also tend to scale with body mass just like those of endotherms. This is difficult to explain with relation to heat retention and heat loss, since ectotherms don't maintain a body temperature different from their environment. The real cause of the relationship between metabolic rate and body mass remains an unsolved mystery.

Energy requirements related to levels of activity

The basal metabolic rate (BMR) or standard metabolic rate (SMR) is a measure of an animal's metabolic rate when it is quiet, not stressed out or excited, and not doing anything active. I don't know about you, but most of the time, that doesn't describe me!

The more active an animal is, the more energy must be expended to maintain that activity, and the higher its metabolic rate. For instance, the hamster running on its wheel in **Figure 9** below would have a higher metabolic rate than a similar hamster snoozing in the corner.

Figure 9. *Phodopus sungorus – Hamsterkraftwerk by Roland Meinecke, CC BY-SA 3.0*

This is something we humans are familiar with from everyday life. For example, if you spend your day going for a long hike or playing sports with friends, you are likely to get pretty hungry (reflecting that you've used up a lot of energy and need more fuel). If, on the other hand, you lie in bed all day reading or watching TV, you'll likely be less hungry because you've used up less energy.

For a typical animal, the average daily rate of energy consumption is much higher than the animal's BMR – by about two to four times. We humans are more sedentary (less active) than the typical animal, so we have an average daily metabolic rate of only about 1.5 times our BMR.

An animal's metabolic rate determines how much food it must consume to maintain its body at a constant mass. If an animal doesn't eat enough food to replace the energy it uses up, it will lose body mass (as glycogen, fats, and other macromolecules are burned for fuel). On the other hand, if an animal eats more food than it needs to replace the energy it uses, there will be leftover chemical energy that is stored by the body as glycogen or fat. This is the basis of weight loss and weight gain in humans as well as other animals.

Scientist Spotlight: Dr. Cara Ocobock

Cara Ocobock (Photo by Mary Kate McGuirk/University of Notre Dame)

Woman the Hunter – Lunch Break Science featuring Dr. Cara Ocobock

Watch this fascinating interview with Cara Ocobock on *Lunch Break Science**. Dr. Ocobock is an associate professor and the director of the Human Energetics Laboratory at Notre Dame University and is an award-winning science communicator. She studies the evolutionary, physiological and behavioral underpinnings of humans in extreme environments (climate) and under extreme conditions (physical activity). In this interview, Dr. Ocobock discusses how her research on women's physical capabilities and endurance challenges traditional narratives of their role in human evolution.

**Lunch Break Science is a web series featuring short talks and interviews with scientists affiliated with the non-profit Leaky Foundation, which supports scientific research and education on human evolution.*

Torpor, hibernation, and estivation

Some animals respond to environmental cues by slowing down their metabolic processes and reducing their body temperature, entering what's known as torpor. **Torpor** is a state of decreased activity and metabolism that allows animals to survive unfavorable conditions and/or conserve energy.

Torpor may be used over long periods. For instance, some animals go into **hibernation**, a state in which they slow their metabolism and maintain a reduced body temperature during the winter. Cues that cause animals to enter hibernation include drops in temperature and the shortening of days. **Figure 10** below shows a Norway bat in its winter hibernation.

Figure 10. *Eptesicus nilssonii hibernating, by Magne Flåten, CC BY-SA 4.0*

Different animals have different hibernation patterns. For instance, the abdominal temperature of a hibernating ground squirrel may drop as low as 0°C (32°F), but the squirrel must wake up periodically during its hibernation period – possibly to sleep, eat, or do other body maintenance. In contrast, a bear's internal temperature stays higher, at 31°C (88°F) or above, but the bear can hibernate for its entire winter period without needing to awaken.

The family of alpine marmots in the next video from PBS *Nature* is preparing for a half-year hibernation underground:

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Learn how a Vancouver Island marmot wakes up from a 7-month hibernation in this clip from the BBC wildlife show *Animals: The Inside Story*:

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Some animals enter an extended period of torpor during the summer months, when there are high temperatures and little water. In this case, the extended torpor is called **estivation**. Some desert animals estivate in response to dry conditions, and this shift helps them survive the harshest months of the year. The snails in **Figure 11** below climb to the tops of fence posts to estivate.

Figure 11. *Kadina snails climb fence, by Vladimir Menkov, CC BY-SA 4.0*

Torpor can also last for short periods. **Daily torpor** can be sporadic, in response to unfavorable conditions, or can repeat in a predictable pattern. For instance, some small endotherms such as dormice reduce the amount of energy they need (and thus, food they must consume) by entering torpor during the part of the day that is coldest, when they would otherwise need to use a lot of energy to produce metabolic heat and maintain body temperature.

Did I Get It?

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Thermoregulation

Why do lizards sunbathe? Why do jackrabbits have huge ears? Why do dogs pant when they're hot? Animals have quite a few different ways to regulate body temperature! These **thermoregulatory** strategies let them live in different environments, including some that are pretty extreme.

Polar bears and penguins, for instance, maintain a high body temperature in their chilly homes at the poles, while kangaroo rats, iguanas, and rattlesnakes thrive in Death Valley, where summertime highs are over 100°F (38°C) (**Figure 12**).

Let's take a closer look at some behavioral strategies, physiological processes, and anatomical features that help animals regulate body temperature.

Figure 12. *Left, polar bear jumping between ice floes; right, lizard in Death Valley. Image credits: left, Polar bear jumping by Arturo de Frias Marques, CC BY-SA 4.0; right, Lézard à queue de zèbre by Jon Sullivan, public domain*

Mechanisms of thermoregulation

Both endotherms and ectotherms have **adaptations**—features that arose by natural selection—that help them maintain a healthy body temperature. These adaptations can be behavioral, anatomical, or physiological. Some adaptations increase heat production in endotherms when it's cold. Others, in both endotherms and ectotherms, increase or decrease exchange of heat with the environment.

We will look at three broad categories of thermoregulatory mechanisms in this article:

- Changing behavior
- Increasing metabolic heat production
- Controlling the exchange of heat with the environment

Behavioral strategies

How do *you* regulate your body temperature using behavior? On a hot day, you might go for a swim, drink some cold water, or sit in the shade. On a cold day, you might put on a coat, sit in a cozy corner, or eat a bowl of hot soup.

Nonhuman animals have similar types of behaviors. For instance, elephants spray themselves with water to cool down on a hot day, and many animals seek shade when they get too warm. On the other hand, lizards often bask on a hot rock to warm up, and penguin chicks huddle in a group to retain heat.

Some ectotherms are so good at using behavioral strategies for temperature regulation that they maintain a fairly stable body temperature, even though they don't use metabolic heat to do so.

Figure 13. *Examples of behavioral temperature regulation, from top left: basking in the sun, cooling off with water, seeking shade, and huddling for warmth. Image credits (from top left): Iguana by Skeeze, public domain; Elephant cooling off by Jean Beaufort, public domain; Chickens seeking shade by Geoffrey McKim, CC BY-SA 2.0; Penguin chicks huddling, by David Stanley, CC BY 2.0*

Increasing heat production—thermogenesis

Endotherms have various ways of increasing metabolic heat production, or **thermogenesis**, in response to cold environments.

One way to produce metabolic heat is through muscle contraction—for example, if you shiver uncontrollably when you're very cold. Both deliberate movements—such as rubbing your hands together or going for a brisk walk—and shivering increase muscle activity and thus boost heat production.

Nonshivering thermogenesis provides another mechanism for heat production. This mechanism depends on specialized fat tissue known as **brown fat**, or brown adipose tissue. Some mammals, especially hibernators and baby animals, have lots of brown fat. Brown fat contains many mitochondria with special proteins that let them release energy from fuel molecules directly as heat instead of channeling it into formation of the energy carrier ATP.

Controlling the loss and gain of heat

Animals also have body structures and physiological responses that control how much heat they exchange with the environment:

- Circulatory mechanisms, such as altering blood flow patterns
- Insulation, such as fur, fat, or feathers
- Evaporative mechanisms, such as panting and sweating

Circulatory mechanisms

The body's surface is the main site for heat exchange with the environment. Controlling the flow of blood to the skin is an important way to control the rate of heat loss to—or gain from—the surroundings.

In endotherms, warm blood from the body's core typically loses heat to the environment as it passes near the skin. Shrinking the diameter of blood vessels that supply the skin, a process known as **vasoconstriction**, reduces blood flow and helps retain heat (**Figure 14**).

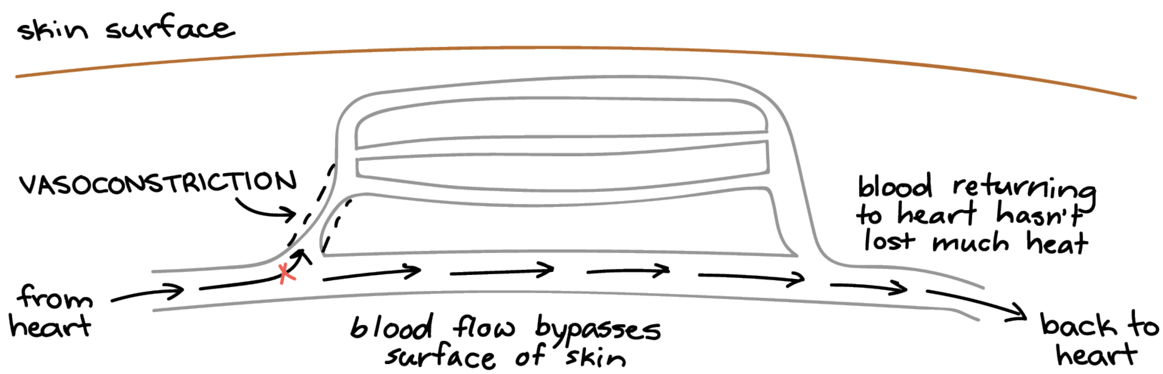

Figure 14. *Diagram based on similar diagrams in Gillam.*

On the other hand, when an endotherm needs to get rid of heat—say, after running hard to escape a predator—these blood vessels get wider, or dilate. This process is called **vasodilation**. Vasodilation increases blood flow to the skin and helps the animal lose some of its extra heat to the environment (**Figure 15**).

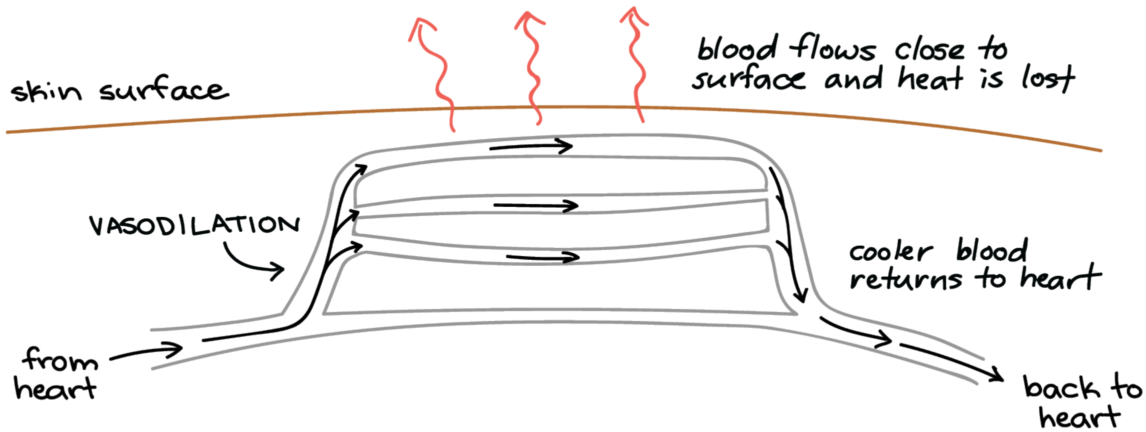

Figure 15. *Diagram based on similar diagrams in Gillam.*

Furry mammals often have special networks of blood vessels for heat exchange located in areas of bare skin. For example, jackrabbits have large ears with an extensive network of blood vessels that allow rapid heat loss. This adaptation helps them live in hot desert environments (**Figure 16**).

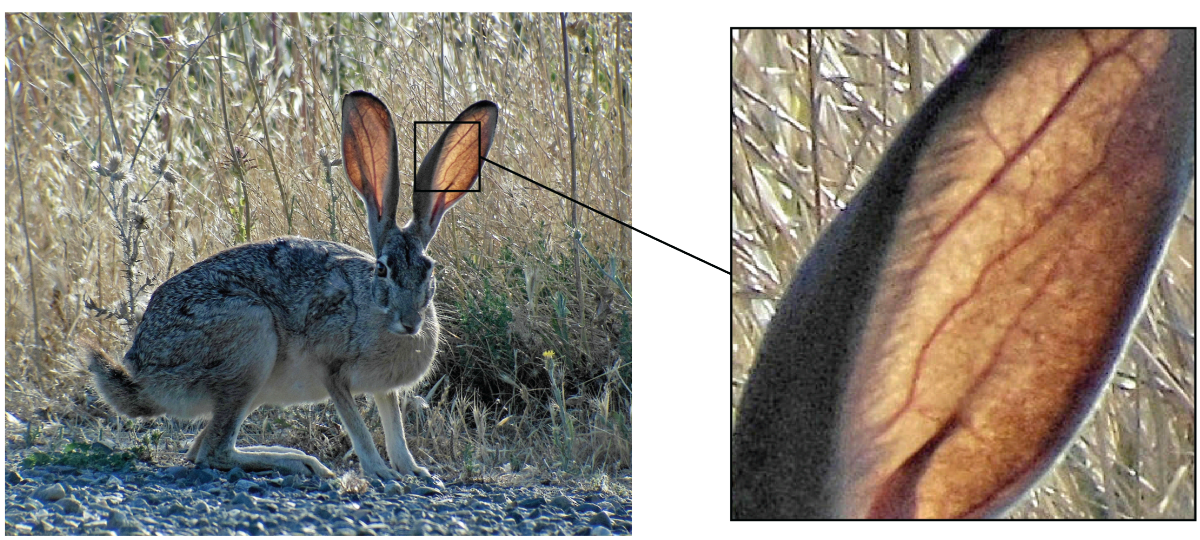

Figure 16. *Modified from Black-tailed jackrabbit by K. Schneider, CC BY-NC 2.0*

Some ectotherms also regulate blood flow to the skin as a way to conserve heat. For instance, iguanas reduce blood flow to the skin when they go swimming in cold water to help retain the heat they soaked up while on land.

Many birds and mammals have **countercurrent heat exchangers**, circulatory adaptations that allow heat to be transferred from blood vessels containing warmer blood to those containing cooler blood. To see how this works, let's look at an example.

In the leg of a wading bird, the artery that runs down the leg carries warm blood from the body. The artery is positioned right alongside a vein that carries cold blood up from the foot. The descending, warm blood passes much of its heat to the ascending, cold blood by conduction (**Figure 17**). This means that less heat will be lost in the foot due to the reduced temperature difference between the cooled blood and the surroundings and that the blood moving back into the body's core will be relatively warm, keeping the core from getting cold.

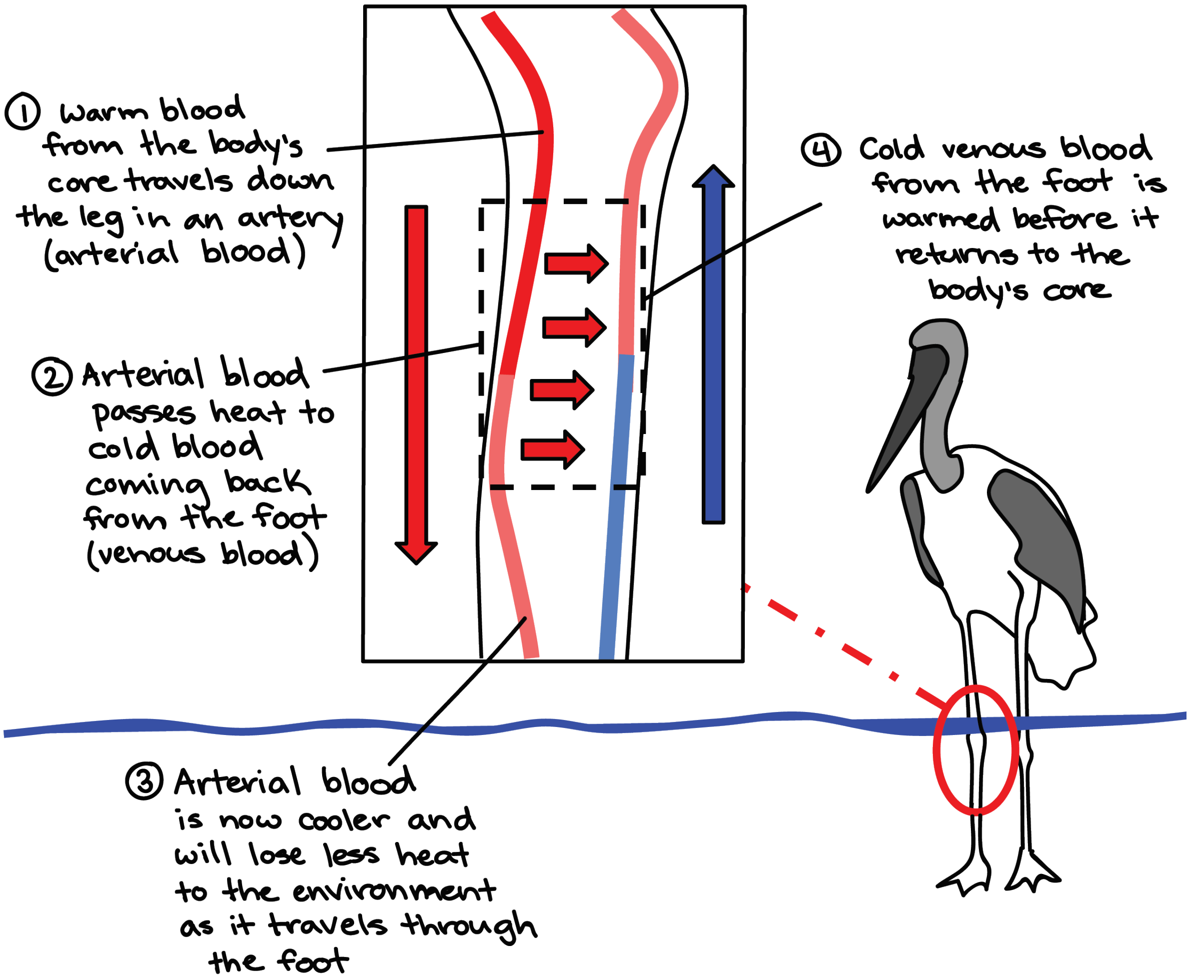

Figure 17. *Diagram modified from [Counter current exchange in birds](#) by Ekann, CC BY-SA 4.0; the modified image is licensed under a CC BY-SA 4.0 license*

Insulation

Another way to minimize heat loss to the environment is through **insulation**. Birds use feathers, and most mammals use hair or fur, to trap a layer of air next to the skin and reduce heat transfer to the environment. Marine mammals like whales use blubber, a thick layer of fat, as a heavy-duty form of insulation.

In cold weather, birds fluff their feathers and animals raise their fur to thicken the insulating layer. The same response in people—goosebumps—is not so effective because of our limited body hair (**Figure 18**). So, most of us wear sweaters!

Figure 18. *Left, a pigeon fluffs its feathers for warmth; right, human goosebumps are an attempt to increase insulation by trapping air near the skin—but are not very effective due to lack of hair! Image credits: left, [Parrow cold big bird](#) by Mike Sandoval, public domain; right, [Goose bumps](#), by Ildar Sagdejev, CC BY-SA 3.0*

Evaporative mechanisms

Land animals often lose water from their skin, mouth, and nose by evaporation into the air. Evaporation removes heat and can act as a cooling mechanism.

For instance, many mammals can activate mechanisms like sweating and panting to increase evaporative cooling in response to high body temperature (**Figure 19**).

In sweating, glands in the skin release water containing various ions—the "electrolytes" we replenish with sports drinks. Only mammals sweat. Learn more about why sweating cools you down in this video from Khan Academy with LeBron James. Then, check out the next video from the BBC *Planet Earth* to learn about a unique evaporative body-cooling behavior in kangaroos!

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In panting, an animal breathes rapidly and shallowly with its mouth open to increase evaporation from the surfaces of the mouth. Both mammals and birds pant, or at least use similar breathing strategies to cool down.

In some species, such as dogs, evaporative cooling from panting combined with a countercurrent heat exchanger helps keep the brain from overheating!

Although panting and sweating are effective cooling mechanisms, these active processes have the unwanted side effect of increasing the metabolic rate and thereby heat production. In addition, panting and sweating cause the animal to lose water and can result in dehydration—always make sure your dog has lots of water available on a hot day! Sweating also depletes the body of electrolytes, which must be replaced to avoid an imbalance.

Figure 19. *Left, wolf panting to lose heat; right, beads of sweat on a human arm. Image credits: left, [Panting wolf] by Mark Dumont, CC BY-NC 2.0; right, [Photo of sweating at Wilson Trail Stage 1] by Minghong, CC BY-SA 3.0*

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V

Ecology

This module contains the following chapters:

- Community Ecology
- Ecosystem Ecology
- The Carbon Cycle

Adapted from:

Community Ecology

Section Goals

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

- Discuss the predator-prey cycle
- Give examples of defenses against predation and herbivory
- Define the competitive exclusion principle
- Compare and contrast the different types of symbiotic relationships between species

Populations rarely, if ever, live in isolation from populations of other species. In most cases, numerous species share a habitat. The interactions between these populations play a major role in regulating population growth and abundance. All populations occupying the same habitat form a community: populations inhabiting a specific area at the same time. The number of species occupying the same habitat and their relative abundance is known as species diversity. Areas with low diversity, such as the glaciers of Antarctica, still contain a wide variety of living things. In contrast, the diversity of tropical rainforests is so great that it cannot be counted. Ecology is studied at the community level to understand how species interact with each other and compete for the same resources.

Predation and Herbivory Perhaps the classical example of species interaction is predation: the consumption of prey by its predator. Nature shows on television highlight the drama of one living organism killing another. Populations of predators and prey in a community are not constant over time; in most cases, they vary in cycles that appear to be related. The most often cited example of predator-prey dynamics is seen in the cycling of the lynx (predator) and the snowshoe hare (prey), using nearly 200-year-old trapping data from North American forests (**Figure 1**). This cycle of predator and prey lasts approximately ten years, with the predator population lagging 1–2 years behind that of the prey population. As the hare numbers increase, there is more food available for the lynx, allowing the lynx population to increase as well. When the lynx population grows to a threshold level, however, they kill so many hares that the hare population begins to decline, followed by a decline in the lynx population because of scarcity of food. When the lynx population is low, the hare population size begins to increase due, at least in part, to low predation pressure, starting the cycle anew.

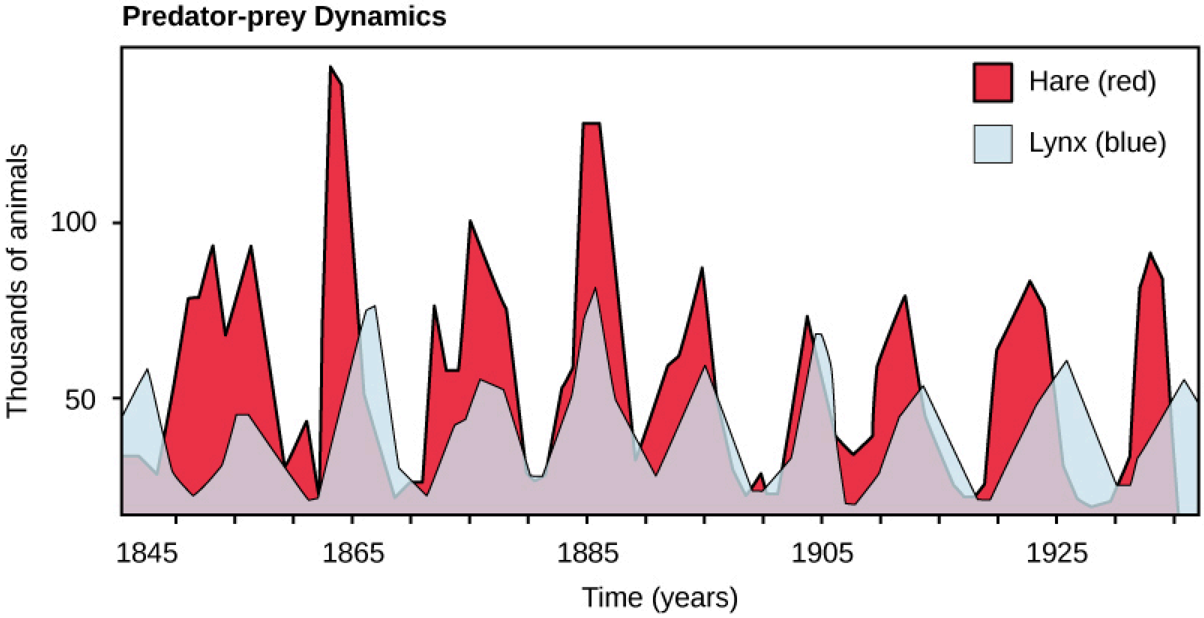

Figure 1. *The cycling of lynx and snowshoe hare populations in Northern Ontario is an example of predator-prey dynamics.*

Some researchers question the idea that predation models entirely control the population cycling of the two species. More recent studies have pointed to undefined density-dependent factors as being important in cycling, in addition to predation. One possibility is that cycling is inherent in the hare population due to density-dependent effects such as lower fecundity (maternal stress) caused by crowding when the hare population gets too dense. The hare cycling would then induce the cycling of the lynx because it is the lynxes' major food source. The more we study communities, the more complexities we find, allowing ecologists to derive more accurate and sophisticated models of population dynamics.

Herbivory describes the consumption of plants by insects and other animals, and it is another interspecific relationship that affects populations. Unlike animals, most plants cannot outrun predators or use mimicry to hide from hungry animals. Some plants have developed mechanisms to defend against herbivory. Other species have developed mutualistic relationships; for example, herbivory provides a mechanism of seed distribution that aids in plant reproduction.

Defense Mechanisms against Predation and Herbivory

The study of communities must consider evolutionary forces that act on the members of the various populations contained within it. Species are not static but slowly changing and adapting to their environment by natural selection and other evolutionary forces. Species have evolved numerous mechanisms to escape predation and herbivory. These defenses may be mechanical, chemical, physical, or behavioral.

Mechanical defenses, such as the presence of thorns on plants or the hard shells on turtles, discourage animal predation and herbivory by causing physical pain to the predator or by physically preventing the predator from being able to eat the prey. Chemical defenses are produced by many animals as well as plants, such as the foxglove, which is extremely toxic when eaten. **Figure 2** shows some organisms' defenses against predation and herbivory.

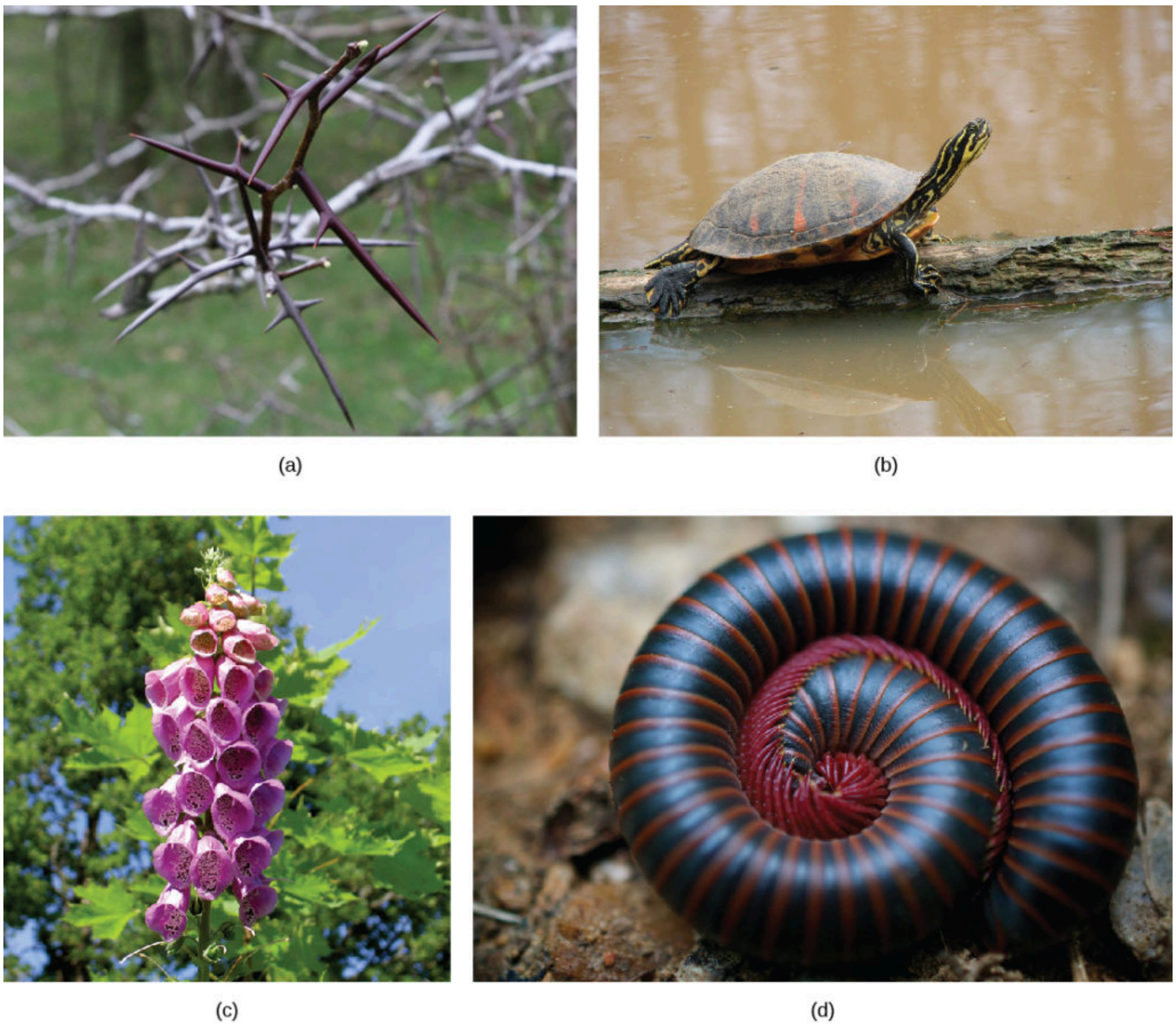

Figure 2. *The (a) honey locust tree (Gleditsia triacanthos) uses thorns, a mechanical defense, against herbivores, while the (b) Florida red-bellied turtle (Pseudemys nelsoni) uses its shell as a mechanical defense against predators. (c) Foxglove (Digitalis sp.) uses a chemical defense: toxins produced by the plant can cause nausea, vomiting, hallucinations, convulsions, or death when consumed. (d) The North American millipede (Narceus americanus) uses both mechanical and chemical defenses: when threatened, the millipede curls into a defensive ball and produces a noxious substance that irritates the eyes and skin.*

Many species use physical appearance, such as body shape and coloration, to avoid being detected by predators. The tropical walking stick is an insect with the coloration and body shape of a twig, which makes it very hard to see when stationary against a background of real twigs (**Figure 3a)**. In another example, the chameleon can, within limitations, change its color to match its surroundings (**Figure 3b**). Both of these are examples of **camouflage** or avoiding detection by blending in with the background. There are many behavioral adaptations to avoid or confuse predators. Playing dead and traveling in large groups, like schools of fish or flocks of birds, are both behaviors that reduce the risk of being eaten.

Figure 3. *(a) The tropical walking stick and (b) the chameleon use body shape and/or coloration to prevent detection by predators.*

Some species use coloration as a way of warning predators that they are not good to eat. For example, the cinnabar moth caterpillar, the fire-bellied toad, and many species of beetle have bright colors that warn of a foul taste, the presence of toxic chemicals, and the ability to sting or bite, respectively. Predators that ignore this coloration and eat the organisms will experience their unpleasant taste or the presence of toxic chemicals and learn not to eat them in the future. This type of defensive mechanism is called **aposematic coloration** or warning coloration (**Figure 4**).

Figure 4. *(a) The strawberry poison dart frog (Oophaga pumilio) uses aposematic coloration to warn predators that it is toxic, while the (b) striped skunk (Mephitis mephitis) uses aposematic coloration to warn predators of the unpleasant odor it produces.*

While some predators learn to avoid eating certain potential prey because of their coloration, other species have evolved mechanisms to mimic this coloration to avoid being eaten, even though they themselves may not be unpleasant to eat or contain toxic chemicals. In **Batesian mimicry**, a harmless species imitates the warning coloration of a harmful one. Assuming they share the same predators, this coloration then protects the harmless ones, even though they do not have the same level of physical or chemical defenses against predation as the organisms they mimic. Many insect species mimic the coloration of wasps or bees, which are stinging, venomous insects, thereby discouraging predation (**Figure 5**).

Figure 5. *Batesian mimicry occurs when a harmless species mimics the coloration of a harmful species, as is seen with the (a) bumblebee and (b) bee-like robber fly.*

In **Müllerian mimicry**, multiple species share the same warning coloration, but all of them actually have defenses. **Figure 6** shows a variety of foul-tasting butterflies with similar coloration. In **Emsleyan/ Mertensian mimicry**, a deadly prey mimics a less dangerous one, such as the venomous coral snake mimicking the nonvenomous milk snake. This type of mimicry is extremely rare and more difficult to understand than the previous two types. For this type of mimicry to work, it is essential that eating the milk snake has unpleasant but not fatal consequences. Then, these predators learn not to eat snakes with this coloration, protecting the coral snake as well. If the snake were fatal to the predator, there would be no opportunity for the predator to learn not to eat it, and the benefit for the less toxic species would disappear.

Figure 6. *Several unpleasant-tasting Heliconius butterfly species share a similar color pattern with better-tasting varieties, an example of Müllerian mimicry.*

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Competitive Exclusion Principle

Resources are often limited within a habitat, and multiple species may compete to obtain them. All species have an ecological niche in the ecosystem, which describes how they acquire the resources they need and how they interact with other species in the community. The **competitive exclusion principle** states that two species cannot occupy the same niche in a habitat. In other words, different species cannot coexist in a community if they are competing for all the same resources. An example of this principle is shown in **Figure 7**, with two protozoan species, *Paramecium aurelia* and *Paramecium caudatum*. When grown individually in the laboratory, they both thrive. But when they are placed together in the same test tube (habitat), *P. aurelia* outcompetes *P. caudatum* for food, leading to the latter's eventual extinction.

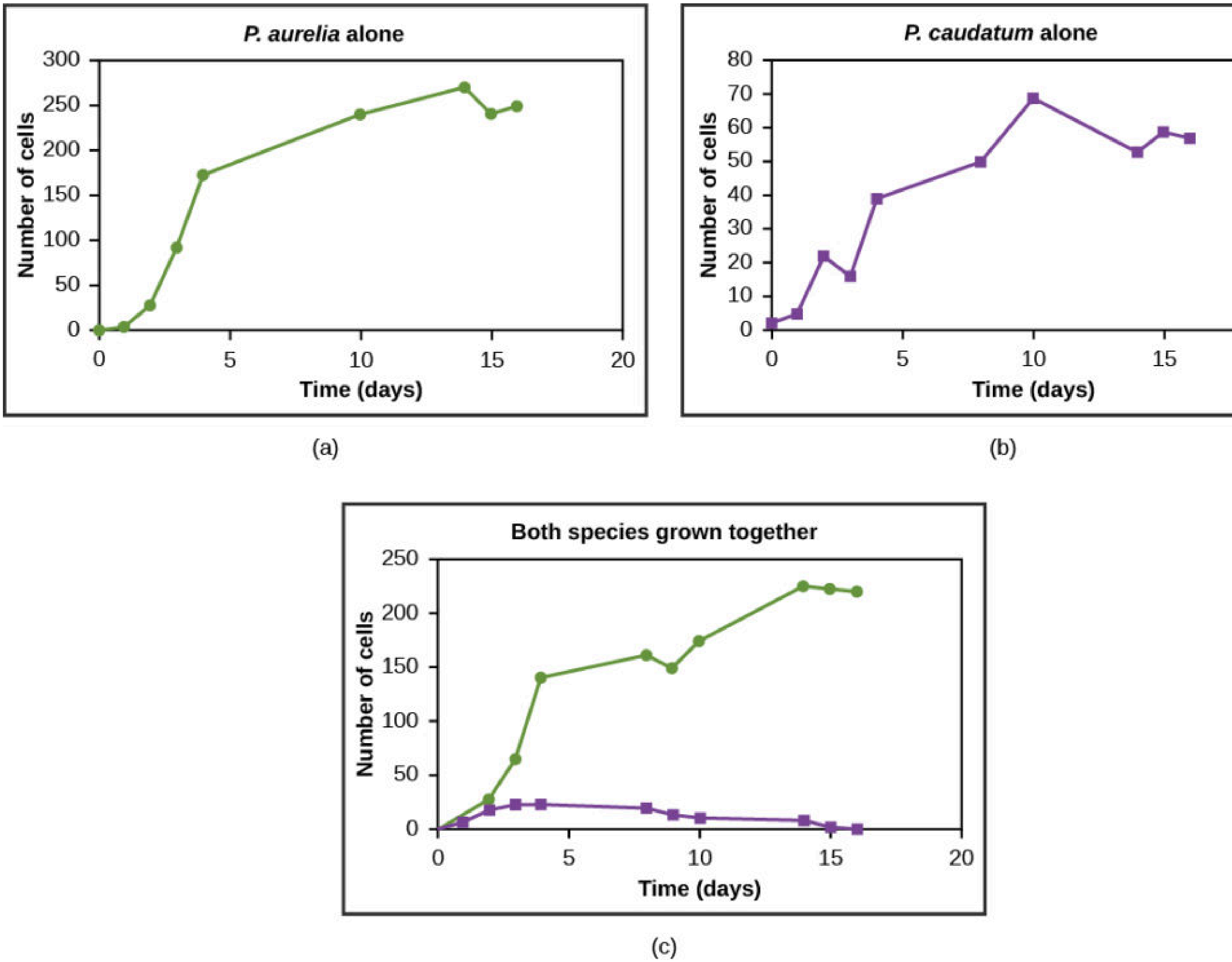

Figure 7. *Paramecium aurelia and Paramecium caudatum grow well individually, but when they compete for the sa resources, the P. aurelia outcompetes the P. caudatum.*

This exclusion may be avoided if a population evolves to make use of a different resource, a different area of the habitat, or feeds during a different time of day, called resource partitioning. The two organisms are then said to occupy different microniches. These organisms coexist by minimizing direct competition.

Resource Partitioning

Competitive exclusion may be avoided if one or both of the competing species evolves to use a different resource, occupy a different area of the habitat, or feed during a different time of day. The result of this kind of evolution is that two similar species use largely non-overlapping resources and thus have different microniches. This situation is called **resource partitioning**, and it helps the species coexist because there is less direct competition between them. These organisms coexist by minimizing direct competition.

The anole lizards found on the island of Puerto Rico are a good example of resource partitioning. In this group, natural selection has led to the evolution of different species that make use of different resources. The figure below shows resource partitioning among 11 species of anole lizards. Each species lives in its own preferred habitat, which is defined by the type and height of vegetation (trees, shrubs, cactus, etc.), sunlight, and moisture, among other factors.

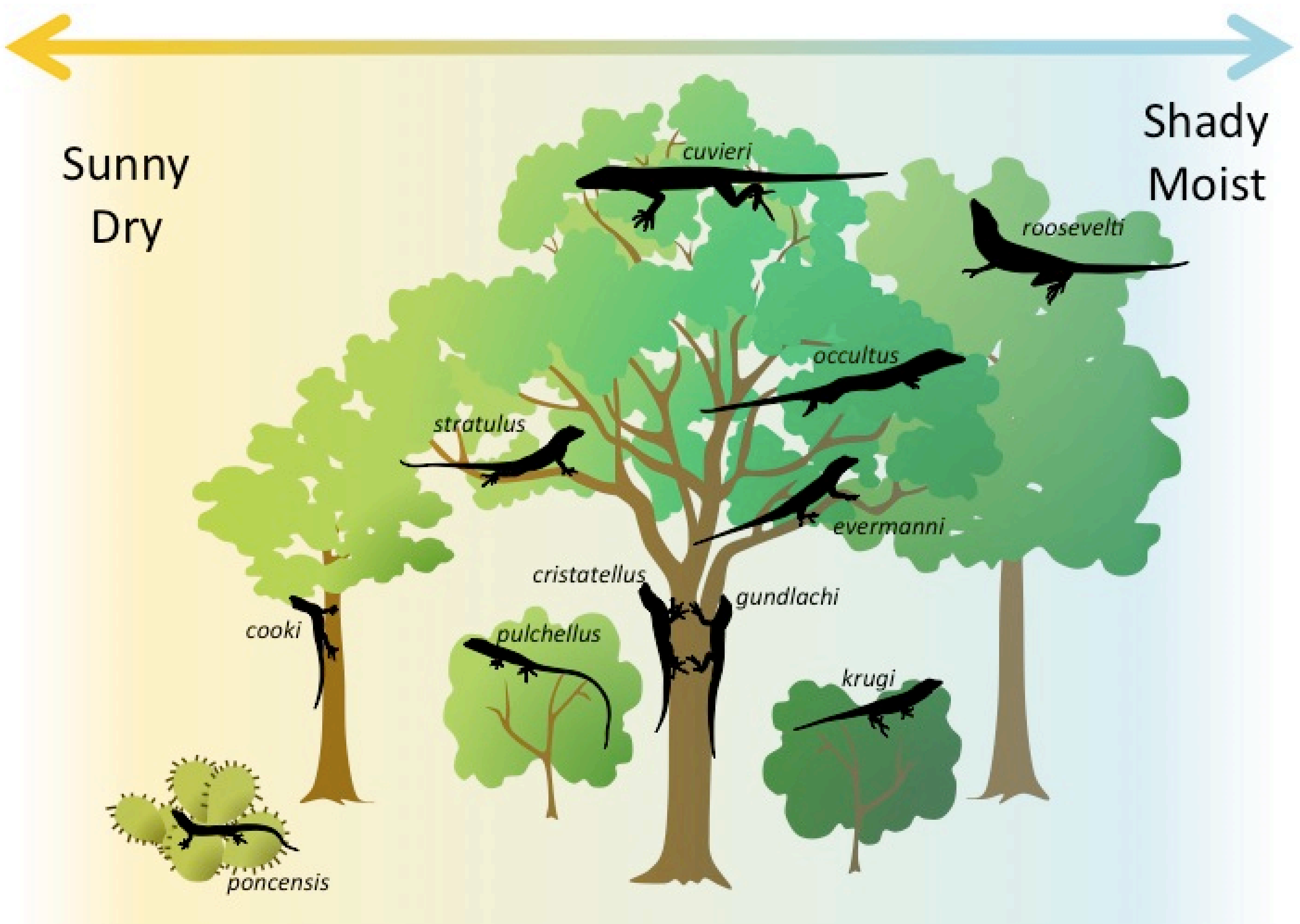

Figure 8. *Resource partitioning among anole lizards, showing a type that lives in sunny, dry areas, such as tops of trees, and another type that lives in shady, moist areas of trees.*

Watch this video to review competition and how populations share resources in a community:

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Symbiosis

Symbiotic relationships, or **symbioses** (plural), are close interactions between individuals of different species over an extended period of time that impact the abundance and distribution of the associating populations. Most scientists accept this definition, but some restrict the term to only those species that are mutualists in a situation in which both individuals benefit from the interaction. In this discussion, the broader definition will be used.

Commensalism

A **commensal** relationship occurs when one species benefits from the close, prolonged interaction while the other neither benefits nor is harmed. Birds nesting in trees provide an example of a commensal relationship (**Figure 9**). The tree is not harmed by the presence of the nest among its branches. The nests are light and produce little strain on the structural integrity of the branch, and most of the leaves, which the tree uses to get energy by photosynthesis, are above the nest, so they are unaffected. The bird, on the other hand, benefits greatly. If the bird had to nest in the open, its eggs and young would be vulnerable to predators. Another example of a commensal relationship is the pilot fish and the shark. The pilot fish feed on the leftovers of the host's meals, and the host is not affected in any way.

Figure 9. *The southern masked weaver bird is starting to make a nest in a tree in Zambezi Valley, Zambia, which is an example of a commensal relationship in which one species (the bird) benefits while the other (the tree) neither benefits nor is harmed.*

Mutualism

A second type of symbiotic relationship is called **mutualism**, where two species benefit from their interaction. Some scientists believe that these are the only true examples of symbiosis. For example, termites have a mutualistic relationship with protozoa that live in the insect's gut (**Figure 10a**). The termite benefits from the ability of bacterial symbionts within the protozoa to digest cellulose. The termite itself cannot do this, and without the protozoa, it would not be able to obtain energy from its food (cellulose from the wood it chews and eats). The protozoa and the bacterial symbionts benefit by having a protective environment and a constant supply of food from the wood-chewing actions of the termite. Lichens have a mutualistic relationship between fungi and photosynthetic algae or bacteria (**Figure 10b**). As these symbionts grow together, the glucose produced by the algae provides nourishment for both organisms. In contrast, the physical structure of the lichen protects the algae from the elements and makes certain nutrients in the atmosphere more available to the algae.

Figure 10. (a) *Termites form a mutualistic relationship with symbiotic protozoa in their guts, which allow both organisms to obtain energy from the cellulose the termite consumes. (b) Lichen is a fungus that has symbiotic photosynthetic algae living inside its cells.*

One of the most remarkable examples of mutualism is between vascular plants and a type of fungi called *mycorrhizae*. The name mycorrhiza is derived from the Greek words *myco* meaning "fungus" and *rhizo* meaning "root." In a mycorrhizal association, the fungi use their extensive network of hyphae (long, branching, filamentous structures that spread underground) and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus. Nearly 90 percent of all vascular plant species have mycorrhizal partners. A well-supported theory proposes that these fungi were instrumental in the evolution of the root system in plants and contributed to the overwhelming success of flowering plants. The plants benefited from the association because mycorrhizae allowed them to move into new habitats and allowed the increased uptake of nutrients, which gave them an enormous selective advantage over plants that did not establish symbiotic relationships.

The Human Microbiome

Human life is only possible due to the action of microbes, both those in the environment and those species that call us home. Internally, they help us digest our food, produce crucial nutrients for us, protect us from pathogenic microbes, and help train our immune systems to function correctly. Each individual has a **normal microbial flora** (also known as a **gut microbiota**)—these terms simply refer to the collective of the bacteria living in each person's stomach. When these bacteria counts change, it can cause digestive problems.

The bacteria that inhabit our skin and gastrointestinal tract do a host of good things for us. They protect us from pathogens, help us digest our food, and produce some of our vitamins and other nutrients. These activities have been known for a long time. More recently, scientists have gathered evidence that these bacteria may also help regulate our moods, influence our activity levels, and even help control weight by affecting our food choices and absorption patterns. The Human Microbiome Project has begun the process of cataloging our normal bacteria (and archaea) so we can better understand these functions.

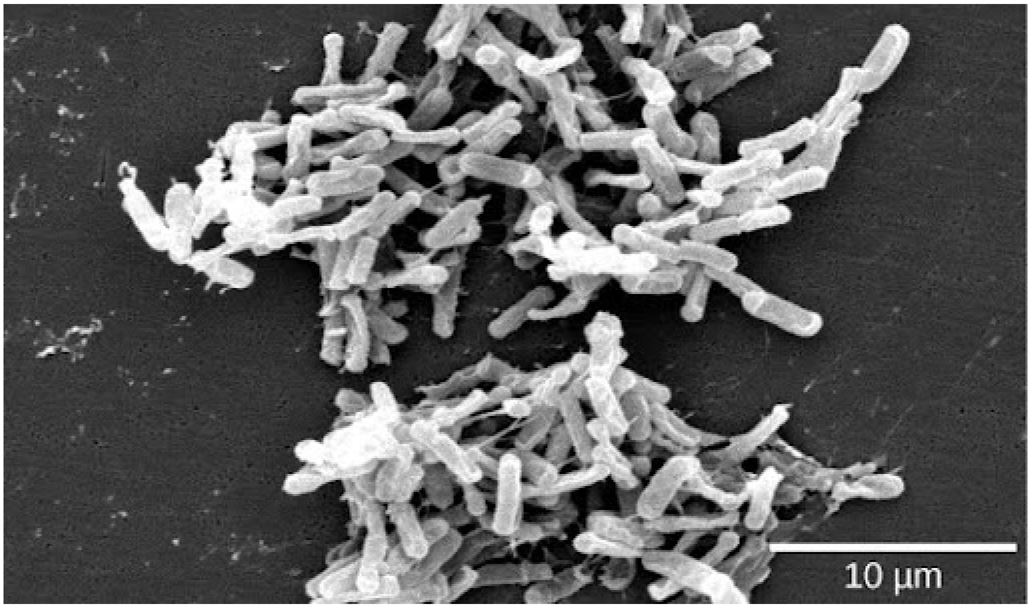

Figure 11. *This scanning electron micrograph shows Clostridium difficile, a Gram-positive, rod-shaped bacterium that causes severe diarrhea. Infection commonly occurs after the normal gut fauna is eradicated by antibiotics. (credit: modification of work by CDC, HHS; scale-bar data from Matt Russell)*

A particularly fascinating example of our normal flora relates to our digestive systems. People who take high doses of antibiotics tend to lose many of their normal gut bacteria, allowing a naturally antibiotic-resistant species called *Clostridium difficile* to overgrow and cause severe gastric problems, especially chronic diarrhea (**Figure 11**). Obviously, trying to treat this problem with antibiotics only makes it worse. However, it has been successfully treated by giving the patients fecal transplants from healthy donors to reestablish the normal intestinal microbial community. Clinical trials are underway to ensure the safety and effectiveness of this technique.

Scientists are also discovering that the absence of certain key microbes from our intestinal tract may set us up for a variety of problems. This seems to be particularly true regarding the appropriate functioning of the immune system. There are intriguing findings that suggest that the absence of these microbes is an important contributor to the development of allergies and some autoimmune disorders. Research is currently underway to test whether adding certain microbes to our internal ecosystem may help in the treatment of these problems as well as in treating some forms of autism.

Parasitism

A **parasite** is an organism that lives in or on another living organism and derives nutrients from it. In this relationship, the parasite benefits, but the **host** is harmed. The parasite usually weakens the host as it siphons resources the host would normally use to maintain itself. The parasite, however, is unlikely to kill the host, especially not quickly, because this would allow no time for the organism to complete its reproductive cycle by spreading to another host.

The reproductive cycles of parasites are often very complex, sometimes requiring more than one host species. A tapeworm is a parasite that causes disease in humans when contaminated, undercooked meat is consumed (**Figure 12**). The tapeworm can live inside the intestine of the host for several years, benefiting from the food the host is eating, and may grow to be over 50 ft long by adding segments. The parasite moves from species to species in a cycle, making two hosts necessary to complete its life cycle.

Another common parasite is *Plasmodium falciparum*, the protozoan cause of malaria, a significant disease in many parts of the world. Living in the human liver and red blood cells, the organism reproduces asexually in the gut of blood-feeding mosquitoes to complete its life cycle. Thus malaria is spread from human to human by mosquitoes, one of many arthropod-borne infectious diseases.

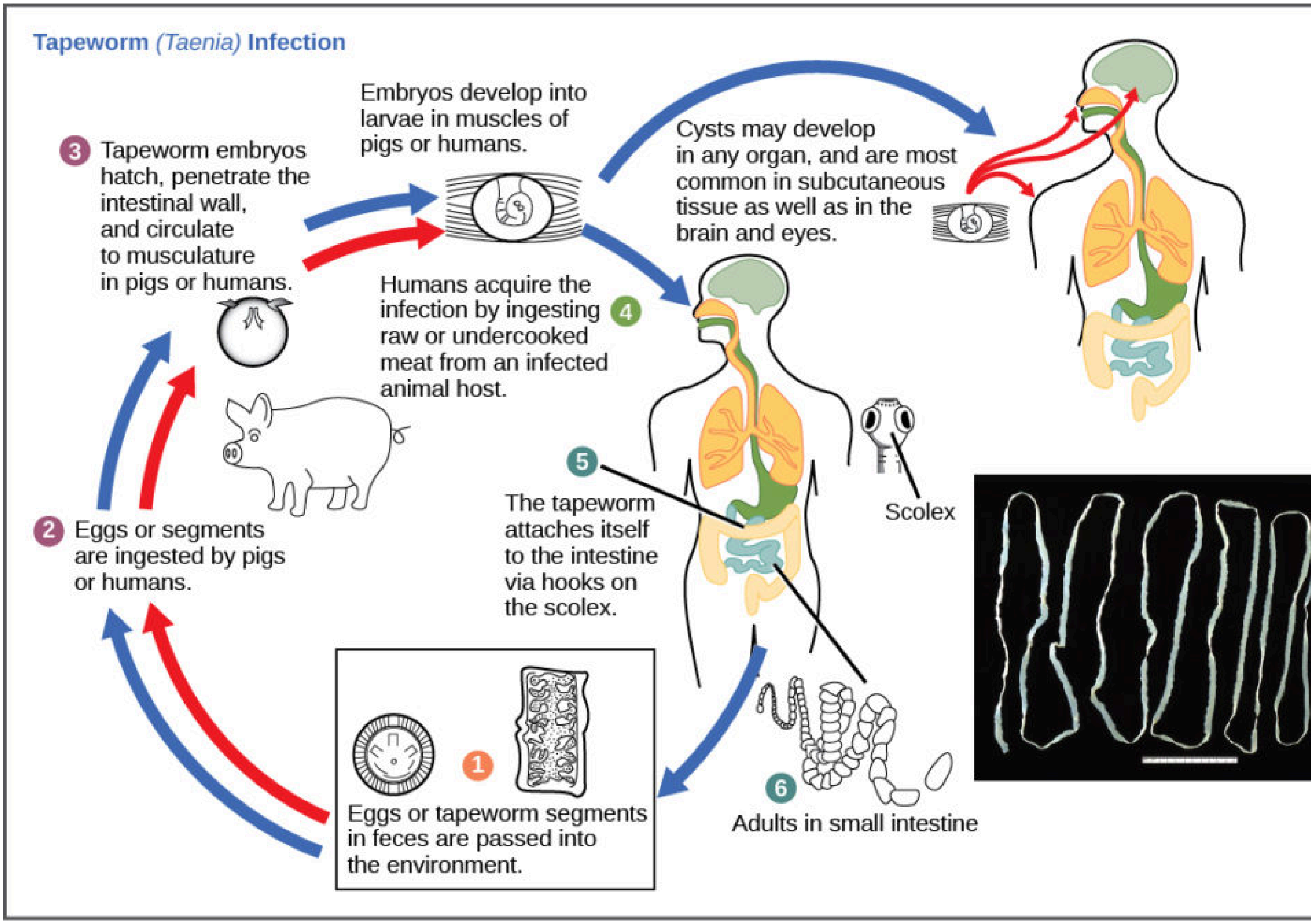

Figure 12. *This diagram shows the life cycle of a pork tapeworm (Taenia solium), a human worm parasite.*

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Scientist Spotlight: Lawrence David

Computational biologist Lawrence David studies the human microbiome. Research in his lab is focused on understanding how the microbial community in and on the human body behaves and changes over time and under varying conditions. Read about his fascinating yearlong study of his own gut microbiome in the *Science News* articles Lawrence David's gut check gets personal and How one scientist's gut microbes changed over a year, and check out the next video where David explains why he studies poop!

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Characteristics of Communities

Communities are complex entities that can be characterized by their structure (the types and numbers of species present) and dynamics (how communities change over time). Understanding community structure and dynamics enables community ecologists to manage ecosystems more effectively.

Foundation Species

Foundation species are considered the "base" or "bedrock" of a community, having the greatest influence on its overall structure. They are usually the primary producers: organisms that bring most of the energy into the community. Kelp, or brown algae, is a foundation species, forming the basis of the kelp forests off the coast of California (**Figure 13**).

Figure 13. *A kelp forest with tall stalks reaching the water surface, mainly exhibiting Ecklonia maxima from below.*

Foundation species may physically modify the environment to produce and maintain habitats that benefit the other organisms that use them. An example is the photosynthetic corals of the coral reef (**Figure 14**). Corals themselves are not photosynthetic but harbor symbionts within their body tissues (dinoflagellates called zooxanthellae) that perform photosynthesis; this is another example of a mutualism. The exoskeletons of living and dead coral make up most of the reef structure, which protects many other species from waves and ocean currents.

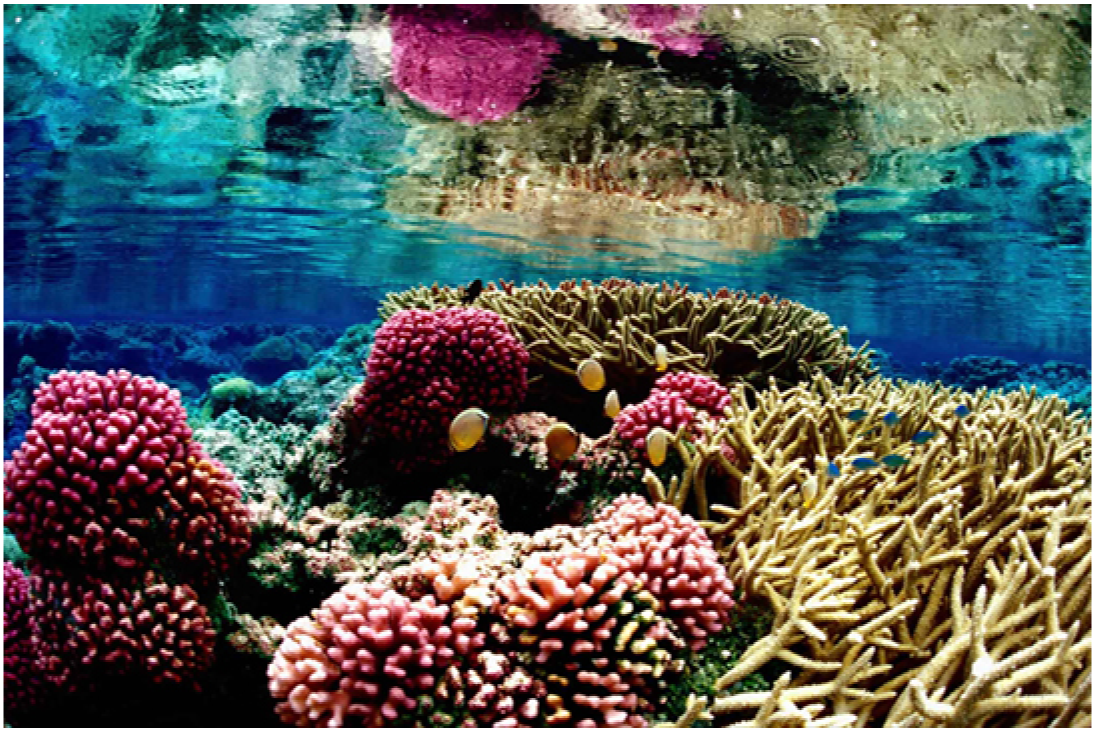

Figure 14. *Coral is the foundation species of coral reef ecosystems.*

In the next video from TEDx Youth, high school student John Ye presents the impact of climate change on coral reefs, and the solutions that are being explored by scientists.

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Biodiversity, Species Richness, and Relative Species Abundance

Biodiversity describes a community's biological complexity: it is measured by the number of different species (species richness) in a particular area and their relative abundance (species evenness). The area in question could be a habitat, a biome, or the entire biosphere. **Species richness** is the term that is used to describe the number of species living in a habitat or biome. Species richness varies across the globe (**Figure 15**). One factor in determining species richness is latitude, with the greatest species richness occurring in ecosystems near the equator, which often have warmer temperatures, large amounts of rainfall, and low seasonality. The lowest species richness occurs near the poles, which are much colder, drier, and thus less conducive to life in Geologic time (time since glaciations). The predictability of climate or productivity is also an important factor. Other factors influence species richness as well. For example, the study of **island biogeography** attempts to explain the relatively high species richness found in certain isolated island chains, including the Galápagos Islands that inspired the young Darwin. **Relative species abundance** is the number of individuals in a species relative to the total number of individuals in all species within a habitat, ecosystem, or biome. Foundation species often have the highest relative abundance of species.

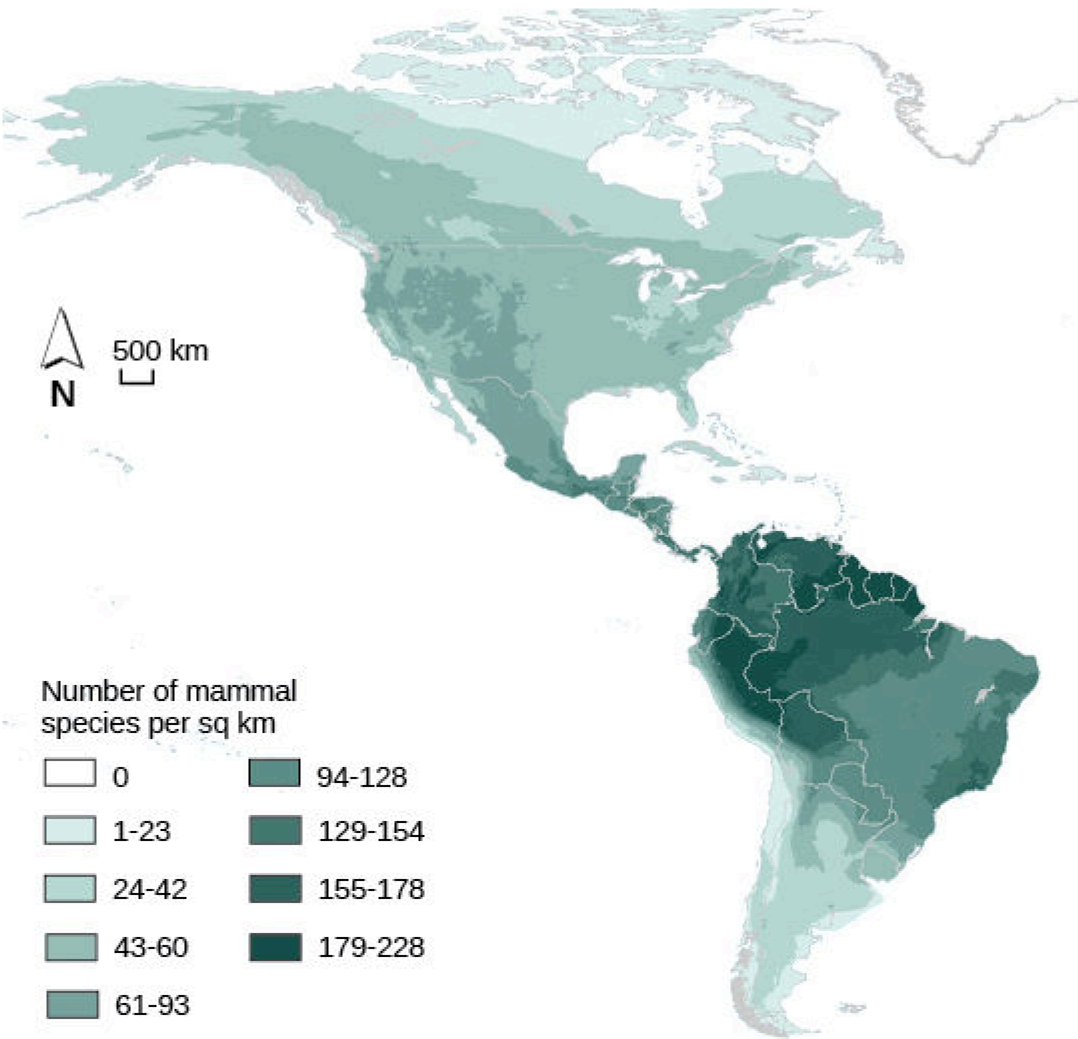

Figure 15. *The greatest species richness for mammals in North and South America is associated with the equatorial latitudes.*

Keystone Species

A **keystone species** is one whose presence is key to maintaining biodiversity within an ecosystem and to upholding an ecological community's structure. The intertidal sea star, *Pisaster ochraceus*, of the northwestern United States is a keystone species (**Figure 16**). Studies have shown that when this organism is removed from communities, populations of their natural prey (mussels) increase, completely altering the species composition and reducing biodiversity. Another keystone species is the banded tetra, a fish in tropical streams, which supplies nearly all of the phosphorus, a necessary inorganic nutrient, to the rest of the community. If these fish were to become extinct, the community would be greatly affected.

Figure 16. *The Pisaster ochraceus sea star is a keystone species.*

Scientist Spotlight: Ynés Mexía

Figure 17. *Photograph of Ynés Mexía with her plant press. Image Source: National Park Service*

When retracing the history of ecology, it is easy to come to a full stop at Charles Darwin's *On the Origin of Species*. His theory of evolution by natural selection shook the scientific community to its core, and observations used to synthesize this theory were collected on a five-year voyage around the world. However, Darwin was not the only one to achieve an expedition of such a grand scale.

Ynés Mexía was a Mexican-American botanist and adventurer. Motivated by a newfound interest in science, Ynes Mexia enrolled in classes at UC Berkeley in 1921. She was 51 years old at the time. By the age of 55, she was engaged in a series of botanical expeditions in remote Alaska and South/Central America. Alongside a Stanford University botanist, Mexia collected 500 plant specimens on her first trip to Mexico. She went on to collect about 145,000 specimens over the next 13 years, 500 of which were new species. Charles Darwin collected a mere 500 specimens on his famed five-year voyage. In addition to the sheer number of Mexia's samples, she was a natural scientist whose research contributed immensely to the modern classification of plants in North America.

Despite her impressive fieldwork, Mexia never received recognition comparable to that of her male counterparts. However, of the 500 plant species she discovered, 50 were named after her, as well as the entire genus *Mexianthus* (**Figure 18**).

Figure 18. *A Mexianthus mexicanus specimen collected by Ynes E. J. Mexia. Image source: [Smithsonian Institution]*

Learn more about this trailblazing botanist in the *Massive Science* article [Meet Ynes Mexia, late-blooming botanist whose adventures rivaled Darwin's], in the UNLADYLIKE2020 [profile of Ynes Mexia], and [this episode] of *Celebrating Science* from the Detroit Zoo!

Ecosystem Ecology

Section Goals

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

- Describe how organisms acquire energy in a food web and associated food chains
- Explain how the efficiency of energy transfers between trophic levels affects ecosystem structure and dynamics
- Discuss trophic levels and how ecological pyramids are used to model them

An **ecosystem** is a community of living organisms and their interactions with their abiotic (non-living) environment. Ecosystems can be small, such as the tide pools found near the rocky shores of many oceans, or large, such as the Amazon Rainforest in Brazil. In this section, we'll learn about ecosystems and how energy moves within a system.

This next video provides a quick introduction to the concepts we'll be learning.

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How Organisms Acquire Energy in a Food Web

All living things require energy in one form or another. Energy is required by most complex metabolic pathways (often in the form of ATP), especially those responsible for building large molecules from smaller compounds. Life itself is an energy-driven process. Living organisms would not be able to assemble macromolecules (proteins, lipids, nucleic acids, and complex carbohydrates) without a constant energy input.

Energy is acquired by living things in three ways: photosynthesis, chemosynthesis, and the consumption and digestion of other living or previously living organisms by heterotrophs.

Photosynthetic and chemosynthetic organisms are both grouped into a category known as autotrophs: organisms capable of synthesizing their own food (more specifically, capable of using inorganic carbon as a carbon source). Photosynthetic autotrophs (photoautotrophs) use sunlight as an energy source, whereas chemosynthetic autotrophs (chemoautotrophs) use inorganic molecules as an energy source. Autotrophs are critical for all ecosystems. Without these organisms, energy would not be available to other living organisms, and life itself would not be possible.

Photoautotrophs, such as plants, algae, and photosynthetic bacteria, serve as the energy source for a majority of the world's ecosystems. These ecosystems are often described as grazing food webs. Photoautotrophs harness the solar energy of the sun by converting it to chemical energy in the form of ATP (and NADP). The energy stored in ATP is used to synthesize complex organic molecules, such as glucose.

Chemoautotrophs are primarily bacteria that are found in rare ecosystems where sunlight is not available, such as in those associated with dark caves or hydrothermal vents at the bottom of the ocean (**Figure 1**). Many chemoautotrophs in hydrothermal vents use hydrogen sulfide (H2S), which is released from the vents as a source of chemical energy. This allows chemoautotrophs to synthesize complex organic molecules, such as glucose, for their own energy and in turn supplies energy to the rest of the ecosystem.

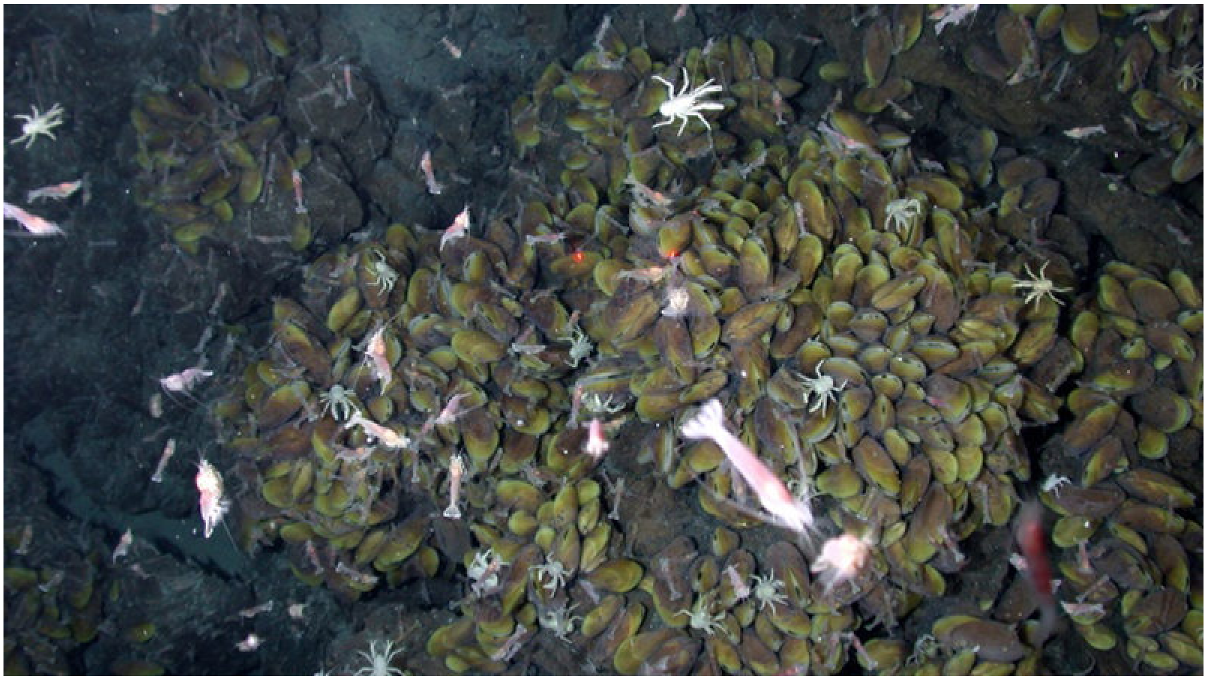

Figure 1. *Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This picture was taken in 2006 at the submerged NW Eifuku volcano off the coast of Japan by the National Oceanic and Atmospheric Administration (NOAA). The summit of this highly active volcano lies 1535 m below the surface.*

Food Chains and Food Webs

Now that we have reviewed how organisms acquire energy, it is important to understand how that energy is passed from one organism to another in the community. In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass. There is a single path through the chain. For example, if you had a hamburger for lunch, you might be part of a food chain that looks like this: grass → cow → human. Each organism in a food chain occupies what is called a **trophic level**. Depending on their role as producers or consumers, species or groups of species can be assigned to various trophic levels.

In many ecosystems, the bottom of the food chain consists of photosynthetic organisms (plants and/or phytoplankton), which are called **primary producers**. The organisms that consume the primary producers are herbivores: the **primary consumers**. **Secondary consumers** are usually carnivores that eat the primary consumers. **Tertiary consumers** are carnivores that eat other carnivores. Higher-level consumers feed on the next lower trophic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. We can see examples of these levels in **Figure 2**. The green algae are primary producers that get eaten by mollusks—the primary consumers. The mollusks then become lunch for the slimy sculpin fish, a secondary consumer, which is itself eaten by a larger fish, the Chinook salmon—a tertiary and in this case, “apex” consumer.

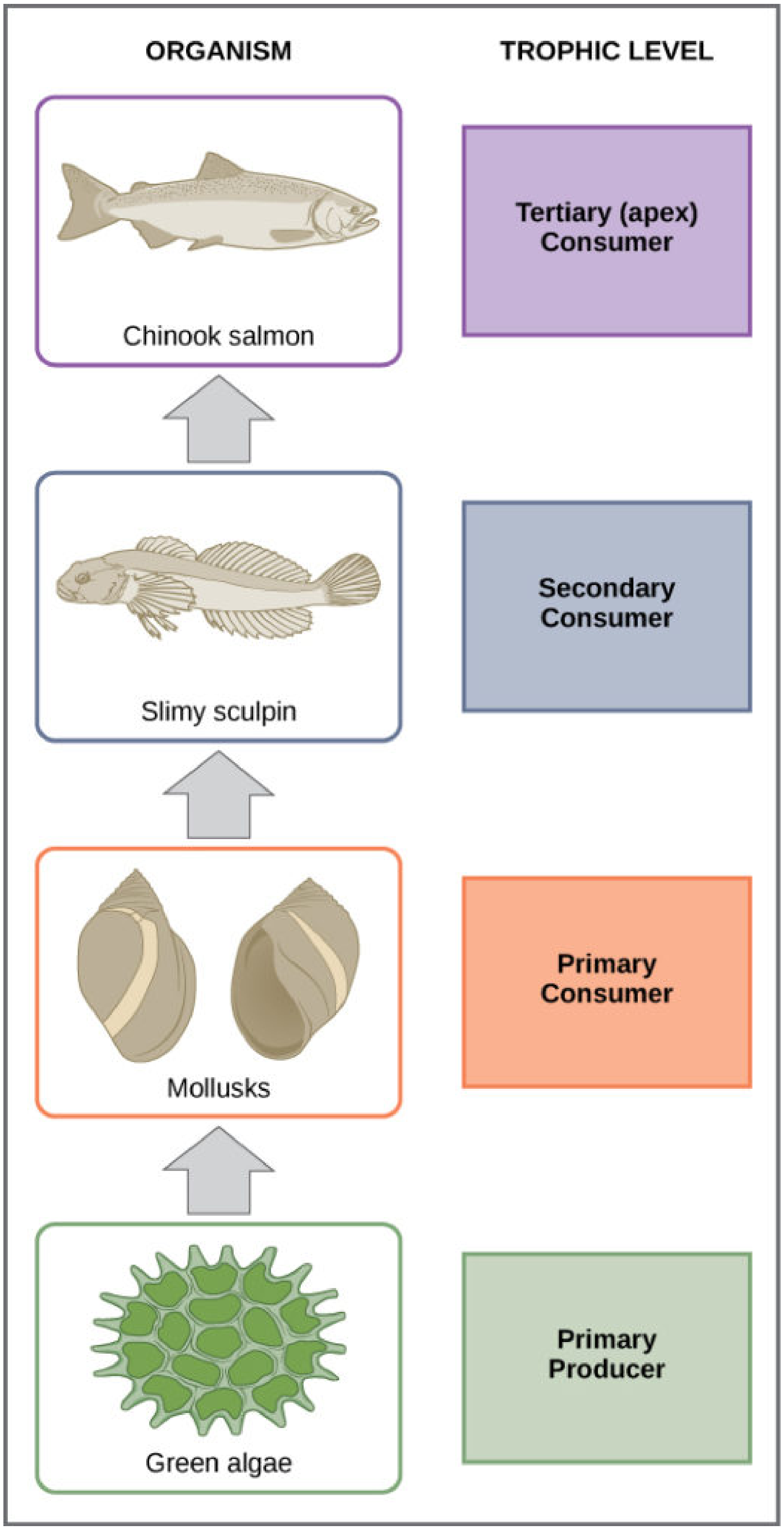

Figure 2. *These are the trophic levels of a food chain in Lake Ontario at the United States-Canada border. Energy and*

nutrients flow from photosynthetic green algae at the bottom to the top of the food chain: the Chinook salmon.

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While food chains are flexible for analytical modeling, are easier to follow, and are easier to experiment with, there are problems with using food chains to accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, some of these organisms can feed on species from more than one trophic level. Consider the hamburger example from above. The source of the hamburger patty is a cow, which is a primary consumer, but the bun is made from wheat, a primary producer. Likewise, any one organism can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not a true representation of ecosystem structure. Instead, a food *web* is a holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment. A **food web** is a graphic representation of a non-linear web of primary producers, primary consumers, and higher-level consumers (**Figure 3**). Food webs more accurately represent ecosystem structure and dynamics, and data can be directly used as input for simulation modeling.

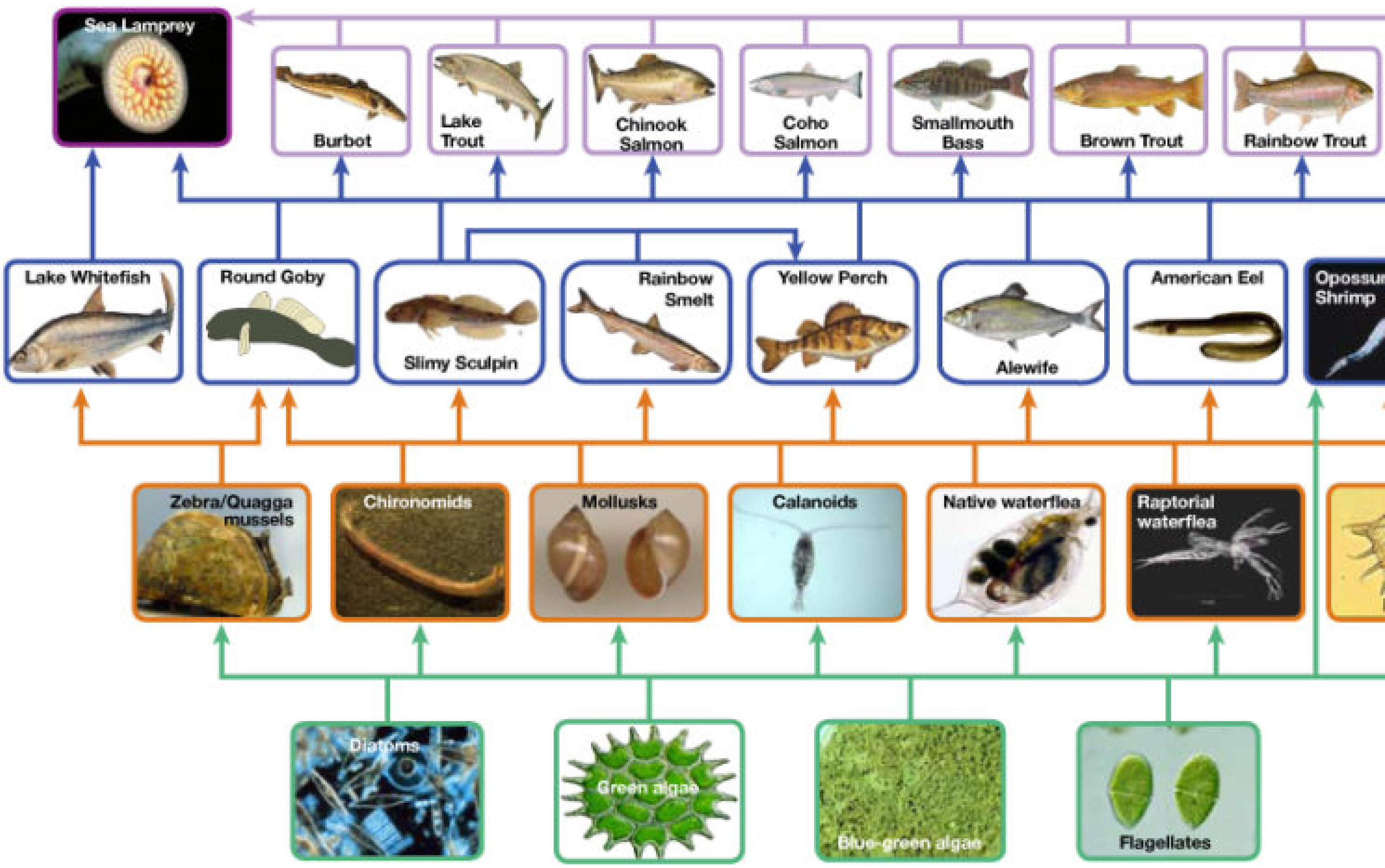

Figure 3. *This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosyst green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opos and primary consumers.*

Ecosystems are often depicted as having **bottom-up control**, where the most biomass exists in producers that then support progressively smaller populations of herbivores, carnivores, and so on. In other words, the lowest trophic level dictates the community structure above it based on how much energy it can fix in photosynthesis. However, you might also find **top-down control** in an ecosystem. With top-down control, the predators/top carnivores are controlling things. Their numbers and behavior dictate how many prey are found, which in turn dictates how many plants and autotrophs are consumed. In this way, in ecosystems, top predators, often at the highest trophic level, play a critical role in regulating the populations of species at lower trophic levels. They do so by controlling the abundance of herbivores or lower-level consumers. When top predators are present and exert their influence, they can limit the populations of herbivores, which in turn can lead to changes in the abundance of primary producers (plants) that are the primary food source for herbivores. These effects can cascade through the ecosystem, affecting multiple trophic levels. In some ecosystems, these top predators control the herbivore populations so that the herbivore populations do not explode, which could lead to overgrazing of plant communities, which can have detrimental effects on ecosystem structure and diversity.

In the next video, enter a kelp forest to see an example of top-down control and to explore the effects of changes in the dynamics of organisms in this diverse ecosystem using food web models. Be sure to pause the video when prompted to formulate your own predictions for the questions presented!

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Another classic example of top-down control theory is the reintroduction of wolves into Yellowstone National Park in the United States. With the return of wolves, the populations of elk, which were overgrazing and affecting plant communities, were controlled.

So the return of wolves had cascading effects, leading to a more diverse and balanced ecosystem, as illustrated in the next video:

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Transfer of Energy Between Trophic Levels

One major factor that limits the length of any given food chain is energy. Energy can pass from one trophic level to the next when organic molecules from an organism's body are eaten by another organism. However, the transfer of energy between trophic levels is not usually very efficient. The loss of energy between trophic levels is illustrated in **Figure 4** below.

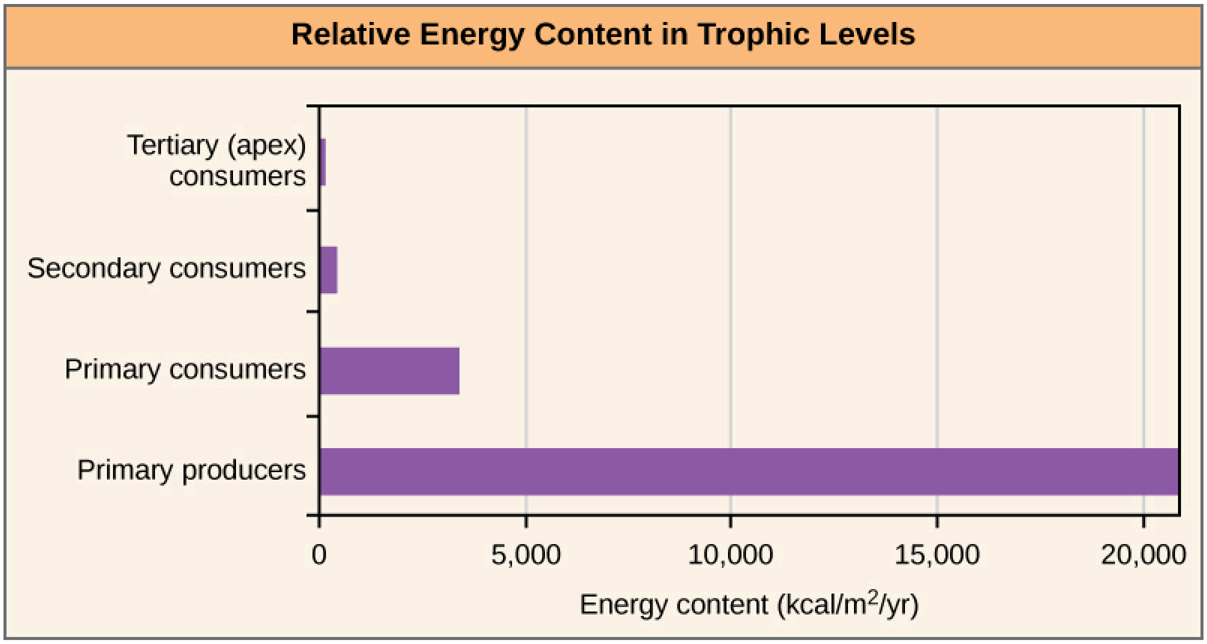

Figure 4. *The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.*

On average, only about 10% of the energy stored as biomass in one trophic level (e.g., primary producers) is converted into biomass and becomes available as food for the next trophic level (e.g., primary consumers). That means that at the first trophic level, autotrophs are using ~90% of the energy that they fix during photosynthesis. They are using the energy to grow taller, grow more roots, produce flowers, and engage in metabolic processes. During such conversions, some energy may be lost as heat. When a primary consumer eats the plants, they will not be able to successfully assimilate all the energy as well. Some molecules are not digestible by the consumer and are lost in its feces (poop). Further, of the energy-carrying molecules that do get absorbed by the consumer, some are used in cellular respiration (instead of being stored as biomass). This is why the amount of energy decreases so quickly as you move up the trophic levels and why you will find a limited number of trophic levels in any one ecosystem or community. There may not be enough energy remaining in the food chain to support viable populations at a higher trophic level. This concept is called the **10% rule** and is a fundamental concept in ecosystem ecology.

The efficiency of energy use by each trophic level also varies. That is, how well organisms use and incorporate the energy from food into biomass to fuel the next trophic level. In general, cold-blooded animals (ectotherms), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than warm-blooded animals (endotherms), such as birds and mammals. The extra heat generated in endotherms, although an advantage in terms of the activity of these organisms in colder environments, is a major disadvantage in terms of efficiency. Therefore, many endotherms have to eat more than ectotherms to get the energy they need for survival.

The inefficiency of energy use by warm-blooded animals has broad implications for the world's food supply. It is widely accepted that the meat industry uses large amounts of crops to feed livestock, and because the energy efficiency is low, much of the energy from animal feed is lost. For example, it costs about $0.01 to produce 1000 dietary calories (kcal) of corn or soybeans, but approximately $0.19 to produce a similar number of calories growing cattle for beef consumption. The same energy content of milk from cattle is also costly, at approximately $0.16 per 1000 kcal. Thus, there has been a growing movement worldwide to promote the consumption of nonmeat and nondairy foods so that less energy is wasted feeding animals for the meat industry.

Ecological Pyramids: Modeling Ecosystem Energy Flow

Ecological pyramids provide an intuitive, visual picture of how the trophic levels in an ecosystem compare for a particular parameter (such as energy flow, biomass, or number of organisms). Let's take a look at these three types of pyramids and see how they reflect the structure and function of ecosystems.

1. **Energy pyramids** represent energy flow through trophic levels. For instance, the pyramid below shows gross productivity for each trophic level in the Silver Springs ecosystem. An energy pyramid usually shows *rates* of energy flow through trophic levels, not absolute amounts of energy stored. It can have energy units, such as kcal/m2/yr, or biomass units, such as g/m2/yr.

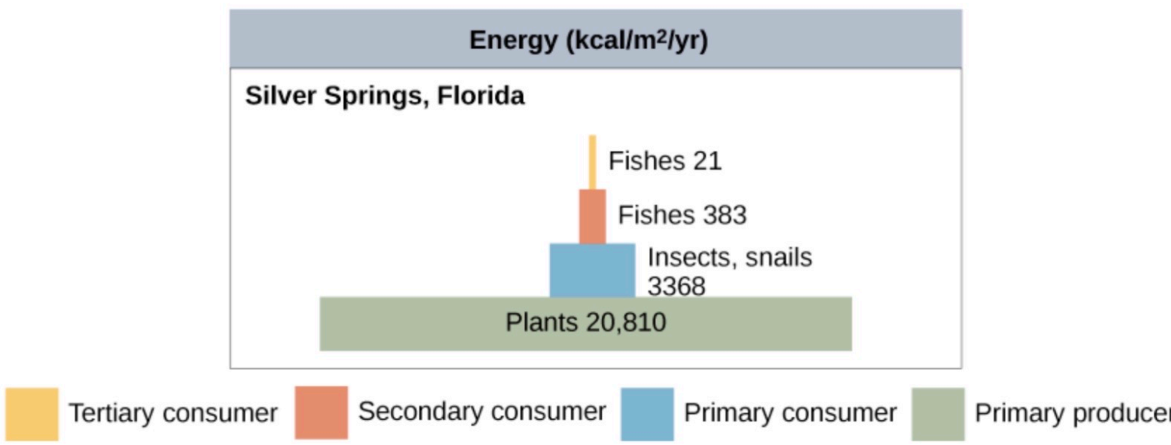

Figure 5. *Image modified from "Energy flow: Figure 3," by OpenStax College, Biology CC BY 4.0.*

Energy pyramids are always upright, that is, narrower at each successive level (unless organisms enter the ecosystem from elsewhere). This pattern reflects the laws of thermodynamics, which tell us that new energy can't be created, and that some must be converted to a form that cannot be used to do work (e.g., heat) in each transfer. An ecosystem without sufficient primary productivity cannot be supported.

2. Another way to visualize ecosystem structure is with **biomass pyramids**. Biomass is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. A biomass pyramid measures the amount of energy converted into living tissue at the different trophic levels.Below on the left, we can see a biomass pyramid for the Silver Springs ecosystem. This pyramid, like many biomass pyramids, is upright. However, the biomass pyramid shown on the right – from a marine ecosystem in the English Channel – is upside-down (inverted).

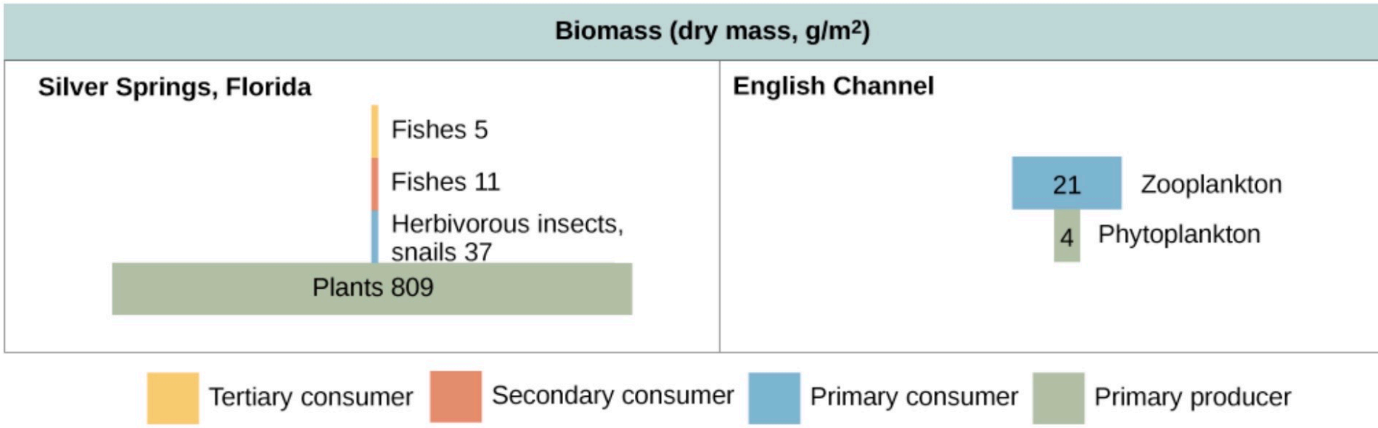

Figure 6. *Image modified from "[Energy flow: Figure 3,]()" by OpenStax College, Biology CC BY 4.0.*

The inverted pyramid is possible because of the high turnover rate of the phytoplankton. They get rapidly eaten by the primary consumers (zooplankton), so their biomass at any point in time is small. However, they reproduce so fast that, despite their low steady-state biomass, they have high primary productivity that can support large numbers of zooplankton.

3. **Numbers pyramids** show how many individual organisms there are in each trophic level. They can be upright, inverted, or kind of lumpy, depending on the ecosystem.As shown in the figure below, a typical grassland during the summer has a base of numerous plants, and the numbers of organisms decrease at higher trophic levels. However, during the summer in a temperate forest, the base of the pyramid instead consists of a few plants (mostly trees) that are vastly outnumbered by primary consumers (mostly insects). Because individual trees are big, they can support the other trophic levels despite their small numbers.

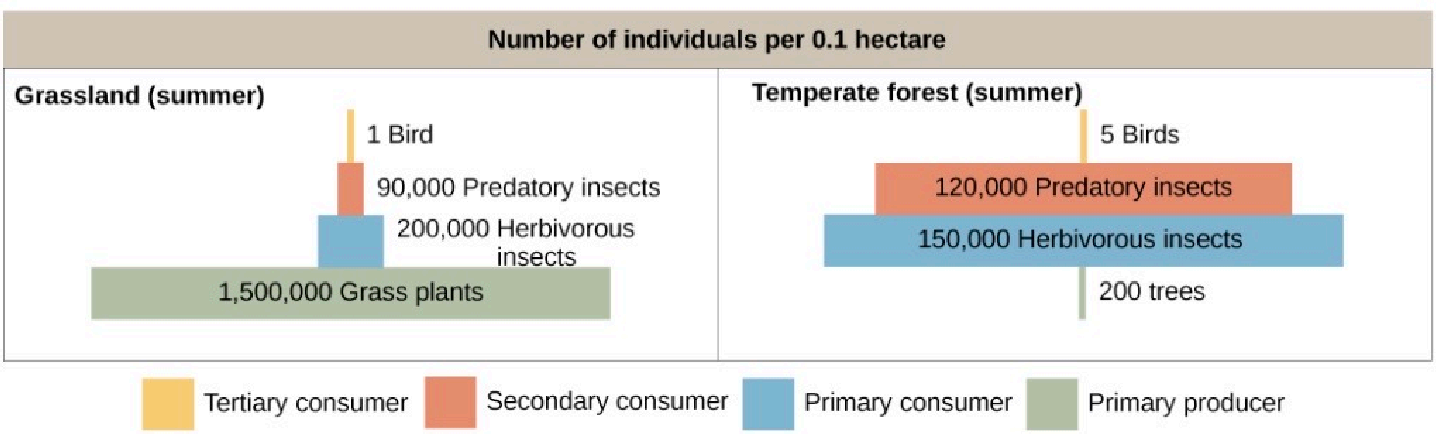

Figure 7. *Image modified from "[Energy flow: Figure 3,]()" by OpenStax College, Biology CC BY 4.0.*

To review, pyramids of organisms may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of organisms can sustain a larger biomass at the next trophic level because the organisms reproduce rapidly and thus supply continuous nourishment. Energy pyramids, however, must always be upright because of the laws of thermodynamics. The first law of thermodynamics states that energy can neither be created nor destroyed; thus, each trophic level must acquire energy from the trophic level below. The second law of thermodynamics states that, during the transfer of energy, some energy is always lost as heat; thus, less energy is available at each higher trophic level.

So which type of pyramid is best? Each type of pyramid provides slightly different information about an ecosystem and how energy is stored in, and moves through, that ecosystem's trophic levels. There is no one "best pyramid," and the pyramid that's most useful will depend on what question we are asking about the ecosystem.

Biological Amplification or Biomagnification

One of the most important environmental consequences of ecosystem dynamics is biomagnification. **Biomagnification** is the increasing concentration of persistent, toxic substances in organisms at each trophic level, from the primary producers to the apex consumers. Many substances have been shown to bioaccumulate, including the pesticide **d**ichloro**d**iphenyl**t**richloroethane (DDT), which was described in the 1960s bestseller *Silent Spring* by marine biologist Rachel Carson. DDT was a commonly used pesticide before its dangers became known. In some aquatic ecosystems, organisms from each trophic level consumed many organisms of the lower level, which caused DDT to increase in birds (apex consumers) that ate fish. Thus, the birds accumulated sufficient amounts of DDT to cause fragility in their eggshells. This effect increased egg breakage during nesting and was shown to have adverse effects on these bird populations. Carson's combination of scientific knowledge and illuminating writing helped raise awareness about overall environmental issues as well as the specifics of the pesticide. The use of DDT was banned in the United States in the 1970s.

Para-Cats!

In the early 1950s, there was an outbreak of malaria in Borneo (now Indonesia). The World Health Organization tried to solve the problem. They sprayed large amounts DDT to kill the mosquitoes that carried the malaria. The mosquitoes indeed died and there was less malaria. That was good. However, there were side effects. One of the first effects was that the roofs of people's houses (which were thatched roofs) began to fall down on their heads. It turned out that the DDT was also killing a parasitic wasp that ate thatch-eating caterpillars. Without the wasps to eat them, there were more and more thatch-eating caterpillars. Worse than that, the insects that died from being poisoned by DDT were eaten by gecko lizards, this caused the geckos nerve damage which slowed their reflexes and made them more likely to be eaten by cats. The cats started to die of DDT poisoning, the rats flourished, and the people were threatened by outbreaks of two new serious diseases carried by the rats, Sylvatic plague and Typhus. To cope with these problems, which it had itself created, the World Health Organization had to parachute live cats into Borneo to eat the rats!

O'Shaughnessy PT. Parachuting cats and crushed eggs the controversy over the use of DDT to control malaria. Am J Public Health. 2008 Nov;98(11):1940-8. doi: 10.2105/AJPH.2007.122523.

Watch this whiteboard animation telling the cautionary tale of cats in Borneo and what can happen when decisions are made without understanding the interconnectedness in nature:

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Other substances that biomagnify are polychlorinated biphenyls (PCBs), which were used in coolant liquids in the United States until their use was banned in 1979, and heavy metals, such as mercury, lead, and cadmium. These substances were best studied in aquatic ecosystems, where fish species at different trophic levels accumulate toxic substances brought through the ecosystem by the primary producers. As illustrated in a study performed by the National Oceanic and Atmospheric Administration (NOAA) in the Saginaw Bay of Lake Huron (**Figure 8**), PCB concentrations increased from the ecosystem's primary producers (phytoplankton) through the different trophic levels of fish species. The apex consumer (walleye) has more than four times the amount of PCBs compared to phytoplankton. Also, based on results from other studies, birds that eat these fish may have PCB levels at least one order of magnitude higher than those found in the lake fish.

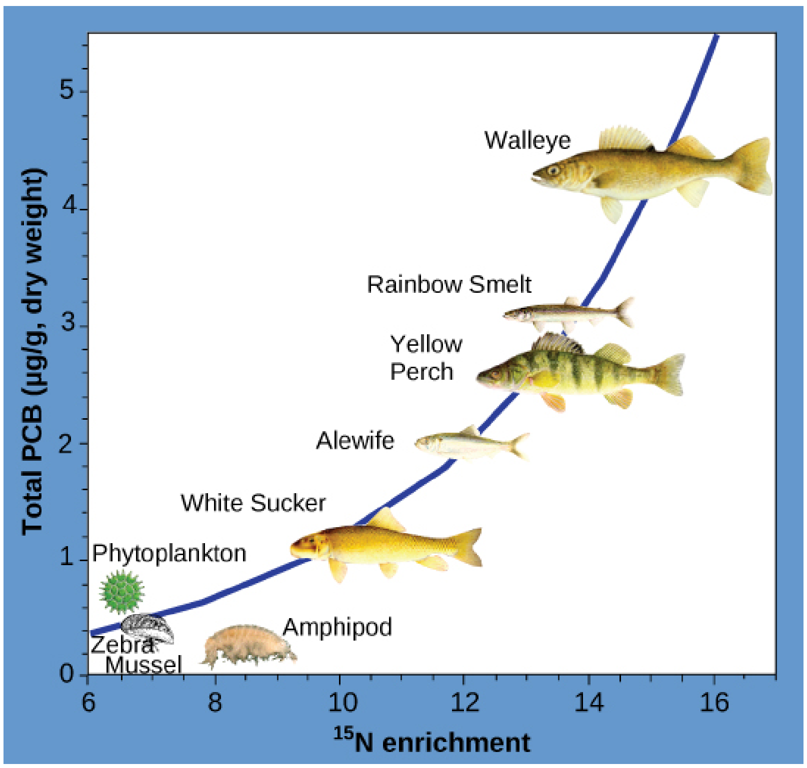

Figure 8. *This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (15N), which is a marker for increasing trophic levels. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels.*

Other concerns have been raised by the accumulation of heavy metals, such as mercury and cadmium, in certain types of seafood. The United States Environmental Protection Agency (EPA) recommends that pregnant people and young children should not consume any swordfish, shark, king mackerel, or tilefish because of their high mercury content. These individuals are advised to eat fish low in mercury: salmon, tilapia, shrimp, pollock, and catfish. Biomagnification is a good example of how ecosystem dynamics can affect our everyday lives, even influencing the food we eat.

The Carbon Cycle

Learning Objectives

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

- Discuss the biological carbon cycle and why carbon is essential to all living things

Energy flows directionally through ecosystems, entering as sunlight (or inorganic molecules for chemoautotrophs) and leaving as heat during the many transfers between trophic levels. However, the matter that makes up living organisms is conserved and recycled. The six most common elements associated with organic molecules—carbon, nitrogen, hydrogen, oxygen, phosphorus, and sulfur—take a variety of chemical forms and may exist for long periods in the atmosphere, on land, in water, or beneath the Earth’s surface.

Carbon is one of the basic building blocks of life and the most abundant element in organisms, accounting for about half of typical dry biomass. Carbon is present in all organic molecules, and its role in the structure of macromolecules is of primary importance to living organisms. Carbon compounds contain especially high energy, particularly those derived from fossilized organisms, mainly plants, which humans use as fuel. Since the 1800s, the number of countries using massive amounts of fossil fuels has increased. Since the beginning of the Industrial Revolution, global demand for the Earth’s limited fossil fuel supplies has risen; therefore, the amount of carbon dioxide in our atmosphere has increased. This increase in carbon dioxide has been associated with climate change and other disturbances of the Earth’s ecosystems and is a major environmental concern worldwide. Thus, the “carbon footprint” is based on how much carbon dioxide is produced and how much fossil fuel countries consume.

The carbon cycle is most easily studied as two interconnected sub-cycles: one dealing with rapid carbon exchange among living organisms and the other dealing with the long-term cycling of carbon through geologic processes. The entire carbon cycle is shown in **Figure 1**.

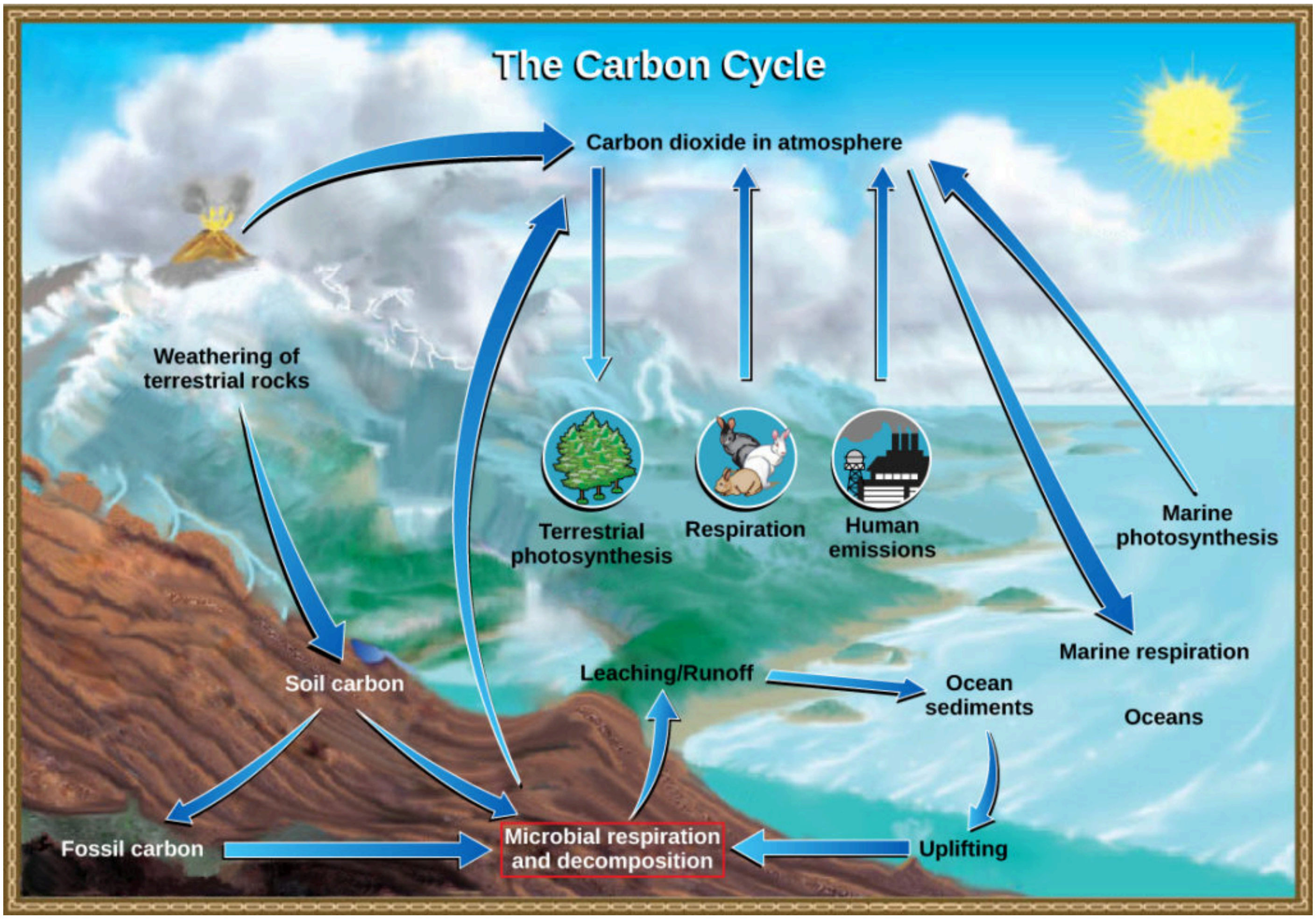

Figure 1. *Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions bring this stored carbon back into the carbon cycle.*

Click this link to read information about the United States Carbon Cycle Science Program.

The Biological Carbon Cycle

Living organisms are connected in many ways, even between ecosystems. A good example of this connection is the exchange of carbon between autotrophs and heterotrophs within and between ecosystems by way of atmospheric carbon dioxide.

Carbon dioxide is the basic building block that most autotrophs use to build multi-carbon, high-energy compounds, such as glucose. The energy harnessed from the sun is used by these organisms to form the covalent bonds that link carbon atoms together. These chemical bonds thereby store this energy for later use in the process of respiration. Most terrestrial autotrophs obtain their carbon dioxide directly from the atmosphere, while marine autotrophs may acquire it in the dissolved form (bicarbonate, HCO_3^-). However carbon dioxide is acquired, a by-product of the process is oxygen. Photosynthetic organisms are responsible for bringing the Earth's atmosphere to the approximately 21 percent oxygen content that we observe today.

Heterotrophs and autotrophs are partners in biological carbon exchange (especially the primary consumers, largely herbivores). Heterotrophs acquire the high-energy carbon compounds from the autotrophs by consuming them, and breaking them down by respiration to obtain cellular energy, such as ATP. The most efficient type of respiration, aerobic respiration, requires oxygen obtained from the atmosphere or dissolved in water. Thus, there is a constant exchange of oxygen and carbon dioxide between the autotrophs (which need the carbon) and the heterotrophs (which need the oxygen). Gas exchange through the atmosphere and water is one way that the carbon cycle connects all living organisms on Earth.

The Biogeochemical Carbon Cycle

The movement of carbon through the land, water, and air is complex, and in many cases, it occurs much more slowly geologically than as seen between living organisms. Carbon is stored for long periods in what are known as carbon reservoirs, which include the atmosphere, bodies of liquid water (mostly oceans), ocean sediment, soil, land sediments (including fossil fuels), and the Earth's interior.

As stated, the atmosphere is a major reservoir of carbon in the form of carbon dioxide and is essential to the process of photosynthesis. The level of carbon dioxide in the atmosphere is greatly influenced by the reservoir of carbon in the oceans. The exchange of carbon between the atmosphere and ocean influences how much carbon is found in each location, and each one affects the other reciprocally. Carbon dioxide (CO_2) from the atmosphere dissolves in seawater, forming bicarbonate ions (HCO_3^-) which can be taken up and fixed by photosynthetic algae and bacteria, which are the base of the marine food web. More than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these bicarbonate ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), the main mineral in marine organisms' shells, and the primary component of coral reefs (the corals use calcium carbonate to build their stony skeletons). These organisms eventually form sediments on the ocean floor. Over geologic time, the calcium carbonate forms limestone, which comprises the largest carbon reservoir on Earth.

On land, carbon is stored in soil as a result of the decomposition of living organisms (by decomposers) or from weathering of terrestrial rock and minerals. This carbon can be leached into the water reservoirs by surface runoff. Deeper underground, on land and at sea, are fossil fuels: the anaerobically decomposed remains of plants that take millions of years to form. Fossil fuels are considered a nonrenewable resource because their use far exceeds their rate of formation. A non-renewable resource, such as fossil fuel, is either regenerated very slowly or not at all. Another way for carbon to enter the atmosphere is from land (including land beneath the surface of the ocean) by the eruption of volcanoes and other geothermal systems. Carbon sediments from the ocean floor are taken deep within the Earth by the process of subduction: the movement of one tectonic plate beneath another. Carbon is released as carbon dioxide when a volcano erupts or from volcanic hydrothermal vents.

Over almost all of geological time, the amount of CO_2 absorbed by the global biota from the atmosphere was similar to that released through respiration and decomposition. Consequently, the cycling of this nutrient can be viewed as a steady-state system. In modern times, however, anthropogenic emissions (those caused by humans) have changed the atmospheric carbon balance. Global emissions of CO_2 and CH_4 are now larger than the uptake of these gasses, an imbalance that has resulted in increasing concentrations in the atmosphere. This phenomenon intensifies the greenhouse effect of Earth and results in a warming climate.

Animal husbandry by humans also increases atmospheric carbon. The large numbers of land animals raised to feed the Earth's growing population results in increased carbon dioxide levels in the atmosphere due to farming practices and respiration and methane production. This is another example of how human activity indirectly affects biogeochemical cycles in a significant way. Although much of the debate about the future effects of increasing atmospheric carbon on climate change focuses on fossil fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

For an explanation of the cyclical relationship of carbon, humans and the environment, check out this animated lesson from TED-Ed:

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VI

Reproduction in Populations

This module contains the following chapters:

Adapted from:

Modes of Reproduction

Section Goals

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

- Compare and contrast asexual and sexual reproduction methods
- Describe the advantages and disadvantages of asexual and sexual reproduction
- Discuss external and internal methods of fertilization

A Note on Sex and Gender

The chapters of this text that highlight topics regarding reproduction and sex do not refer to *gender*, which is a different concept.

Although the terms are sometimes used interchangeably, sex and gender refer to two different ideas. According to the American Psychological Association: "Sex is typically assigned at birth (or before during ultrasound) based on the appearance of external genitalia. When the external genitalia is ambiguous, other indicators (e.g., internal genitalia, chromosomal and hormonal sex) are considered to assign a sex, with the aim of assigning a sex that is most likely to be congruent with the child's gender identity." Gender is "a person's deeply felt, inherent sense of being a girl, woman, or female; a boy, a man, or male; a blend of male or female; or an alternative gender[1]."

Gender influences how people perceive themselves and each other, how they act and interact, and the distribution of power and resources in society. Gender identity is not confined to a binary (girl/woman, boy/man), nor is it static; it exists along a continuum and can change over time. There is considerable diversity in how individuals and groups understand, experience, and express gender through their roles, the expectations placed on them, their relations with others, and the complex ways that gender is institutionalized in society.

Just like there are many individuals for whom chromosomal, hormonal, gonadal, and anatomical sex do not align, so too are there individuals whose innate gender identity or gender expression differs from their phenotypic sex as determined by external genitalia. This situation is called transgender. Individuals for whom their gender identity is the same as their phenotypic sex are cisgender.

Historically, the biology of gender has not been as well studied as sex, and, as such, it is poorly understood. However, a number of studies provide strong evidence that gender is innate, with both genetic and other biological causes. For example, transgender individuals may have brain structures that more closely match their gender than their phenotypic sex. A majority of individuals with 5-alpha-reductase deficiency choose to live as male after puberty, despite culturally having been raised as female to that point. XY babies with abnormal genitalia who are surgically assigned a female sex (a practice more common in previous decades) have a much higher incidence of transgender. And twin studies and adoption studies – standard ways to determine whether genetic factors affect a trait – strongly suggest a genetic component to gender.

Sexual and Asexual Reproduction

Reproduction is the production of offspring. Reproduction can happen in a variety of ways and is usually separated into sexual and asexual reproduction. Both methods have advantages and disadvantages.

Asexual reproduction produces offspring that are genetically identical to the reproducing individual. Note that this is a different term from human asexual identity.

A single individual can produce offspring asexually, and large numbers of offspring can be produced quickly. In a stable or predictable environment, asexual reproduction is an effective means of reproduction because all the offspring will be adapted to that environment. In an unstable or unpredictable environment, asexually reproducing species may be at a disadvantage because all the offspring are genetically identical and may not have the genetic variation to survive in new or different conditions. On the other hand, the rapid rates of asexual reproduction may allow for a speedy response to environmental changes if individuals have mutations. An additional advantage of asexual reproduction is that colonization of new habitats may be easier when an individual does not need to find a mate to reproduce.

During **sexual reproduction,** the genetic material of two individuals is combined to produce genetically diverse offspring that differ from their parents. (Sexual reproduction involves meiosis, a cell division process that creates sex cells). The genetic diversity of sexually produced offspring is thought to give species a better chance of surviving in an unpredictable or changing environment. Species that reproduce sexually must maintain two different types of individuals, males, and females, which can limit the ability to colonize new habitats as both sexes must be present.

Try It!

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Asexual Reproduction

Asexual reproduction occurs in prokaryotic microorganisms (bacteria) and some eukaryotic single-celled and multi-celled organisms. There are a number of ways that animals reproduce asexually.

Fission

Fission, also called binary fission, occurs in prokaryotic microorganisms and in some invertebrate, multi-celled organisms. After a period of growth, an organism splits into two separate organisms. Some unicellular eukaryotic organisms undergo binary fission by mitosis. In other organisms, part of the individual separates and forms a second individual. This process occurs, for example, in many asteroid echinoderms through the splitting of the central disk. Some sea anemones and some coral polyps (Figure 1) also reproduce through fission.

Figure 1. *Coral polyps reproduce asexually by fission. (credit: G. P. Schmahl, NOAA FGBNMS Manager)*

Budding

Budding is a form of asexual reproduction that results from the outgrowth of a part of a cell or body region leading to a separation from the original organism into two individuals. Budding occurs commonly in some invertebrate animals such as corals and hydras. In hydras, a bud forms that develops into an adult and breaks away from the main body, as illustrated in Figure 2, whereas in coral budding, the bud does not detach and multiplies as part of a new colony.

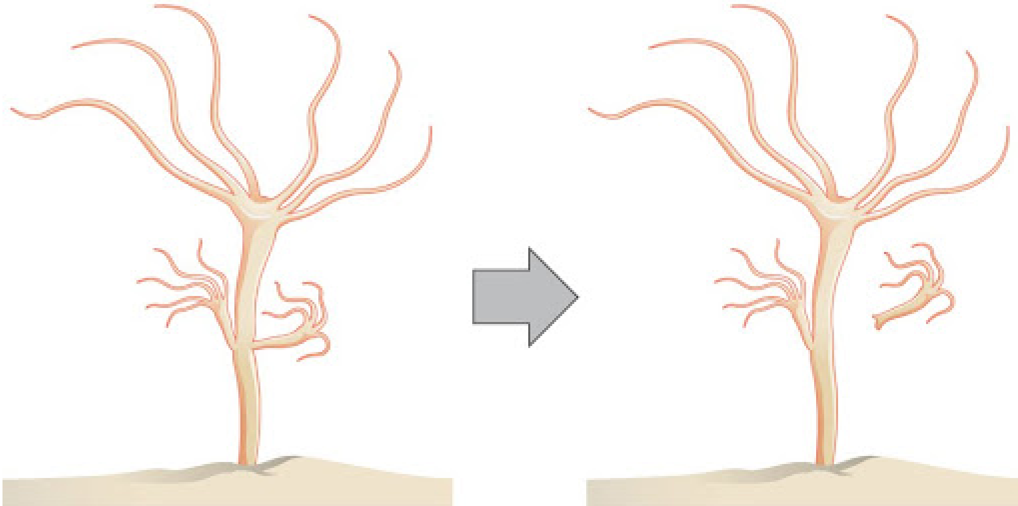

Figure 2. *Hydra reproduce asexually through budding.*

Watch this video of a hydra budding! Note that there is no audio in this video.

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Fragmentation

Fragmentation is the breaking of the body into two parts with subsequent regeneration. If the animal is capable of fragmentation, and the part is big enough, a separate individual will regrow.

For example, in many sea stars, asexual reproduction is accomplished by fragmentation. Figure 3 illustrates a sea star for which an arm of the individual is broken off and regenerates a new sea star. Fisheries workers have been known to try to kill the sea stars eating their clam or oyster beds by cutting them in half and throwing them back into the ocean. Unfortunately for the workers, the two parts can each regenerate a new half, resulting in twice as many sea stars to prey upon the oysters and clams. Fragmentation also occurs in annelid worms, turbellarians, and poriferans.

Figure 3. *Sea stars can reproduce through fragmentation. The large arm, a fragment from another sea star, is developing into a new individual.*

Note that in fragmentation, there is generally a noticeable difference in the size of the individuals, whereas in fission, two individuals of approximate size are formed.

Parthenogenesis

Parthenogenesis is a form of asexual reproduction where an egg develops into a complete individual without being fertilized. The resulting offspring can be either haploid or diploid, depending on the process and the species. Parthenogenesis occurs in invertebrates such as water fleas, rotifers, aphids, stick insects, some ants, wasps, and bees. Bees use parthenogenesis to produce haploid males (drones). If eggs are fertilized, diploid females develop, and if the fertilized eggs are fed a special diet (so called royal jelly), a queen is produced.

Some vertebrate animals—such as certain reptiles, amphibians, and fish—also reproduce through parthenogenesis. Although more common in plants, parthenogenesis has been observed in animal species that were segregated by sex in terrestrial or marine zoos. Two female Komodo dragons, a hammerhead shark, and a blacktip shark have produced parthenogenic young when the females have been isolated from males.

Did I Get It?

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Sexual Reproduction

Sexual reproduction is the combination of (usually haploid) reproductive cells from two individuals to form a third (usually diploid) unique offspring. Sexual reproduction produces offspring with novel combinations of genes. This can be an adaptive advantage in unstable or unpredictable environments. As humans, we are used to thinking of animals as having two separate sexes—male and female—determined at conception. However, in the animal kingdom, there are many variations on this theme.

Sex Cells

Most sexually reproducing species have two sex cell types that differ in size: in animals these are egg and sperm. Eggs and sperm for each species are identified by the size of the sex cell rather than the characteristics of the individual possessing the sex cells: egg cells are larger than sperm cells. The difference in size is due to how the cytoplasm- the material in the cell- in a cell divides. For sperm cells, during meiosis, the cytoplasm divides evenly across the four cells. For egg cells, most of the cytoplasm goes into one cell; the other three that are produced via meiosis cannot be fertilized.

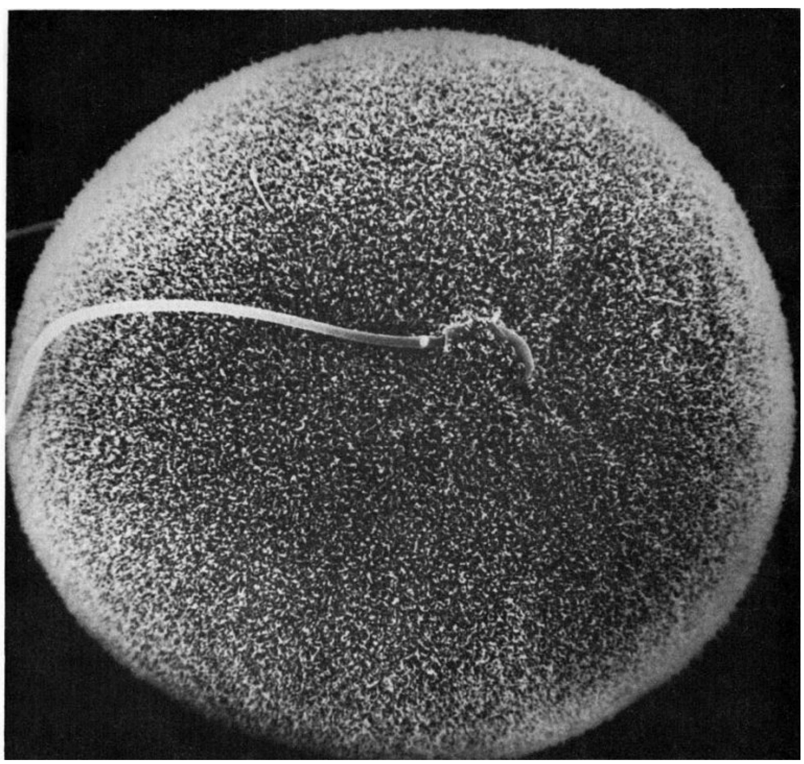

Figure 4. *Sperm fertilizing an egg. The large sphere is the egg and the thin fiber with a head going across it horizontally is the sperm. Notice the difference in size between these two sex cells.*

Some individuals only produce one type of sex cell (identified as males or females) while others may produce both sperm and eggs. Those that produce both types are hermaphroditic. Hermaphroditism can be either sequential (they can switch from producing one sex cell to producing another sex cell) or simultaneous (they can produce both sex cells at one time).

External Fertilization

External fertilization usually occurs in aquatic environments where both eggs and sperm are released into the water. After the sperm reaches the egg, fertilization takes place. Most external fertilization happens during the process of spawning where one or several females release their eggs and the male(s) release sperm in the same area, at the same time. The release of the reproductive material may be triggered by water temperature or the length of daylight. Nearly all fish spawn, as do crustaceans (such as crabs and shrimp), mollusks (such as oysters), squid, and echinoderms (such as sea urchins and sea cucumbers). Figure 5a shows salmon spawning in a shallow stream. Frogs, like those shown in Figure 5b, corals, mayflies, and mosquitoes also spawn.

(a) (b)

Figure 5. *(a) Salmon reproduce through spawning. (b) During sexual reproduction in toads, the male grasps the female from behind and externally fertilizes the eggs as they are deposited. (credit a: Dan Bennett; credit b: "OakleyOriginals"/Flickr)*

Pairs of fish that are not broadcast spawners may exhibit courtship behavior. This allows the female to select a particular male. The trigger for egg and sperm release (spawning) causes the egg and sperm to be placed in a small area, enhancing the possibility of fertilization.

External fertilization in an aquatic environment protects the eggs from drying out. Broadcast spawning can result in a greater mixture of the genes within a group, leading to higher genetic diversity and a greater chance of species survival in a hostile environment. For sessile aquatic organisms like sponges, broadcast spawning is the only mechanism for fertilization and colonization of new environments. The presence of the fertilized eggs and developing young in the water provides opportunities for predation resulting in a loss of offspring. Therefore, millions of eggs must be produced by individuals, and the offspring produced through this method must mature rapidly. The survival rate of eggs produced through broadcast spawning is low.

Internal Fertilization

Internal fertilization occurs most often in land-based animals, although some aquatic animals also use this method. There are three ways that offspring are produced following internal fertilization. In **oviparity**, fertilized eggs are laid outside the female's body and develop there, receiving nourishment from the yolk that is a part of the egg. This occurs in most bony fish, many reptiles, some cartilaginous fish, most amphibians, two mammals, and all birds. Reptiles and insects produce leathery eggs, while birds and turtles produce eggs with high concentrations of calcium carbonate in the shell, making them hard. Chicken eggs are an example of this second type.

In **ovoviparity**, fertilized eggs are retained in the female, but the embryo obtains its nourishment from the egg's yolk and the young are fully developed when they are hatched. This occurs in some bony fish (like the guppy *Lebistes reticulatus*), some sharks, some lizards, some snakes (such as the garter snake *Thamnophis sirtalis*), some vipers, and some invertebrate animals (like the Madagascar hissing cockroach *Gromphadorhina portentosa*).

In **viviparity** the young develop within the female, receiving nourishment from the mother's blood through a placenta. The offspring develops in the female and is born alive. This occurs in most mammals, some cartilaginous fish, and a few reptiles.

Internal fertilization has the advantage of protecting the fertilized egg from dehydration on land. The embryo is isolated within the female, which limits predation on the young. Internal fertilization enhances the fertilization of eggs by a specific male. Fewer offspring are produced through this method, but their survival rate is higher than that for external fertilization.

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Chromosomes and Sex Development

Section Goals

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

- Compare and contrast mechanisms of sex determination in different species.

Introduction to sex chromosomes: it's not just X

and Y

Sex chromosomes were historically distinguished from autosomal chromosomes because they were easily visible under the microscope, and depending on the species of the organism being studied, these distinctive chromosomes tracked with sex through generations. Geneticists later found that these chromosomes carry genes associated with the development of sex structures, called sex-determination genes.

In humans and other mammals, males typically have one X and one Y chromosome and are said to be heterogametic. Females typically have two X chromosomes and are homogametic.

Note 1: In this text, you'll see the XX genotype described as "typically" or "most commonly" associated with a female phenotype and the XY genotype with males. The reason for the "typically" or "most commonly" description is that there are many exceptions to this, both in humans and other organisms. For example, there are individuals with sex chromosome aneuploidies (SCAs), with only one X chromosome (described sometimes as XO) or more than two sex chromosomes (XXX, XXY, or XXXX, for example). There are also many individuals for whom their sex chromosome pair (XY or XX) does not align with either the appearance of sex-associated traits or gender.

Did I Get It?

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Note 2: Although humans and many other species (including some plants

Charlesworth, D. Plant sex determination and sex chromosomes. *Heredity* 88, 94–101 (2002).

!) use X and Y sex chromosomes, other organisms use different systems of sex determination. Birds, for example, use Z and W sex chromosomes. In yet other species, sex can be determined by environmental conditions or even the ploidy of an organism. In honeybees, for example, males are typically haploid, and females are diploid

Sex Determination in Honeybees | Learn Science at Scitable. http://www.nature.com/scitable/topicpage/sex-determination-in-honeybees-2591764.

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The X and Y chromosomes share similar DNA sequences at the ends

During meiosis I, the autosomes are paired with their homolog. For both autosomes and sex chromosomes, the pairing happens due to sequence similarities between the sister homologs. This pairing is discussed in more detail in the chapter on meiosis and mitosis. The pairing is possible, even when that "pairing" is between XY or ZW chromosomes because the very ends of the sex chromosomes contain homologous sequences. These are called pseudoautosomal (PAR) regions because both males and females have two copies of all the genes in those regions. The pseudoautosomal regions of the X and Y chromosomes are shown in **Figure 1**.

During meiosis, chromosome pairs – including XX or XY pairs – are separated into different daughter cells. This results in haploid daughter cells. Each daughter cell ultimately contains one copy of each autosome and one sex chromosome. For mammals, eggs typically carry an X chromosome and sperm carry either an X or Y chromosome. For birds, eggs typically contain either a Z or a W chromosome, while all sperm contain a Z chromosome.

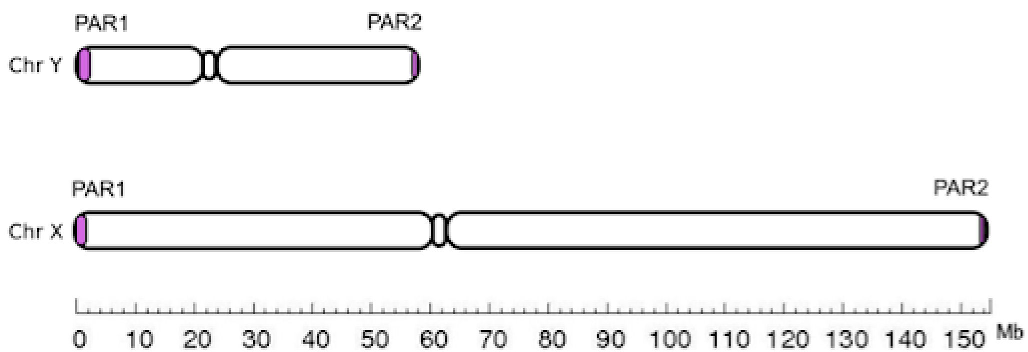

Figure 1. *In humans and other mammals, the X and Y chromosomes share regions of homology at their very ends, called pseudoautosomal regions (PAR). Image Source: Kelkar A, Thakur V, Ramaswamy R, Deobagkar D (2009) Characterisation of Inactivation Domains and Evolutionary Strata in Human X Chromosome through Markov Segmentation. PLoS ONE 4(11): e7885.*

Sex is a phenotype, like any other observable trait. **Sex-determination genes** are genes that control the development of sex-associated traits.

In mammals, fruit flies, and some flowering plant embryos, females usually (but not always) have an XX genotype, while males usually (but not always) have an XY genotype. In birds and some reptiles and amphibians, males typically have a ZZ genotype, and females have a ZW genotype. Note that females are not always the homogametic sex – they don't always have two of the same chromosome.

These genotypes are associated with either male or female phenotypes due to the presence of sex-determination genes located on the sex chromosomes. However, the mechanism for the development of sex-associated phenotypes is different depending on species. For example, although humans and Drosophila both have X and Y sex chromosomes, they have different mechanisms for determining sex.

Table 1 lists chromosomal methods of sex determination in several species. In humans and other mammals, the SRY gene on the Y chromosome triggers the development of testes in the early embryo.

Fruit flies and certain other insects also use an XY system of sex determination, but the mechanism of sex determination is different. For fruit flies, the ratio of X chromosomes to autosomes determines sex phenotype due to the expression of autosomal genes that, in turn, influence the expression of sex-determination genes on the X chromosome.

In other insects, there's no Y chromosome at all! The number of X chromosomes influences maleness. In birds and some other species, the DMRT1 gene on the Z chromosome initiates the process of sex development. Still, it is **haploinsufficient**: one copy of the gene does not produce enough gene product to trigger maleness, so ZW individuals will typically develop female anatomy.

Note: some species do not use sex chromosomes! Sex in some species can be determined by autosomes or even environmental conditions. In honeybees, sex is determined by whether eggs are fertilized: unfertilized eggs develop into males, while fertilized eggs develop into females. In many turtles, sex is determined by environmental temperature: cooler temperatures are associated with male development, and warmer temperatures with female development

US Department of Commerce, N. O. and A. A. What causes a sea turtle to be born male or female? https://oceanservice.noaa.gov/facts/temperature-dependent.html.

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Table 1. Chromosomal systems of sex determination

Organism	**Humans and other mammals**	**Drosophila (fruit fly)**	**Some insects and other organisms**	**Birds, reptiles, some fishes and amphibians**
Chromosomal System	XX-XY	XX-XY (XA system)	XX-XO	ZZ-ZW
Chromosomal method of determination	The presence of the Y chromosome triggers maleness during fetal development.	The ratio of X: autosomal chromosomes determines sex.	Number of X chromosomes determines sex; there is no Y chromosome.	Two Z chromosomes are required for maleness
Mechanism	SRY gene on the Y chromosome sets off a series of events leading to development of testes. (Other genes, both autosomal and sex-linked, are also involved)	Expression of sex-determining genes on the X-chromosome is affected by timing (and level) of expression of autosomal genes.	May vary among species: In *C. elegans,* it is related to the amount of an X-encoded protein which can inhibit maleness.	The DMRT1 gene on the Z chromosome is haploinsufficient; one copy of the gene can't produce enough protein to trigger male development

In all organisms, the sex chromosomes are associated with sex determination because they house some, but not all, of the genes responsible for determining sex. Other sex-determination genes are located on the autosomes. The sex chromosomes also house genes not responsible for sex determination at all. These are called **sex-linked genes**, but they have nothing to do with sex beyond their chromosomal locus. Some examples in humans are a gene linked with color blindness and a gene that affects the strength of tooth enamel.

In the next video, hear a short talk from evolutionary biologist Joan Roughgarden on sexual

diversity in nature. Then check out the article On the Originality of Species from *Stanford Magazine* to learn more about Roughgarden and her work!

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Sex Development in Humans

Section Goals

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

- Recognize that both sex-linked and autosomal genes play a role in sex development in humans
- Explain how disruptions in the sex development pathway can lead to differences in sex development.

Sex differentiation during human development

So, given what we know about genes, chromosomes, and gene expression, why does the presence of a Y chromosome typically trigger maleness during human development? The answer to that involves a network of both sex-linked and autosomal genes.

Sex is a phenotype. Typically, in most sexually dimorphic species, multiple characteristics, in addition to sex organs, distinguish male from female individuals. Those sex-associated traits are phenotypes, just like hair color, eye color, or wing shape. Those phenotypes can be genetically (or in some cases environmentally) determined.

In humans and other mammals, the Y chromosome carries the SRY gene. The SRY protein encoded by the gene is a transcription factor. In the early stages of human development, a human embryo develops a bi-potential genital ridge – that is, tissue that has the potential to become either ovaries or testes. Early embryos also have two systems of ducts, Wolffian and Müllerian, which can develop into the male and female reproductive tracts, respectively.

If a Y chromosome is present, the transcription factor SRY is produced. In turn, SRY activates the expression of Sox9, which is also a transcription factor. Sox9 in turn activates other genes, which eventually lead to the development of testes.

The testes, in turn, produce testosterone and anti-Müllerian hormone, or AMH. Testosterone (and other hormones, including 5α-dihydrotestosterone) trigger the formation of other organs in the male reproductive system from the Wolffian duct tissue, while AMH causes degeneration of the Müllerian duct and suppresses the development of female sex structures.

In the absence of SRY (as in individuals with an XX genotype), an alternative set of molecular signals is typically activated, including WNT4, RSPO1, DHH (Desert Hedgehog), and β-catenin. These lead to the development of ovaries. The ovaries then produce estrogen and trigger the development of the uterus, oviducts, and cervix from the Müllerian duct.

The sequential activation of these genes is illustrated in **Figure 1**, below.

Thus, in humans and other mammals, the SRY protein product sets into motion this cascade of events that leads to maleness. However, SRY is not the only gene involved in this process – and, in fact, all the other genes shown in **Figure 1** are autosomal, not sex-linked! A loss of function in any of the autosomal genes will disrupt the sex determination pathway, leading to differences in sex development, discussed in greater detail below.

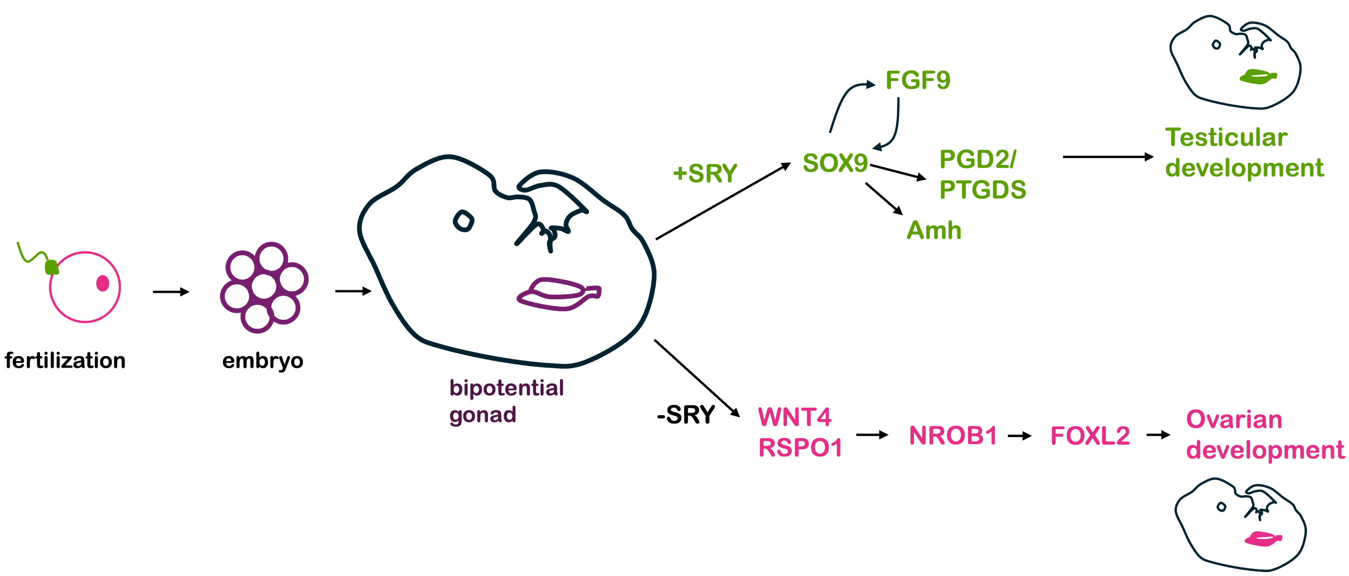

Figure 1. *Selected genes required for sex determination and differentiation in humans and other mammals.*

Differences in sex development in humans

Although the term "biological sex" is used quite often, this term is an oversimplification of the biology underlying the development of sex characteristics. There are a number of ways males and females differ from one another. As a result, there are many ways “biological sex” might be defined.

In this module, we’ve so far been focused on chromosomal sex, where an XY individual is considered male and an XX individual is considered female. But sex is usually determined or assigned at birth based on the visible presence of a penis or a vulva in a newborn. Sex can be determined by genitalia even before birth, when genitals are clearly visible by ultrasound.

Genitalia define anatomical sex. This is also sometimes called phenotypic sex, although this is an oversimplification of the term phenotype. Gonadal sex refers to the presence of either testes or ovaries. Although individuals show a range of hormonal levels, human males and females tend to have different ranges of androgens (males typically have more, females typically have less) and estrogens (females typically have more, males typically have less). This is hormonal sex.

At puberty, both males and females develop secondary sex characteristics. In males, this includes deepening of the voice, growth of facial and body hair, and broadening of the shoulders. In females, secondary sex characteristics include the growth of breast tissue, widening of hips, and onset of menses. These secondary sex characteristics typically (though not always) develop according to hormonal sex.

You might expect that these ways of defining biological sex (chromosomal, anatomical, gonadal, and hormonal) all align: XY individuals would have a penis, have testes, have relatively high levels of androgens like testosterone and low levels of estrogens, and develop male secondary sex characteristics at puberty. But this is not always true: it is possible to have an XY genotype but have female genitalia, gonads, and secondary sex characteristics. It is possible to have an XX genotype and have male genitalia, gonads, and secondary sex characteristics. It is possible to have female external genitalia and internal testes. It is possible to have genitalia with both male and female characteristics, or indeterminate characteristics. In fact, it is possible to have almost any combination of chromosomal, genital, gonadal, and hormonal sex.

Genetically, these sex phenotypes are due to genotypic changes in any one of the networks of genes responsible for sex determination and differentiation – and because there are so many genes involved in the process, there are many Differences in Sex Development (DSDs) in the human population. Another term for DSD is intersex. Some examples of DSDs in humans are listed in the section below, although this is not an exhaustive list.

Click the arrow below to read the next section

Examples of DSDs and Resulting Phenotypes in Humans

Sex chromosome aneuploidy. Remember that aneuploidy refers to an atypical number of chromosomes. They often result from nondisjunction during meiosis or mitosis: either homologous pairs or sister chromatids fail to separate during anaphase. Aneuploidies of autosomes are relatively rare in the human population, since additional copies – or too few copies – of most chromosomes would have lethal effects on a developing embryo. (Some exceptions are Trisomy 21 – Down syndrome, Trisomy 13, and Trisomy 18, all of which have significant phenotypic effects and are linked with shortened lifespan.) Aneuploidies of sex chromosomes, however, are by far more common. This is likely because the Y chromosome has very few genes – none required for life – and any extra copies of the X chromosome can be inactivated (discussed more in the next section).

Sex chromosome aneuploidies are the most common DSDs in the human population as well as the most common aneuploidies in the human population. Humans with sex chromosome aneuploidies usually have a normal lifespan but may be infertile, may have neurological and/or cognitive disabilities, or they may have few or no measurable phenotypic differences. It's estimated that 50-75% of people with sex chromosome abnormalities never even know they have a sex chromosome aneuploidy.

Individuals without a Y chromosome typically – but not always – show a female phenotype, regardless of the total number of sex chromosomes. This is because the SRY gene on the Y chromosome is needed to initiate the development of male reproductive structures. Individuals with one or more Y chromosomes typically – but not always – show a male phenotype since the presence of SRY triggers the development of male reproductive structures during embryogenesis.

A selected list of human sex chromosome abnormalities is listed in **Table 1**, below, with associated phenotype.

Table 1: Sex chromosome aneuploidies in humans

Genotype	**Phenotype**
XO (One sex chromosome only)	Turner syndrome. Anatomical females present with symptoms that vary in severity but may include short stature, ovarian failure, cardiac defects, and/or infertility that may be corrected with fertility treatment.
XXY	Klinefelter syndrome. Anatomical males present with signs and symptoms that vary in severity but may include taller than average stature, weak bones, delayed puberty, decreased muscle mass, and low sex drive. Some may go undiagnosed.
XYY	XYY syndrome. Anatomical males with normal fertility and sexual development. May be taller than average, have an increased risk of cystic acne, ADHD, and, to a lesser extent, autism spectrum disorder. May go undiagnosed.
XXX	Triple X syndrome. Anatomical females who are generally taller than average, some with subtle physical differences including wide-spaced eyes. Some patients may have learning disabilities and medical problems including infertility due to premature ovarian failure, but others may have mild or no symptoms and go undiagnosed.

Translocation of SRY. In some anatomical males with an XX genotype, the SRY gene has been translocated to one of the X chromosomes or an autosome. This is often the result of an aberrant recombination event – crossing over between the X and Y chromosomes (or the Y and an autosome) during meiosis in the father. Such individuals appear phenotypically male but may have small testes or a urethra opening on the underside of the penis. Affected individuals may be shorter than average, require hormone treatments at puberty to trigger development of secondary sex characteristics, and may be infertile, but are otherwise healthy.

Swiyer syndrome. XY individuals who are phenotypically female, with functional vagina, uterus, and fallopian tubes but lacking ovaries. Because they lack ovaries, women with Swiyer syndrome are usually diagnosed in adolescence when they do not undergo a first period. Secondary sex characteristics do not develop without hormonal supplementation, but women can become pregnant with donated embryos. Women with Swiyer syndrome often have a deletion on the Y chromosome that inactivates the SRY gene, but the syndrome is also associated with mutations in the gene NROB1 on the X chromosome and several autosomal genes as well.

Complete androgen insensitivity (CAIS). 46, XY female phenotype. Mutations in the androgen receptor gene prevent cells of a developing embryo from responding to androgens, including testosterone. Although people with CAIS have normal-appearing female external genitalia and secondary sex characteristics, they have internal, undescended testes, and usually have a shortened vagina and lack a uterus.

Congenital adrenal hyperplasia (CAH). Mutations in the enzyme 21-hydroxylase block one step of cortisol synthesis. This in turn leads to a build-up of testosterone since cortisol and testosterone share parts of their biosynthetic pathway. This causes masculinization of the external genitalia in XX individuals, who may have ambiguous genitalia or even the appearance of normal male external genitalia. Such XX individuals have female gonads and internal genitalia.

5-alpha-reductase deficiency. These XY individuals have a loss of function mutation in the enzyme that converts testosterone to dihydrotestosterone (DHT). DHT is the hormone required for the development of external male genitalia during fetal development. Children with 5-alpha-reductase deficiency may appear to have female external genitalia or ambiguous external genitalia at birth. However, they have internal testes, and, at puberty, the testes produce much higher levels of testosterone that cause penile and scrotal tissue to grow and male secondary sex characteristics to develop. This particular DSD occurs at high frequency in certain communities in the Dominican Republic, where such people are called “guavedoces”. The term “guavedoces” very loosely translates to “penis at age twelve”, since children assumed to be female appear to grow a penis.

For an awesome infographic that breaks down DSDs and visually highlights the complexity of sex determination, see the article Beyond XX and XY: The Extraordinary Complexity of Sex Determination from the September 2017 issue of *Scientific American*. Click on the infographic and use the zoom tool to enlarge portions of the graphic. If you are interested in graphic design and science communication, and would like to learn more about the development of this particular infographic, check out the post Visualizing Sex as a Spectrum by graphic designer Amanda Montañez.

What is the Frequency of DSDs in the Human Population?

With an expanded understanding of biological sex, it becomes apparent that while individuals with unambiguously male or unambiguously female characteristics make up the majority of the human population, individuals frequently do not completely align with either category. Thus, although sex is often considered binary – male or female – this is not an accurate picture of human biology, since there are many ways differences in sex development can arise. Humans may be chromosomally male but phenotypically female, or vice versa. They may be chromosomally male, hormonally male, but phenotypically female. Or they may have nearly any other combination of chromosomal, anatomical, gonadal, and hormonal sex.

Estimates of how many individuals in the human population have DSDs range depending on who is counted. If only individuals with differences in external genitalia are counted, such individuals make up about 1/4500-1/2000 of the human population. However, DSDs may result in typical external genitalia but atypical alignment of chromosomal, hormonal, or gonadal sex. They may also include individuals with atypical numbers of sex chromosomes – many of whom may not even know they have such a condition. If individuals with atypical sex chromosome ploidy are included, some estimates are that individuals with DSDs make up about 2% of the human population. For comparison, this is about the same frequency as the red hair phenotype worldwide – not as uncommon as one might think. If you know people with red hair, you likely know someone with a difference in sex development, too, making sex not very binary at all.

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VII

Mechanisms of Evolution

This module contains the following chapters:

Variation in Populations

Section Goals

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

- Describe the sources of variation in a population

Figure 1. *The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)*

A population's individuals often display different phenotypes, or express different alleles of a particular gene, which scientists refer to as **polymorphisms**. We call populations with two or more variations of particular characteristics polymorphic. A number of factors, including the population's genetic structure and the environment (**Figure 1**) influence population variation, the distribution of phenotypes among individuals. Understanding phenotypic variation sources in a population is important for determining how a population will evolve in response to different evolutionary pressures.

Heritability is the fraction of phenotype variation that can be attributed to genetic differences, or genetic variance, among individuals in a population. The greater the heritability of a population's phenotypic variation, the more susceptible it is to the evolutionary forces that act on heritable variation.

The diversity of alleles and genotypes within a population is called **genetic diversity**, or **genetic variation**. Genetic diversity in a population comes from two main mechanisms: mutation and sexual reproduction.

Mutations

Mutations are changes to an organism's DNA, and are an important driver of new alleles, or new genetic variation in any population. An organism's DNA affects how it looks, how it behaves, its physiology — all aspects of its life. So a change in an organism's DNA can cause changes in all aspects of its life.

Species evolve because of mutations accumulating over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance. The genetic changes that mutation causes can have one of three outcomes on the phenotype:

1. A mutation affects the organism's phenotype in a way that is harmful or gives it reduced fitness—lower likelihood of survival or fewer offspring. These mutations are often quickly eliminated from the population by natural selection.
2. A mutation may produce a phenotype with a beneficial effect on fitness, and will spread through

the population.
3. Many mutations will also have no effect on the organism's fitness and can linger, unaffected by natural selection, in the genome. We call these neutral mutations.

Mutations may also have a whole range of effect sizes on the organism's fitness that expresses them in their phenotype, from a small effect to a great effect.

Mutations can be beneficial, neutral, or harmful for the organism, but mutations do not "try" to supply what the organism "needs." In this respect, mutations are random — whether a particular mutation happens or not is unrelated to how useful that mutation would be.

Not all mutations matter to evolution. Since all cells in our body contain DNA, there are lots of places for mutations to occur; however, not all mutations matter for evolution. Somatic mutations occur in non-reproductive cells and so won't be passed onto offspring. For example, the yellow color on half of a petal on the red tulip in **Figure 2** was caused by a somatic mutation. The seeds of the tulip do not carry the mutation. Cancer is also caused by somatic mutations that cause a particular cell lineage (e.g., in the breast or brain) to multiply out of control. Such mutations affect the individual carrying them but are not passed directly on to offspring.

Figure 2. *Tulip with somatic mutation causing yellow petal. Photo from Wikipedia, by LepoRello under CC BY-SA 3.0.*

The only mutations that matter for the evolution of life's diversity are those that can be passed onto offspring. These occur in reproductive cells like eggs and sperm and are called germline mutations.

Read more about how mutations are random and the famous Lederberg experiment that demonstrated this. Or read more about how mutations factored into the history of evolutionary thought. Or dig into DNA and mutations in this primer.

Sex and genetic shuffling

Sexual reproduction also leads to genetic diversity: Sex can introduce new gene combinations into a population and is an important source of genetic variation. When two parents reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each offspring.

You probably know from experience that siblings are not genetically identical to their parents or to each other (except, of course, for identical twins). That's because when organisms reproduce sexually, some genetic "shuffling" occurs, bringing together new combinations of genes. For example, you might have bushy eyebrows and a big nose if one of your parents had genes associated with bushy eyebrows and the other parent had genes associated with a big nose (**Figure 3**).

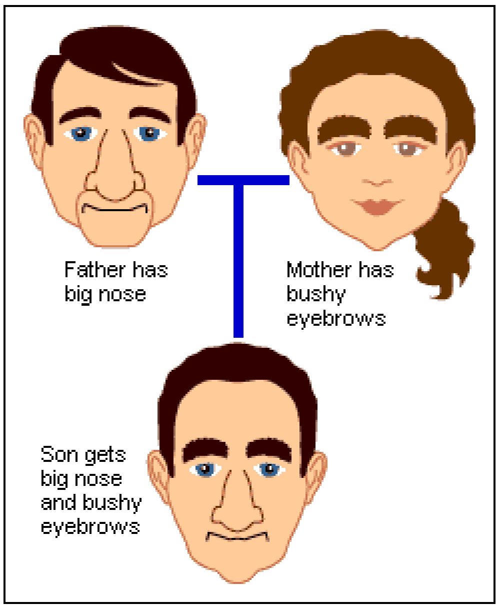

Figure 3. *Genetic "shuffling" brings together new combinations of genes.*

This shuffling is important for evolution because it can introduce new combinations of genes every generation. For example, in a particular population, plants with reddish flowers and plants with longer more tubular flowers might each do fine on their own – but if sex and genetic shuffling produced a plant with both traits (red tubular flowers), the combination might attract a new pollinator (hummingbirds) and alter the evolutionary trajectory of the lineage. Of course, sex and genetic shuffling can also break up good combinations of genes and form bad ones.

When scientists are involved in the breeding of a species, such as with animals in zoos and nature preserves, they try to increase a population's genetic variance to preserve as much of the phenotypic diversity as they can. This also helps reduce the risks associated with **inbreeding**, the mating of closely related individuals, which can have the undesirable effect of bringing together deleterious recessive mutations that can cause abnormalities and susceptibility to disease. For example, a disease that is caused by a rare, recessive allele might exist in a population, but it will only manifest itself when an individual carries two copies of the allele. Because the allele is rare in a normal, healthy population with unrestricted habitat, the chance that two carriers will mate is low, and even then, only 25 percent of their offspring will inherit the disease allele from both parents. While it is likely to happen at some point, it will not happen frequently enough for natural selection to be able to swiftly eliminate the allele from the population, and as a result, the allele will be maintained at low levels in the gene pool. However, if a family of carriers begins to interbreed with each other, this will dramatically increase the likelihood of two carriers mating and eventually producing diseased offspring, a phenomenon known as **inbreeding depression**.

What about genes that impact development?

Development is the process through which a fertilized egg, the earliest stage of an embryo, becomes an adult organism. Throughout development, an organism's genotype is expressed as a phenotype, exposing genes and the genetic elements that control their expression to the action of natural selection. Genetic variation in genes affecting development seems to have played an important role in evolution.

Changes in the genes controlling development can have major effects on the morphology (form and structure) of the adult organism. Because these effects are so significant, scientists suspect that changes in the expression of developmental genes have helped bring about major evolutionary transformations. Developmental changes, as well as new genes, may help explain, for example, how some hoofed mammals evolved into ocean-dwellers, how water plants invaded the land, and how small, armored invertebrates evolved wings.

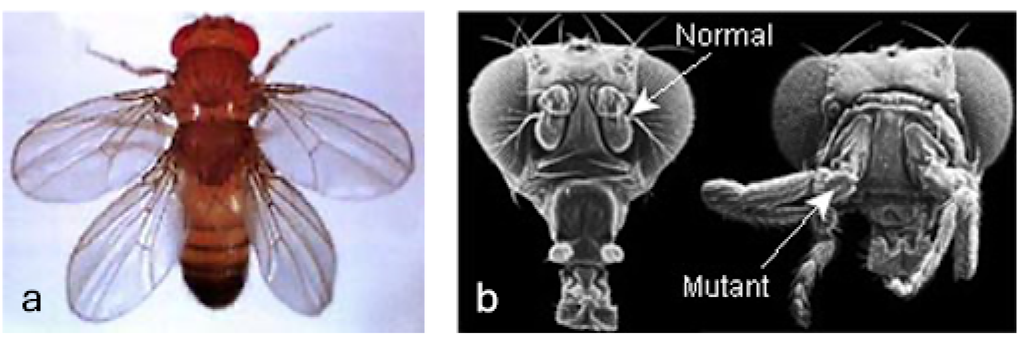

Figure 4. *(a) Mutations in the genes that control fruit fly development can cause major morphology changes, such as two pairs of wings instead of one. (b) Another developmental gene mutation can cause fruit flies to have legs where the antennae normally are, as shown in the fly on the right. Fruit fly images courtesy of Jean-Michel Muratet, Syndicat National des Ophtalmologistes de France (SNOF).*

Developmental processes may also constrain the sorts of phenotypes that genetic variation can lead to, and so might prevent certain characters from evolving in certain lineages. For example, development may help explain why there are no truly six-fingered tetrapods among living species.

Environmental Variance

Genes are not the only players involved in determining population variation. Other factors, such as the environment also influence phenotypes. A beachgoer is likely to have darker skin than a city dweller, for example, due to regular exposure to the sun, an environmental factor. For some species, the environment determines some major characteristics, such as sex (**Figure 5**). For example, some turtles and other reptiles have temperature-dependent sex determination (TSD). TSD means that individuals develop into males if their eggs are incubated within a certain temperature range, or females at a different temperature range.

Figure 5. *The sex of the American alligator (Alligator mississippiensis) is determined by the temperature at which the eggs are incubated. Eggs incubated at 30°C produce females, and eggs incubated at 33°C produce males. (credit: Steve Hillebrand, USFWS)*

Geographic separation between populations can lead to differences in the phenotypic variation between those populations. We see such **geographical variation** between most populations and it can be significant. We can observe one type of geographic variation, a **cline**, as given species' populations vary gradually across an ecological gradient. Species of warm-blooded animals, for example, tend to have larger bodies in the cooler climates closer to the earth's poles, allowing them to better conserve heat. This is a latitudinal cline. Alternatively, flowering plants tend to bloom at different times depending on where they are along a mountain slope. This is an altitudinal cline.

If there is gene flow between the populations, the individuals will likely show gradual differences in phenotype along the cline. Restricted gene flow, alternatively, can lead to abrupt differences, even speciation.

Population Genetics

Section Goals

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

- Describe how population genetics is used in the study of the evolution of populations
- Explain why natural selection can only act upon heritable variation

Recall that a gene for a particular character may have several alleles, or variants, that code for different traits associated with that character. For example, in the ABO blood type system in humans, three alleles determine the particular blood-type carbohydrate on the surface of red blood cells. Each individual in a population of diploid organisms can only carry two alleles for a particular gene, but more than two may be present in the individuals that comprise the population. Mendel followed alleles as they were inherited from parent to offspring. In the early twentieth century, biologists in the area of **population genetics** began to study how selective forces change a population through changes in allele and genotypic frequencies.

Evolution and Flu Vaccines

Every fall, the media starts reporting on flu vaccinations and potential outbreaks. Scientists, health experts, and institutions determine recommendations for different parts of the population, predict optimal production and immunization schedules, create vaccines, and set up clinics to provide immunizations. You may think of the annual flu shot as a lot of media hype, an important health protection, or just a briefly uncomfortable prick in your arm. But do you think of it in terms of evolution?

The media hype of annual flu shots is scientifically grounded in our understanding of evolution. Each year, scientists across the globe strive to predict the flu strains that they anticipate being most widespread and harmful in the coming year. This knowledge is based on how flu strains have evolved over time and the past few flu seasons. Scientists then work to create the most effective vaccine to combat those selected strains. Hundreds of millions of doses are produced in a short period in order to provide vaccinations to key populations at the optimal time.

Because viruses, like the flu, evolve very quickly (especially in evolutionary time), this poses quite a challenge. Viruses mutate and replicate at a fast rate, so the vaccine developed to protect against last year's flu strain may not provide the protection needed against the coming year's strain. The evolution of these viruses means continued adaptations to ensure survival, including adaptations to survive previous vaccines.

The **allele frequency** (or gene frequency) is the rate at which a specific allele appears within a population. Until now, we have discussed evolution as a change in the characteristics of a population of organisms, but behind that, phenotypic change is genetic change. In population genetics, the term evolution is defined as a change in the frequency of an allele in a population. Using the ABO blood type system as an example, the frequency of one of the alleles, *I*A, is the number of copies of that allele divided by all the copies of the ABO gene in the population. For example, a study in Jordan

Sahar S. Hanania, Dhia S. Hassawi, and Nidal M. Irshaid, "Allele Frequency and Molecular Genotypes of ABO Blood Group System in a Jordanian Population," *Journal of Medical Sciences* 7 (2007): 51–58, doi:10.3923/jms.2007.51.58.

found a frequency of *I*A to be 26.1 percent. The *I*Band *I*0 alleles made up 13.4 percent and 60.5 percent of the alleles, respectively, and all of the frequencies added up to 100 percent. A change in this frequency over time would constitute evolution in the population.

See another example in the next video.

https://www.youtube.com/watch?v=Bc9bhLk_AhI

The allele frequency within a given population can change depending on environmental factors; therefore, certain alleles become more widespread than others during the natural selection process. Natural selection can alter the population's genetic makeup. An example is if a given allele confers a phenotype that allows an individual to survive better or have more offspring. Because many of those offspring will also carry the beneficial allele, and often the corresponding phenotype, they will have more offspring of their own that also carry the allele, thus perpetuating the cycle. Over time, the allele will spread throughout the population. Some alleles will quickly become fixed in this way, meaning that every individual in the population will carry the allele. At the same time, detrimental mutations may be swiftly eliminated if derived from a dominant allele from the gene pool. The **gene pool** is the sum of all the alleles in a population.

Sometimes, allele frequencies within a population change randomly with no advantage to the population over existing allele frequencies. We call this phenomenon genetic drift. Natural selection and genetic drift usually occur simultaneously in populations and are not isolated events. It is hard to determine which process dominates because it is often nearly impossible to determine the cause of change in allele frequencies at each occurrence. We call an event that initiates an allele frequency change in an isolated part of the population, which is not typical of the original population, the **founder effect**. Natural selection, random drift, and founder effects can lead to significant changes in a population's genome.

Did I Get It?

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Natural selection and some of the other evolutionary forces can only act on heritable traits, namely an organism's genetic code. Because alleles are passed from parent to offspring, those that confer beneficial traits or behaviors may be selected, while deleterious alleles may not. Acquired traits, for the most part, are not heritable. For example, if an athlete works out in the gym every day, building up muscle strength, the athlete's offspring will not necessarily grow up to be a bodybuilder. If there is a genetic basis for the ability to run fast, on the other hand, a parent may pass this to a child.

Before Darwin's theory of descent with modification became the prevailing theory of evolution, French naturalist Jean-Baptiste Lamarck theorized that acquired traits could, in fact, be inherited (e.g., giraffes stretch to reach leaves higher on trees, causing their offspring to inherit longer necks). This hypothesis has been largely unsupported, but scientists have recently begun to realize that Lamarck was not completely wrong. Epigenetics, the study of how a person's behaviors and environment can change the way their genes work, may help to explain why identical twins, who share the same genes, can have very different health outcomes. Check out the Epigenetics & Inheritance page from the University of Utah's Genetic Science Learning Center to learn more.

Adaptive Evolution

Section Goals

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

- Explain the different ways natural selection can shape populations
- Describe how these different forces can lead to different outcomes in terms of the population variation

Biological evolution, simply put, is *descent with modification*.

Biological evolution is not simply a matter of change over time. Lots of things change over time: trees lose their leaves and mountain ranges rise and erode, but they aren't examples of biological evolution because they don't involve descent through genetic inheritance.

The central idea of biological evolution is that *all life on Earth shares a common ancestor*, just as you and your cousins share a common grandmother.

Through the process of descent with modification, the common ancestor of life on Earth gave rise to the fantastic diversity that we see documented in the fossil record and around us today. Evolution means that we're all distant cousins: humans and oak trees; hummingbirds and whales.

Evolution occurs at different scales:

- **Microevolution** (small-scale evolution): Changes in gene frequency within a population (not resulting in speciation)
- **Macroevolution** (large-scale evolution): Changes in gene frequency that result in speciation (one population is different enough from other populations that it is no longer the same species)

Although the term "evolution" is often used synonymously with "natural selection," they are actually referring to different concepts. Evolution is an observable phenomenon in which gene frequencies change over time, but it does not explain *why* a population is undergoing evolution. This is where natural selection—and other mechanisms—come into play. They explain "the why."

Natural Selection

Natural selection acts on the population's heritable traits: selecting for beneficial alleles that allow for environmental adaptation, thus increasing their frequency in the population, while selecting against deleterious alleles and thereby decreasing their frequency. Scientists call this process **adaptive evolution**. Natural selection acts on entire organisms, not on an individual allele within the organism. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce (fecundity), but if that same individual also carries an allele that results in a fatal childhood disease, that fecundity phenotype will not pass to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the individual's level. It selects for individuals with greater contributions to the gene pool of the next generation. Scientists call this an organism's **evolutionary (Darwinian) fitness**.

Fitness is often quantifiable and is measured by scientists in the field. However, it is not an individual's absolute fitness that counts, but rather how it compares to the other organisms in the population. Scientists call this concept **relative fitness**, which allows researchers to determine which individuals are contributing additional offspring to the next generation, and thus, how the population might evolve.

There are several ways selection can affect population variation: stabilizing selection, directional selection, diversifying selection, frequency-dependent selection, and sexual selection. As natural selection influences the allele frequencies in a population, individuals can either become more or less genetically similar and the phenotypes can become more similar or more disparate.

Stabilizing Selection

If natural selection favors an average phenotype, selecting against extreme variation, the population will undergo **stabilizing selection** (**Figure 1**). In a mouse population that lives in the woods, for example, natural selection is likely to favor mice that best blend in with the forest floor and are less likely for predators to spot. Assuming the ground is a fairly consistent shade of brown, those mice whose fur is most closely matched to that color will be most likely to survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them a bit lighter or a bit darker will stand out against the ground and be more likely to fall victim to predation. As a result of this selection, the population's genetic variability will decrease.

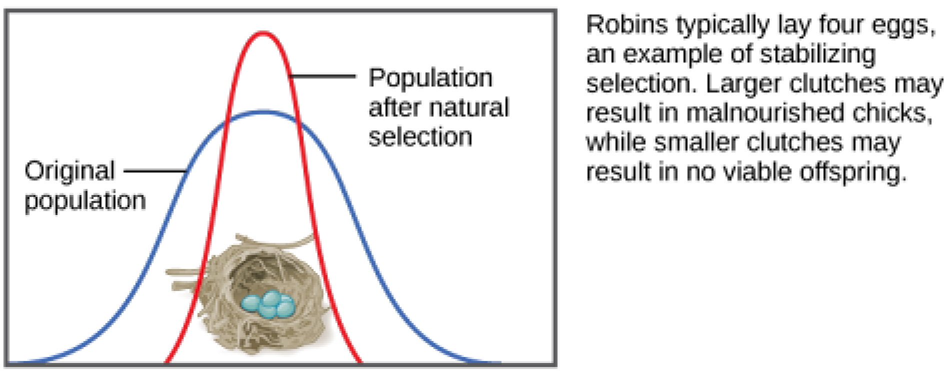

Figure 1. *In stabilizing selection, an average phenotype is favored.*

Directional Selection

When the environment changes, populations will often undergo **directional selection** (**Figure 2**), which selects for phenotypes at one end of the spectrum of existing variation. A classic example of this type of selection is the evolution of the peppered moth in eighteenth- and nineteenth-century England. Prior to the Industrial Revolution, the moths were predominately light in color, which allowed them to blend in with the light-colored trees and lichens in their environment. However, as soot began spewing from factories, the trees darkened, and the light-colored moths became easier for predatory birds to spot. Over time, the frequency of the moth's melanic form increased because they had a higher survival rate in habitats affected by air pollution because their darker coloration blended with the sooty trees. Similarly, the hypothetical mouse population may evolve to take on a different coloration if something were to cause the forest floor where they live to change color. The result of this type of selection is a shift in the population's genetic variability toward the new, fit phenotype.

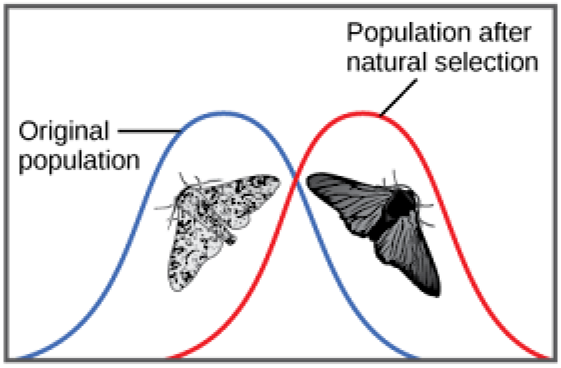

Figure 2. *In directional selection, a change in the environment shifts the spectrum of phenotypes observed.*

Diversifying Selection

Sometimes two or more distinct phenotypes can each have their advantages for natural selection, while the intermediate phenotypes are, on average, less fit. Scientists call this **diversifying selection** (**Figure 3**) We see this in many animal populations that have multiple male forms. Large, dominant alpha males use brute force to obtain mates, while small males can sneak in for furtive copulations with the females in an alpha male's territory. In this case, both the alpha males and the "sneaking" males will be selected for, but medium-sized males, who can't overtake the alpha males and are too big to sneak copulations, are selected against. Diversifying selection can also occur when environmental changes favor individuals on either end of the phenotypic spectrum. Imagine a mouse population living at the beach where there is light-colored sand interspersed with patches of tall grass. In this scenario, light-colored mice that blend in with the sand would be favored, as well as dark-colored mice that can hide in the grass. Medium-colored mice, alternatively, would not blend in with either the grass or the sand, and thus predators would most likely eat them. The result of this type of selection is increased genetic variability as the population becomes more diverse.

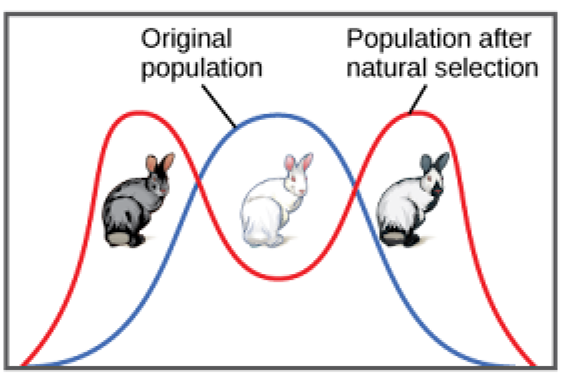

Figure 3. *In diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.*

Different types of natural selection can impact the distribution of phenotypes within a population (refer back to **Figures 1, 2, and 3**). In recent years, factories have become cleaner, and less soot is released into the environment. What impact do you think this has had on the distribution of moth color in the population?

Answer:

Moths have shifted to a lighter color.

Sexual Selection

Darwin noticed that there were many traits and behaviors of organisms that could not just be explained by the ability to survive. For example, the brilliant plumage of peacocks should actually lower their rates of survival. That is, the peacocks' feathers act like a neon sign to predators, advertising "Easy, delicious dinner here!" But if these bright feathers only lower peacocks' chances of survival, why do they have them? The same can be said of similar characteristics of other animals, such as the large antlers of male stags or the wattles of roosters, which also seem to be unfavorable to survival. Again, if these traits only make the animals less likely to survive, why did they develop in the first place? And how have these animals continued to survive with these traits over thousands and thousands of years? Darwin's answer to this conundrum was the theory of sexual selection: the evolution of characteristics, not because of survival advantage, but because of mating advantage.

Intrasexual Selection

Members of one sex compete against each other, and the winner mates with members of the opposite sex. It is "intra-sex" because the competition is occurring within one sex.

Intersexual Selection

If members of one sex are attracted to certain qualities in mates, then those desired qualities get passed on in greater numbers because their possessors mate more often. It is "inter-sex" because one sex affects selection in the other sex.

Did I Get It?

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Sexual selection has shaped many extreme adaptations that help organisms find mates. Perhaps one of the most extreme examples is in Australian redback spiders– also known as Australian black widows (**Figure 4**). The venomous female redback spider poses a danger to humans, and to male redback spiders, which are often eaten by their mates. Males seem to go out of their way to make this happen, flipping themselves over and presenting their abdomens to the female while mating.

Figure 4. *Female redback spider with egg sac at right. A much smaller male (circled) at left. Photo courtesy of Wikimedia.*

This behavior might at first seem like one that selection would act against. After all, how could risking one's life be adaptive? Remember that evolutionary fitness is about getting genes into the next generation, not just survival. Perhaps this strange behavior is favored by sexual selection because it gives males a fitness boost.

Scientist Spotlight: Maydianne Andrade

University Professor
Maydianne CB Andrade

Evolutionary ecologist Maydianne Andrade is known for her work researching the behavior of the cannibalistic Australian redback spiders. Listen to Canada's national public radio interview with Andrade, including a discussion of spiders, unconscious bias, imposter syndrome, and the burden carried by Black scientists.

Frequency-Dependent Selection

Another type of selection, **frequency-dependent selection**, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection). We can observe an interesting example of this type of selection in a unique group of Pacific Northwest lizards. Male common side-blotched lizards come in three throat-color patterns: orange, blue, and yellow. Each of these forms has a different reproductive strategy: orange males are the strongest and can fight other males for access to their females. Blue males are medium-sized and form strong pair bonds with their mates. Yellow males (**Figure 5**) are the smallest, and look a bit like females, which allows them to sneak copulations. Like a game of rock-paper-scissors, orange beats blue, blue beats yellow, and yellow beats orange in the competition for females. That is, the big, strong orange males can fight off the blue males to mate with the blue's pair-bonded females, the blue males are successful at guarding their mates against yellow sneaker males, and the yellow males can sneak copulations from the potential mates of the large, polygynous orange males.

Figure 5. *A yellow-throated side-blotched lizard is smaller than either the blue-throated or orange-throated males and appears a bit like the females of the species, allowing it to sneak copulations. (credit: "tinyfroglet"/Flickr)*

In this scenario, natural selection favors orange males when blue males dominate the population. Blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes—in one generation, orange might predominate, and then yellow males will begin to rise in frequency. Once yellow males comprise a majority of the population, blue males will be selected. Finally, when blue males become common, orange males once again will be favored.

Negative frequency-dependent selection serves to increase the population's genetic variability by selecting for rare phenotypes; whereas, positive frequency-dependent selection usually decreases genetic variability by selecting for common phenotypes.

Did I Get It?

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Adaptation

An adaptation is a feature that arose and was favored by natural selection for its current function. Adaptations help an organism survive and/or reproduce in its current environment.

Adaptations can take many forms: a behavior that allows better evasion of predators, a protein that functions better at body temperature, or an anatomical feature that allows the organism to access a valuable new resource — all of these might be adaptations. A platypus's webbed feet are an adaptation for swimming. A snow leopard's thick fur is an adaptation for living in the cold. A cheetah's fast speed is an adaptation for catching prey.

Many of the things that impress us most in nature are thought to be adaptations.

Figure 6. *A katydid from Costa Rica with wings that mimic leaves.Image © Greg Neise, GE Neise Digital Communication.*

Mimicry of leaves by insects is an adaptation for evading predators (**Figure 6**). The creosote bush is a desert-dwelling plant that produces toxins that prevent other plants from growing nearby, thus reducing competition for nutrients and water. Echolocation in bats is an adaptation for catching insects.

So what's not an adaptation? The answer: a lot of things. One example is vestigial structures. A vestigial structure is a feature that was adaptive for the organism's ancestor, but that evolved to be non-functional because the organism's environment changed. Fish species that live in completely dark caves have vestigial, non-functional eyes. When their sighted ancestors ended up living in caves, there was no longer any natural selection that maintained the function of the fish's eyes. So fish with better sight no longer out-competed fish with worse sight. Today, these fish still have eyes — but they are not functional and are not an adaptation; they are just the by-products of the fishes' evolutionary history.

Misconceptions about natural selection

Because natural selection can produce amazing adaptations, it's tempting to think of it as an all-powerful force, urging organisms on, constantly pushing them in the direction of progress — but this is not what natural selection is like at all.

Natural selection is not all-powerful; it does not produce perfection. It's all about getting genes into the next generation, and if your genes are "good enough" to do that, you don't have to be perfect. This should be clear just by looking around us: human populations carry genes that cause disease, plants may not have the genes to survive a drought, and a predator may not be quite fast enough to catch her prey every time she is hungry. No population or organism is perfectly adapted.

It's more accurate to think of natural selection as a process rather than as a guiding hand. Natural selection is the simple result of variation, differential reproduction, and heredity — it is mindless and mechanistic. It has no goals; it's not striving to produce "progress" or a balanced ecosystem.

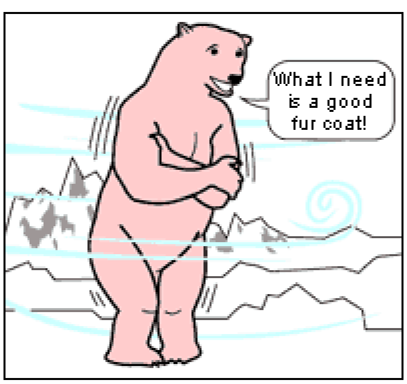

Figure 7. *Evolution does not work this way.*

This is why "need," "try," and "want" are not very accurate words when it comes to explaining evolution. The population or individual does not "want" or "try" to evolve, and natural selection cannot try to supply what an organism "needs." Natural selection can only select from whatever variation already exists in the population. It does not create anything from scratch. Thus, it is limited by a population's existing genetic variability and whatever new alleles arise through mutation and gene flow.

Natural selection is also limited because it works at the individual, not allele level, and some alleles are linked due to their physical proximity in the genome, making them more likely to pass on together (linkage disequilibrium). Any given individual may carry some beneficial and some unfavorable alleles. It is the alleles' net effect, or the organism's fitness, upon which natural selection can act. As a result, good alleles can be lost if individuals who carry them also have several overwhelmingly bad alleles. Likewise, bad alleles can be kept if individuals who have enough good alleles to result in an overall fitness benefit carry them.

Read more about how natural selection does not produce perfectly engineered traits or perfect populations (i.e., populations with no deleterious genes).

At the opposite end of the scale, natural selection is sometimes interpreted as a completely random process. This is also a misconception. The genetic variation that occurs in a population because of mutation is random — but selection acts on that variation in a very non-random way: genetic variants that aid survival and reproduction are much more likely to become common than variants that don't. Natural selection is NOT random!

Finally, it is important to understand that **not all evolution is adaptive**. While natural selection selects the fittest individuals and often results in a more fit population overall, other forces of evolution, including genetic drift and gene flow, often do the opposite: introducing deleterious alleles to the population's gene pool. Evolution has no purpose—it is not changing a population into a preconceived ideal. It is simply the sum of the various forces that we have described in this chapter and how they influence the population's genetic and phenotypic variability.

Non-Adaptive Evolution

Section Goals

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

- Describe genetic drift and two special cases of genetic drift– bottlenecks and founder effects
- Describe gene flow
- Explain how genetic drift and gene flow can influence a population's allele frequencies

Changes in allele frequencies that we identify in a population can shed light on how it is evolving. Recall that *not all evolution is adaptive*. In addition to natural selection, other non-adaptive evolutionary forces, such as genetic drift or gene flow, could be in play.

Genetic Drift

The theory of natural selection stems from the observation that some individuals in a population are more likely to survive longer and have more offspring than others; thus, they will pass on more of their genes to the next generation. A big, powerful male gorilla, for example, is much more likely than a smaller, weaker one to become the population's silverback, the pack's leader who mates far more than the other males of the group. The pack leader will father more offspring, who share half of his genes, and are likely to also grow bigger and stronger like their father. Over time, the genes for bigger size will increase in frequency in the population, and the population will, as a result, grow larger on average. That is, this would occur if this particular **selection pressure**, or driving selective force, were the only one acting on the population. In other examples, better camouflage or a stronger resistance to drought might pose a selection pressure.

Another way a population's allele and genotype frequencies can change is **genetic drift** (**Figure 1**). Genetic drift is one of the basic mechanisms of evolution. By chance, some individuals will have more offspring than others (and leave behind more genes, of course!) —not due to an advantage conferred by some genetically-encoded trait, but just because one male happened to be in the right place at the right time (when the receptive female walked by) or because the other one happened to be in the wrong place at the wrong time (when a fox was hunting).

Genetic drift happens to ALL populations. It affects the genetic makeup of the population, but unlike natural selection, through an entirely random process. So, although genetic drift is a mechanism of evolution, it doesn't work to produce adaptations.

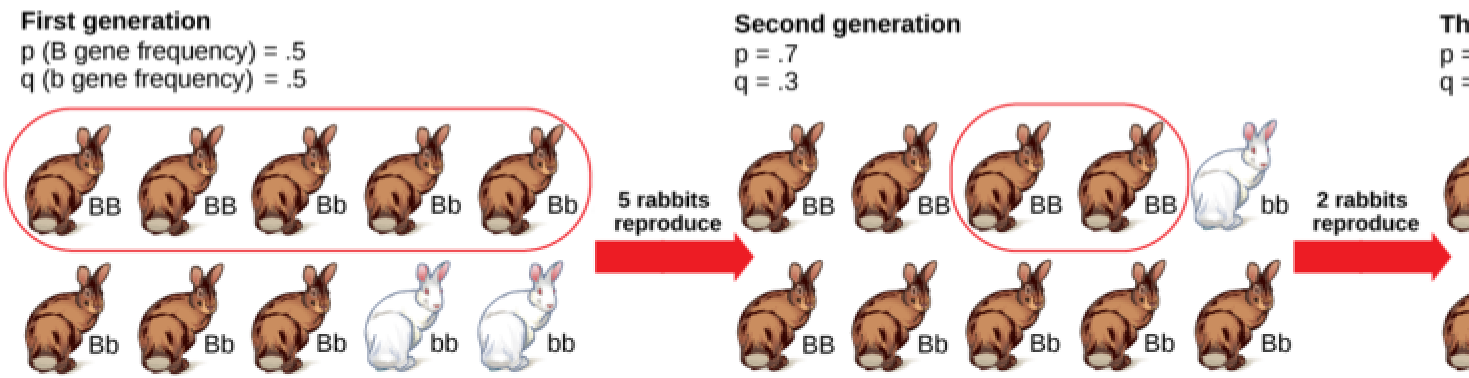

Figure 1. *Click for a larger image. Genetic drift in a population can lead to the elimination of an allele from a popu with the brown coat color allele (B) are dominant over rabbits with the white coat color allele (b). In the first gener frequency in the population, resulting in p and q values of .5. Only half of the individuals reproduce, resulting in a s and .3, respectively. Only two individuals in the second generation reproduce, and by chance these individuals are h As a result, in the third generation the recessive b allele is lost.*

Do you think genetic drift would happen more quickly on an island or on the mainland?

Answer:

Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

Small populations are more susceptible to the forces of genetic drift. Large populations, alternatively, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before it leaves any offspring to the next generation, all of its genes—1/10 of the population's gene pool—will be suddenly lost. In a population of 100, that's only 1 percent of the overall gene pool; therefore, it is much less impactful on the population's genetic structure.

Watch this animation of random sampling and genetic drift in action:

Bottleneck Effect

Genetic drift can also be magnified by natural events, such as a natural disaster that kills—at random—a large portion of the population. Known as the **bottleneck effect**, it results in a large portion of the gene pool suddenly being wiped out (**Figure 2**). In one fell swoop, the genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

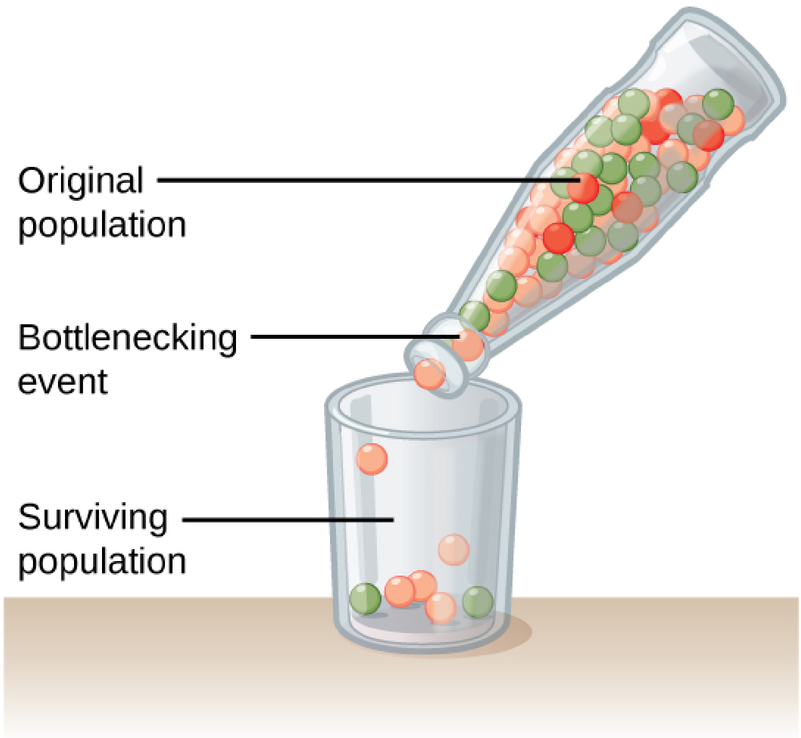

Figure 2. *A chance event or catastrophe can reduce the genetic variability within a population.*

Founder Effect

Another scenario in which populations might experience a strong influence of genetic drift is if some portion of the population leaves to start a new population in a new location or if a physical barrier divides a population. In this situation, those individuals are an unlikely representation of the entire population, which results in the founder effect. The founder effect occurs when the genetic structure changes to match that of the new population's founding fathers and mothers. Researchers believe that the founder effect was a key factor in the genetic history of the Afrikaner population of Dutch settlers in South Africa, as evidenced by mutations that are common in Afrikaners but rare in most other populations. This effect is probably due to the fact that a higher-than-normal proportion of the founding colonists carried these mutations. As a result, the population expresses unusually high incidences of Huntington's disease (HD) and Fanconi anemia (FA), a genetic disorder known to cause blood marrow and congenital abnormalities—even cancer.

Watch this short video to learn more about the founder and bottleneck effects. Note that the video has no audio.

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You can view the descriptive transcript for "Founder and Bottleneck Effect (Evolution)" here.

Gene Flow

Another important evolutionary force is gene flow: the flow of alleles in and out of a population due to the migration of individuals or gametes (**Figure 3**).

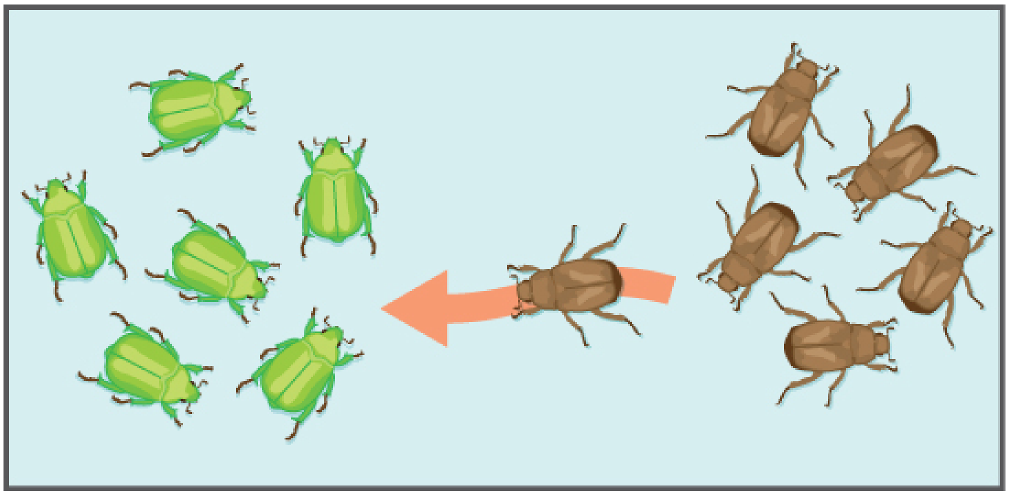

Figure 3. *Gene flow can occur when an individual travels from one geographic location to another.*

While some populations are fairly stable, others experience more flux. Many plants, for example, send their pollen far and wide, by wind or by bird, to pollinate other populations of the same species some distance away. Even a population that may initially appear to be stable, such as a pride of lions, can experience its fair share of immigration and emigration as developing males leave their mothers to seek out a new pride with genetically unrelated females. This variable flow of individuals in and out of the group not only changes the population's gene structure but can also introduce new genetic variation to populations in different geological locations and habitats.

Did I Get It?

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Simulation Exercise

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Evidence for Evolution

Section Goals

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

- Outline physical evidence that supports the theory of evolution
- Outline biological evidence that supports the theory of evolution
- Refute common misconceptions about evolution

The evidence for evolution is compelling and extensive. Looking at every level of organization in living systems, biologists see the signature of past and present evolution. Darwin dedicated a large portion of his book, *On the Origin of Species*, to identifying patterns in nature that were consistent with evolution, and since Darwin, our understanding has become clearer and broader.

Physical Evidence

Fossils

Fossils provide solid evidence that organisms from the past are not the same as those found today, and fossils show a progression of evolution. Scientists determine the age of fossils and categorize them from all over the world to determine when the organisms lived relative to each other. The resulting fossil record tells the story of the past and shows the evolution of form over millions of years (**Figure 1a**). For example, scientists have recovered highly detailed records showing the evolution of humans and horses (**Figure 1b**).

Figure 1. *In this (a) display, fossil hominids are arranged from oldest (bottom) to newest (top). As hominids evolved, the shape of the skull changed. An artist's rendition of (b) extinct species of the genus Equus reveals that these ancient species resembled the modern horse (Equus ferus) but varied in size.*

Anatomy and Embryology

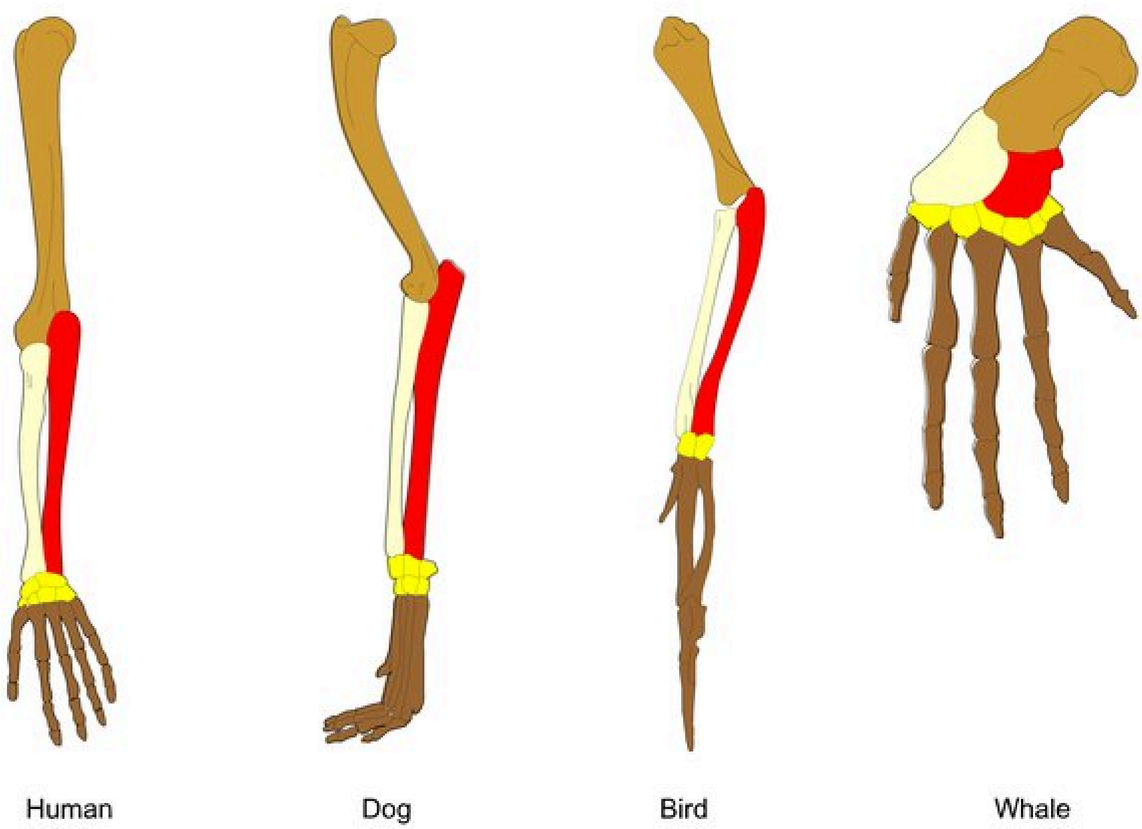

Figure 2. *The similar construction of these appendages indicates that these organisms share a common ancestor.*

Another type of evidence for evolution is the presence of structures in organisms that share the same basic form. For example, the bones in the appendages of a human, dog, bird, and whale all share the same overall construction (**Figure 2**) resulting from their origin in the appendages of a common ancestor. Over time, evolution led to changes in the shapes and sizes of these bones in different species, but they have maintained the same overall layout. Scientists call these synonymous parts homologous structures.

Some structures exist in organisms that have no apparent function at all, and appear to be residual parts from a past common ancestor. These unused structures without function are called vestigial structures. Some examples of vestigial structures are wings on flightless birds, leaves on some cacti, and hind leg bones in whales.

Another evidence of evolution is the convergence of form in organisms that share similar environments. For example, species of unrelated animals, such as the arctic fox and ptarmigan, living in the arctic region have been selected for seasonal white phenotypes during winter to blend with the snow and ice (**Figure 3**). These similarities occur not because of common ancestry, but because of similar selection pressures—the benefits of not being seen by predators.

(a) (b)

Figure 3. *The white winter coat of the (a) arctic fox and the (b) ptarmigan's plumage are adaptations to their environments. (credit a: modification of work by Keith Morehouse)*

Embryology, the study of the development of the anatomy of an organism to its adult form, also provides evidence of relatedness between now widely divergent groups of organisms. Mutational tweaking in the embryo can have such magnified consequences in the adult that embryo formation tends to be conserved. As a result, structures that are absent in some groups often appear in their embryonic forms and disappear by the time the adult or juvenile form is reached. For example, all vertebrate embryos, including humans, exhibit gill slits and tails at some point in their early development. These disappear in the adults of terrestrial groups but are maintained in adult forms of aquatic groups such as fish and some amphibians. Great ape embryos, including humans, have a tail structure during their development that is lost by the time of birth.

Misleading Appearances

Some organisms may be very closely related, even though a minor genetic change caused a major morphological difference to make them look quite different. Similarly, unrelated organisms may be distantly related, but appear very much alike. This usually happens because both organisms in common adaptations that evolved within similar environmental conditions, like the white phenotypes in the Arctic fox and ptarmigan in **Figure 3** above. When similar characteristics occur because of environmental constraints and not due to a close evolutionary relationship, it is an **analogy** or **homoplasy**. For example, insects use wings to fly like bats and birds, but the wing structure and embryonic origin are completely different. These are analogous structures (**Figure 4**). Analogous structures are the result of convergent evolution.

Similar traits can be either homologous or analogous. Homologous structures share a similar embryonic origin. Analogous organs have a similar function. For example, the bones in a whale's front flipper are homologous to the bones in the human arm. These structures are not analogous. A butterfly and a bird's wings are analogous, not homologous. Some structures are both analogous and homologous: bird and bat wings are both homologous and analogous. Bird and bat wings are analogous to wings. As forelimbs, they are homologous. Birds and bats did not inherit wings from a common ancestor with wings, but they did inherit forelimbs from a common ancestor with forelimbs. Scientists must determine which type of similarity a feature exhibits to decipher the organisms' phylogeny.

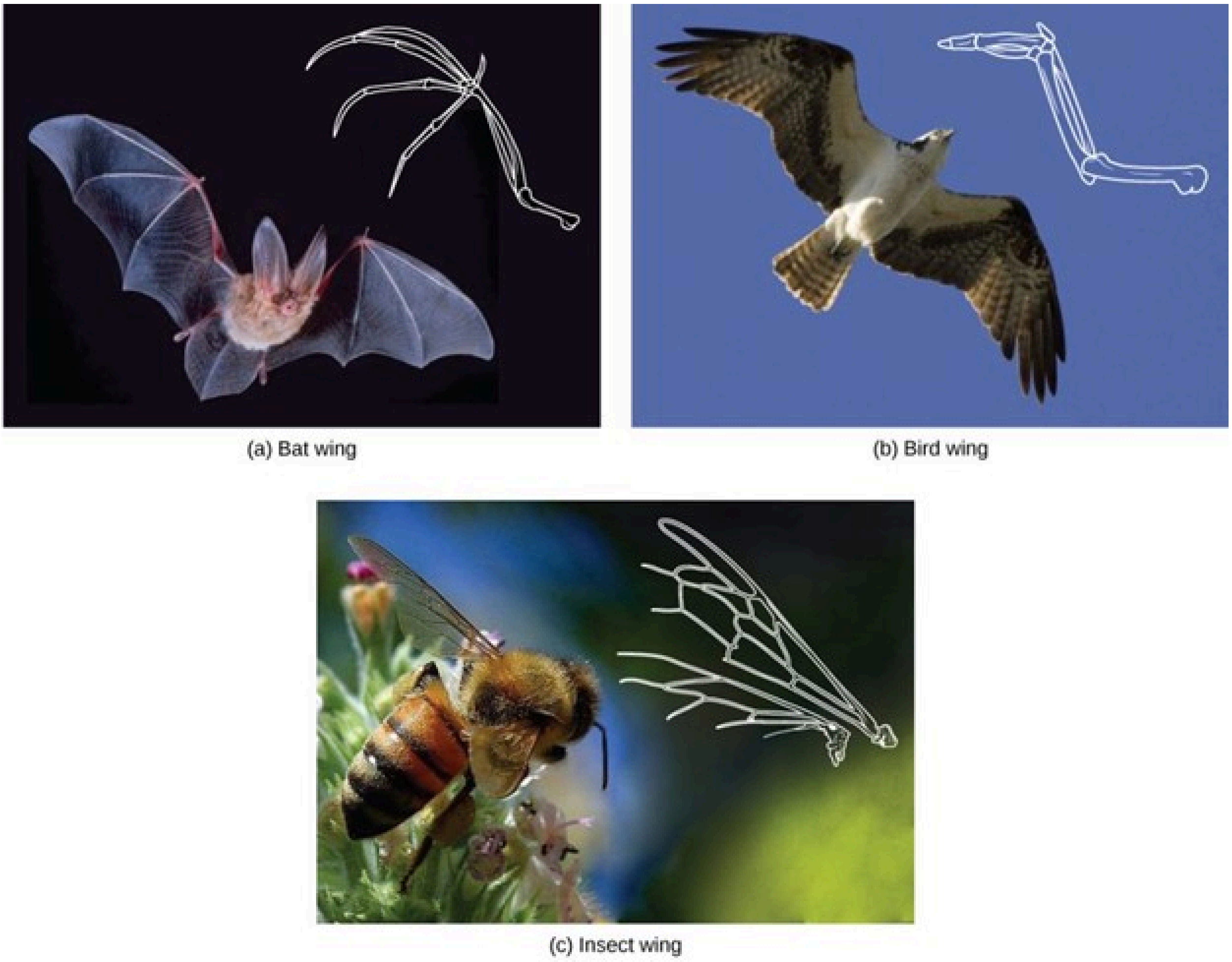

Figure 4. *The (c) wing of a honeybee is similar in shape to a (b) bird wing and (a) bat wing, and it serves the same function. However, the honeybee wing is not composed of bones and has a distinctly different structure and embryonic origin. These wing types (insect versus bat and bird) illustrate an analogy—similar structures that do not share an evolutionary history. (credit a: modification of work by Steve Hillebrand, USFWS; credit b: modification of work by U.S. DOI BLM; credit c: modification of work by Jon Sullivan)*

Click through this interactive module to learn more about homologies and convergent traits, and to test your understanding!

Biological Evidence

Biogeography

The geographic distribution of organisms on the planet follows patterns that are best explained by evolution in conjunction with the movement of tectonic plates over geological time. Broad groups that evolved before the breakup of the supercontinent Pangaea (about 200 million years ago) are distributed worldwide. Groups that evolved since the breakup appear uniquely in regions of the planet, such as the unique flora and fauna of northern continents that formed from the supercontinent Laurasia and of the southern continents that formed from the supercontinent Gondwana. The presence of members of the plant family Proteaceae in Australia, southern Africa, and South America is best due to their appearance prior to the southern supercontinent Gondwana breaking up.

The great diversification of marsupials in Australia and the absence of other mammals reflect Australia's long isolation. Australia has an abundance of endemic species—species found nowhere else—which is typical of islands whose isolation by expanses of water prevents species migration. Over time, these species diverge evolutionarily into new species that look very different from their ancestors that may exist on the mainland. The marsupials of Australia, the finches on the Galápagos, and many species on the Hawaiian Islands are all unique to their one point of origin, yet they display distant relationships to ancestral species on the mainland.

Molecular Evidence

DNA can provide a lot of information to help us study relationships among organisms. We can look at genes from multiple taxa to determine if they are similar or different to help us understand how closely or distantly related they are to one another. **Homeotic genes** are sections of DNA that play a key role in the developmental process as embryos undergo all sorts of changes. Homeotic genes act as on-and-off switches to help with the positioning of cells within the organism's body plan.

One group of homeotic genes that turn out to be very helpful for understanding evolution is **hox genes**. Hox genes determine the form, number, and evolution of repeating parts, such as the number and type of vertebrae in animals. The role of hox genes is to specify positional identity in the embryo, which will lead to corresponding structures in the adult. For example, at least eight different Hox genes are critical for the development of different body segments in fruit flies (**Figure 5**). Hox genes also affect the orientation of segments such that the anterior-to-posterior orientation is maintained. Scientists have learned that hox genes are part of a "toolbox" of genes that can be shuffled and rearranged to create the diversity of species we find on the planet.

When studying animal species, we find animal species with more simple body structures do not have as many hox genes as those species with more complex bodies. For example, a mammal such as a mouse will have many more hox genes than a flatworm. Humans have over 200 homeotic genes, and out of that, 39 are hox genes.

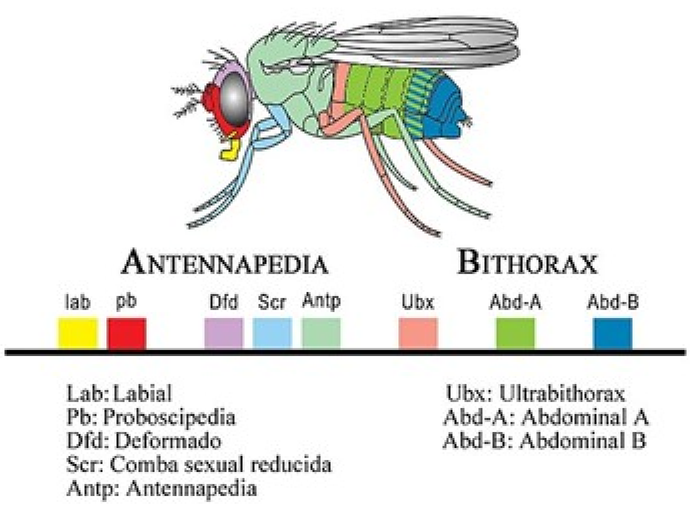

Figure 5. *The hox genes arranged on a chromosome found in the fruit fly. Each box of color represents a gene, a section of DNA, that helps determine the body part on the fly highlighted in the same color. For example, the yellow hox gene "lab" will help to dictate the labial mouth part of the adult fly. Antonio Quesada Díaz, Public domain, via Wikimedia Commons*

When looking more closely at homeotic genes, scientists discovered a 180-base-pair sequence to be identical in a wide array of animal species. This 180 base-pair sequence is called the homeobox and is highly conserved across evolutionary time (and it was first discovered in fruit flies). This suggests that hox genes arose very early in evolutionary time. The shared homeobox sequence suggests an ancestral gene was present and duplicated multiple times over evolutionary time to give rise to what we find today. Scientists get very excited about the homeobox because mutations in this gene can cause dramatic developmental changes in body parts and can lead to speciation.

Hox genes, as mentioned above, are conserved across species. We find some of the human hox genes are homologous to those in the fruit fly. In experiments with mice, the Hox10 genes turn the "rib" genes off which are normally active in the lower back, but not needed. When scientists experimentally manipulate these genes, they can cause ribs to grow in the vertebrae of the lower back. As such, we can see hox genes dictating arms versus legs as well as differentiating specific fingers, like a thumb or a pinky. The variation on the theme of the hox genes will give an organism a variety of traits and can lead to speciation.

Click through this animation to see how these master genes control basic fruit fly body plans. Visit this resource page to further explore how hox genes hold clues about evolutionary relationships!

DNA sequences have also shed light on some of the mechanisms of evolution. For example, it is clear that the evolution of new functions for proteins commonly occurs after gene duplication events that allow the free modification of one copy by mutation, selection, or drift (changes in a population's gene pool resulting from chance), while the other copy continues to produce a functional protein.

Check out the next video to review several varieties of evidence that support the Theory of Evolution:

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Did I Get It?

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Misconceptions about Evolution

Although the theory of evolution generated some controversy when it was first proposed, it was almost universally accepted by biologists, particularly younger biologists, within 20 years after the publication of *On the Origin of Species*. Nevertheless, the theory of evolution is a difficult concept, and misconceptions or misrepresentations about how it works are not uncommon. Here are some of the big ones:

Evolution Is Just a Theory

Critics of the theory of evolution dismiss its importance by purposefully confounding the everyday usage of the word "theory" with the way scientists use the word. In science, a "theory" is understood to be a body of thoroughly tested and verified explanations for a set of observations of the natural world. Scientists have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes understood facts about the world. In the same way, the theory of evolution describes facts about the living world. As such, a theory in science has survived significant efforts to discredit it by scientists.

In contrast, a "theory" in the common vernacular is a word meaning a guess or suggested explanation; this meaning is more akin to the scientific concept of "hypothesis." When critics of evolution say evolution is "just a theory," they are implying that there is little evidence supporting it and that it is still being rigorously tested. This use of the word theory is a mischaracterization.

Individuals Evolve

Evolution is the change in the genetic composition of a population over time, specifically over generations, resulting from the differential reproduction of individuals with certain alleles. Individuals do change over their lifetime, obviously, but this is called development and involves changes programmed by the set of genes the individual acquired at birth in coordination with the individual's environment. When thinking about the evolution of a characteristic, it is probably best to think about it as the change of the average value of the characteristic in the population over time. For example, when natural selection leads to bill-size changes in medium-ground finches in the Galápagos, this does not mean that individual bills on the finches are changing. If one measures the average bill size among all individuals in the population at one time and then measures the average bill size in the population several years later, this average value will be different as a result of evolution. Although some individuals may survive from the first time to the second, they will still have the same bill size; however, there will be many new individuals that contribute to the shift in average bill size.

Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment" are quite common, but such statements can lead to two types of misunderstandings. First, the statement must not be understood to mean that individual organisms evolve. The statement is shorthand for "a population evolves in response to a changing environment." However, a second misunderstanding may arise by interpreting the statement to mean that the evolution is somehow intentional. A changed environment results in some individuals in the population, those with particular phenotypes, benefiting and therefore producing proportionately more offspring than other phenotypes. This results in a change in the population if the characteristics are genetically determined.

It is also important to understand that the variation that natural selection works on is already in a population and does not arise in response to an environmental change. For example, applying antibiotics to a population of bacteria will, over time, select a population of bacteria that are resistant to antibiotics. The resistance, which is caused by a gene, did not arise by mutation because of the application of the antibiotic. The gene for resistance was already present in the gene pool of the bacteria, likely at a low frequency. The antibiotic, which kills the bacterial cells without the resistance gene, strongly selects resistant individuals, since these would be the only ones that survive and divide. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of antibiotics.

In a larger sense, evolution is not goal-directed. Species do not become "better" over time; they simply track their changing environment with adaptations that maximize their reproduction in a particular environment at a particular time. Evolution has no goal of making faster, bigger, more complex, or even smarter species, despite the commonness of this kind of language in popular discourse. What characteristics evolve in a species are a function of the variation present and the environment, both of which are constantly changing in a non-directional way. What trait is fit in one environment at one time may well be fatal at some point in the future. This property of traits holds equally well for a species of insect as it does for the human species.

Evolution Explains the Origin of Life

It is a common misunderstanding that evolution includes an explanation of life's origins. Conversely, some of the theory's critics believe that it cannot explain the origin of life. The theory does not try to explain the origin of life. The theory of evolution explains how populations change over time and how life diversifies the origin of species. It does not shed light on the beginnings of life, including the origins of the first cells, which is how life is defined. The mechanisms of the origin of life on Earth are a particularly difficult problem because it occurred a very long time ago, and presumably it just occurred once. Importantly, biologists believe that the presence of life on Earth precludes the possibility that the events that led to life on Earth can be repeated because the intermediate stages would immediately become food for existing living things.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA either within a cell or pre-cell, these entities would be subject to the principle of natural selection. More effective reproducers would increase in frequency at the expense of inefficient reproducers. So while evolution does not explain the origin of life, it may have something to say about some of the processes operating once pre-living entities acquired certain properties.

Check out this more comprehensive list of common misconceptions about evolution from the *Understanding Evolution* site.

Did I Get It?

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Summary: Evidence for Evolution

Since Darwin developed his ideas on descent with modification and the pressures of natural selection, a variety of evidence has been gathered supporting the theory of evolution. Fossil evidence shows the changes in lineages over millions of years, such as in hominids and horses. Studying anatomy allows scientists to identify homologous structures across diverse groups of related organisms, such as leg bones. Vestigial structures also offer clues to common ancestors. Using embryology, scientists can identify common ancestors through structures present only during development and not in the adult form. Biogeography offers further clues about evolutionary relationships. The presence of related organisms across continents indicates when these organisms may have evolved. For example, some flora and fauna of the northern continents are similar across these landmasses but distinct from those of the southern continents. Islands such as Australia and the Galapagos chain often have unique species that evolved after these landmasses separated from the mainland. Finally, molecular biology provides data supporting the theory of evolution. In particular, the universality of DNA and near universality of the genetic code for proteins shows that all life once shared a common ancestor. DNA also provides clues into how evolution may have happened. Gene duplications allow one copy to undergo mutational events without harming an organism, as one copy continues to produce functional protein.

Many misconceptions exist about the theory of evolution—including some perpetuated by critics of the theory. First, evolution as a scientific theory means that it has years of observation and accumulated data supporting it. It is not "just a theory" as a person may say in common vernacular.

Another misconception is that individuals evolve, though in fact it is populations that evolve over time. Individuals simply carry mutations. Furthermore, these mutations neither arise on purpose nor do they arise in response to environmental pressure. Instead, mutations in DNA happen spontaneously and are already present in individuals of a population when selective pressure occurs. Once the environment begins to favor a particular trait, then those individuals already carrying that mutation will have a selective advantage and are likely to survive better and outproduce others without adaptation.

Finally, the theory of evolution does *not* address the origins of life on this planet. Scientists believe that we cannot repeat the circumstances that led to life on Earth because, at this time, life already exists. The presence of life has so dramatically changed the environment that the origins cannot be totally produced for study.

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VIII

Evolutionary Patterns

This module contains the following chapters:

- Defining Species
- Formation of New Species
- Phylogenetic Trees
- Reconstructing Evolutionary Relationships

Adapted from:

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Defining Species

Section Goals

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

- Define species and describe how species are identified as distinct

A **species** is a group of individual organisms that interbreed and produce fertile, viable offspring. According to this definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile offspring.

Members of the same species share both external and internal characteristics, which develop from their DNA. The closer the relationship two organisms share, the more DNA they have in common, just like people and their families. People’s DNA is likely to be more like their father’s or mother’s DNA than their cousin’s or grandparent’s DNA. Organisms of the same species have the highest level of DNA alignment and therefore share characteristics and behaviors that lead to successful reproduction.

Species’ appearance can be misleading in suggesting an ability or inability to mate. For example, even though domestic dogs (*Canis lupus familiaris*) display phenotypic differences, such as size, build, and coat, most dogs can interbreed and produce viable puppies that can mature and sexually reproduce (**Figure 1**).

(a) (b) (c)

Figure 1. *The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo. (credit a: modification of work by Sally Eller, Tom Reese; credit b: modification of work by Jeremy McWilliams; credit c: modification of work by Kathleen Conklin)*

In other cases, individuals may appear similar although they are not members of the same species. For example, even though bald eagles (*Haliaeetus leucocephalus*) and African fish eagles (*Haliaeetus vocifer*) are both birds and eagles, each belongs to a separate species group (**Figure 2**). If humans were to artificially intervene and fertilize the egg of a bald eagle with the sperm of an African fish eagle and a chick did hatch, that offspring, called a **hybrid** (a cross between two species), would probably be infertile—unable to successfully reproduce after it reached maturity. Different species may have different genes that are active in development; therefore, it may not be possible to develop a viable offspring with two different sets of directions. Thus, even though hybridization may take place, the two species still remain separate.

(a) (b)

Figure 2. *The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species. (credit a: modification of work by Nigel Wedge; credit b: modification of work by U.S. Fish and Wildlife Service)*

Populations of species share a gene pool: a collection of all the gene variants in the species. Again, the basis for any changes in a group or population of organisms must be genetic for this is the only way to share and pass on traits. When variations occur within a species, they can only pass to the next generation along two main pathways: asexual reproduction or sexual reproduction. The change will pass on asexually simply if the reproducing cell possesses the changed trait. For the changed trait to be passed on by sexual reproduction, a gamete, such as a sperm or egg cell, must possess the changed trait. In other words, sexually reproducing organisms can experience several genetic changes in their body cells, but if these changes do not occur in a sperm or egg cell, the changed trait will never reach the next generation. Only heritable traits can evolve. Therefore, reproduction plays a paramount role in genetic change to take root in a population or species. In short, organisms must be able to reproduce with each other to pass new traits to offspring.

What is a Species?

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Read more about the biological species concept and other species concepts.

Did I Get It?

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https://rotel.pressbooks.pub/understanding-organisms/?p=248#h5p-48

Formation of New Species

Section Goals

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

- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Differentiate between allopatric and sympatric speciation

The biological definition of species, which works for sexually reproducing organisms, is a group of actual or potentially interbreeding individuals. There are exceptions to this rule. Many species are similar enough that hybrid offspring are possible and may often occur in nature, but for the majority of species, this rule generally holds. The presence in nature of hybrids between similar species suggests that they may have descended from a single interbreeding species, and the speciation process may not yet be completed.

Given the extraordinary diversity of life on the planet there must be mechanisms for **speciation**: the formation of two species from one original species. Darwin envisioned this process as a branching event and diagrammed the process in the only illustration found in *On the Origin of Species* (**Figure 1a**). Compare this illustration to the diagram of elephant evolution (**Figure 1b**), which shows that as one species changes over time, it branches to form more than one new species, repeatedly, as long as the population survives or until the organism becomes extinct.

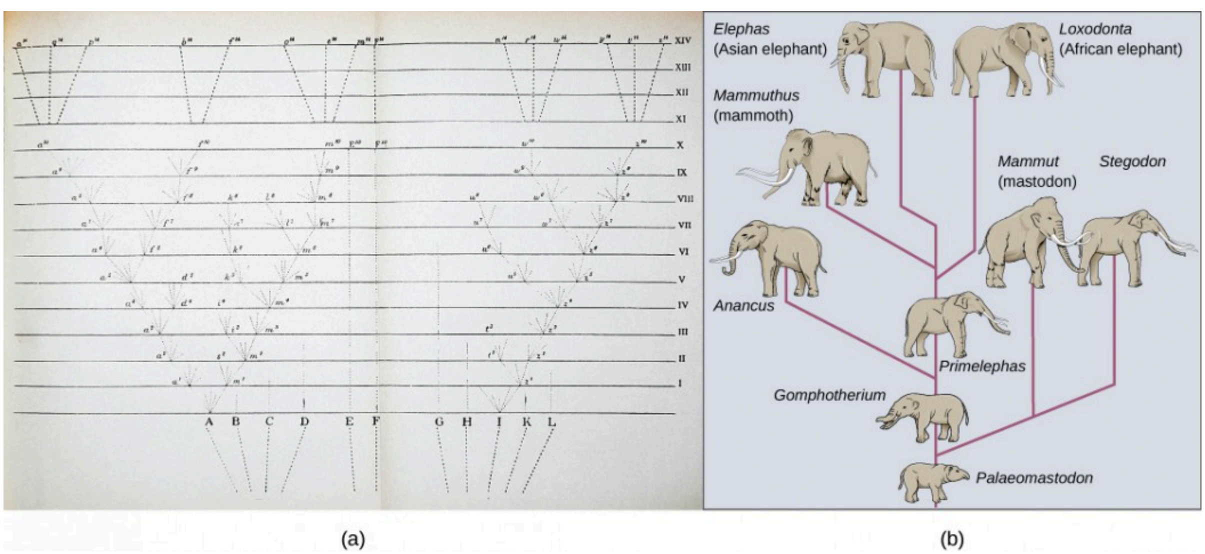

Figure 1. *The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from the Palaeomastodon, a species that lived in Egypt 35–50 million years ago.*

For speciation to occur, two new populations must be formed from one original population and they must evolve in such a way that it becomes impossible for individuals from the two new populations to interbreed. Biologists have proposed mechanisms by which this could occur that fall into two broad categories. **Allopatric speciation** (*allo–* = "other"; *–patric* = "homeland") involves the geographic separation of populations from a parent species and subsequent evolution. **Sympatric speciation** (*sym–* = "same"; *–patric* = "homeland") involves speciation occurring within a parent species remaining in one location.

Biologists think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why more than two species might not form at one time except that it is less likely and we can conceptualize multiple events as single splits occurring close in time.

Watch this video to see how scientists uncover evidence that birds descended from dinosaurs.

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Allopatric Speciation

A geographically continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across a species' range, is relatively free because individuals can move and then mate with individuals in their new location. Thus, an allele's frequency at one end of a distribution will be similar to the allele's frequency at the other end. When populations become geographically discontinuous, it prevents alleles' free flow. When that separation lasts for a period of time, the two populations are able to evolve along different trajectories. Thus, their allele frequencies at numerous genetic loci gradually become increasingly different as new alleles independently arise by mutation in each population. Typically, environmental conditions, such as climate, resources, predators, and competitors for the two populations will differ, causing natural selection to favor divergent adaptations in each group.

Isolation of populations leading to allopatric speciation can occur in a variety of ways: a river forming a new branch, erosion creating a new valley, a group of organisms traveling to a new location without the ability to return, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends entirely on the organism's biology and its potential for dispersal. If two flying insect populations took up residence in separate nearby valleys, chances are, individuals from each population would fly back and forth continuing gene flow. However, if a new lake divided two rodent populations, continued gene flow would be unlikely; therefore, speciation would be more likely.

Biologists group allopatric processes into two categories: dispersal and vicariance. **Dispersal** is when a few members of a species move to a new geographical area, and **vicariance** is when a natural situation arises to physically divide organisms.

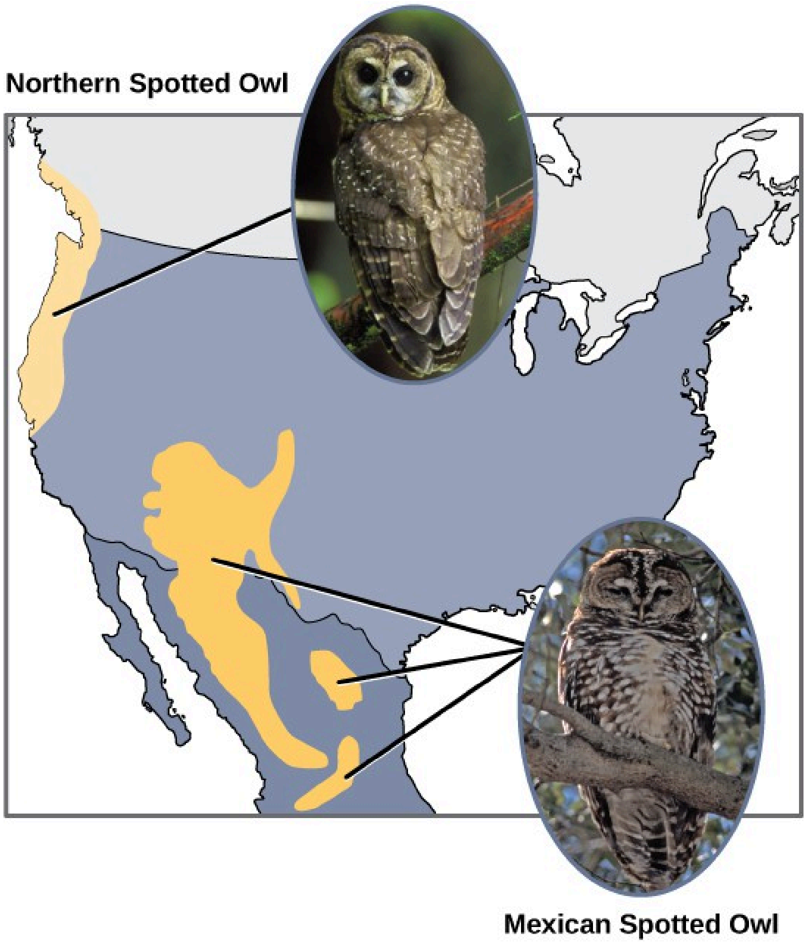

Figure 2. *The northern spotted owl and the Mexican spotted owl inhabit geographically separate locations with different climates and ecosystems. The owl is an example of allopatric speciation. (credit "northern spotted owl": modification of work by John and Karen Hollingsworth; credit "Mexican spotted owl": modification of work by Bill Radke)*

Scientists have documented numerous cases of allopatric speciation. For example, along the west coast of the United States, two separate spotted owl subspecies exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south (**Figure 2**).

Additionally, scientists have found that the further the distance between two groups that once were the same species, the more likely it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would likely have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south. The types of organisms in each ecosystem differ, as do their behaviors and habits. Also, the hunting habits and prey choices of the southern owls vary from the northern owls. These variances can lead to evolved differences in the owls, and speciation likely will occur.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area, and each finds a distinct niche or isolated habitat. Over time, the varied demands of their new lifestyles lead to multiple speciation events originating from a single species. We call this **adaptive radiation** because many adaptations evolve from a single point of origin, thus causing the species to radiate into several new ones. Island archipelagos like the Hawaiian Islands provide an ideal context for adaptive radiation events because water surrounds each island which leads to geographical isolation for many organisms. The Hawaiian honeycreeper illustrates one example of adaptive radiation. From a single species, the founder species, numerous species have evolved, including the six in **Figure 3**.

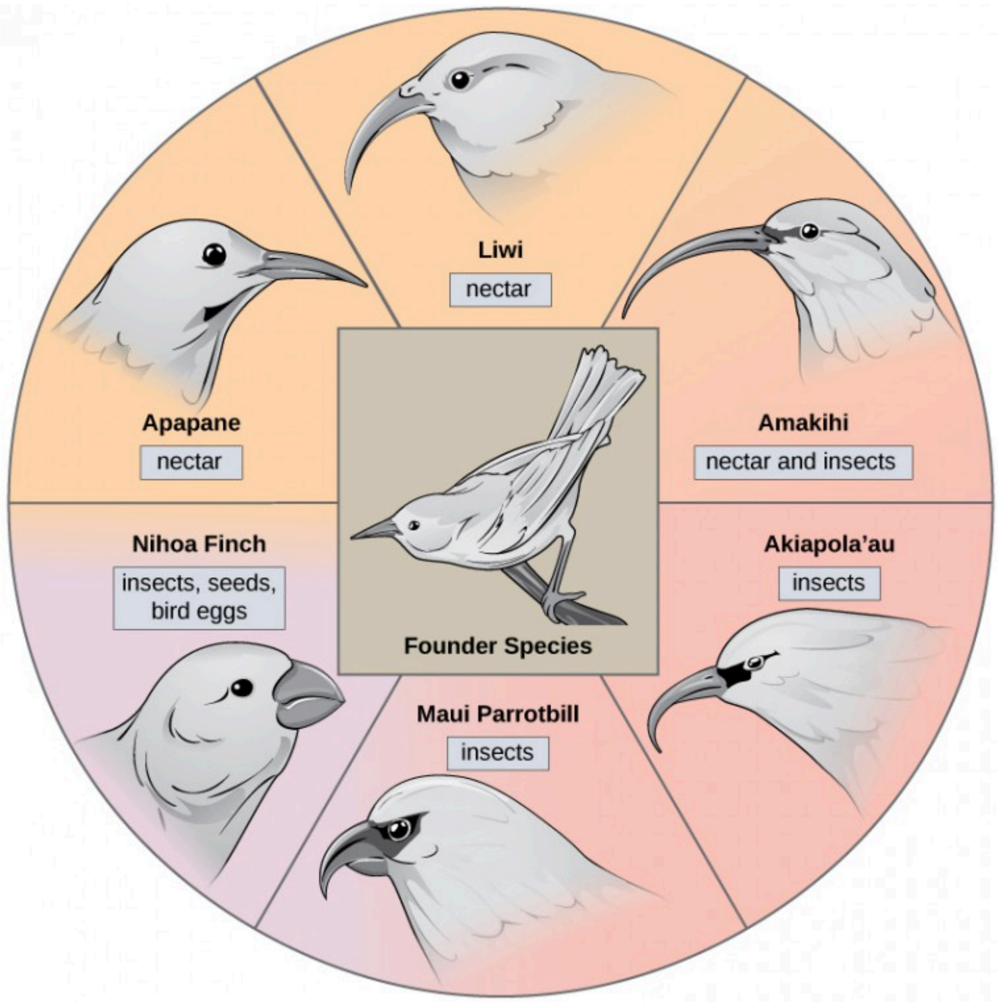

Figure 3. *The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.*

Notice the differences in the species' beaks in **Figure 3**. Evolution in response to natural selection based on specific food sources in each new habitat led to the evolution of a different beak suited to the specific food source. The seed-eating bird has a thicker, stronger beak which is suited to break hard nuts. The nectar-eating birds have long beaks to dip into flowers to reach the nectar. The insect-eating birds have beaks like swords, appropriate for stabbing and impaling insects. Darwin's finches are another example of adaptive radiation in an archipelago.

In the next video, the process of speciation is illustrated in Birds-of-paradise.

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Sympatric Speciation

Can divergence occur if no physical barriers are in place to separate individuals who continue to live and reproduce in the same habitat? The answer is yes. We call the process of speciation within the same space sympatric. The prefix "sym" means same, so "sympatric" means "same homeland" in contrast to "allopatric" meaning "other homeland." Scientists have proposed and studied many mechanisms.

One form of sympatric speciation can begin with a serious chromosomal error during cell division. In a normal cell division event chromosomes replicate, pair up, and then separate so that each new cell has the same number of chromosomes. However, sometimes the pairs separate and the end cell product has too many or too few individual chromosomes in a condition that we call **aneuploidy** (**Figure 4**).

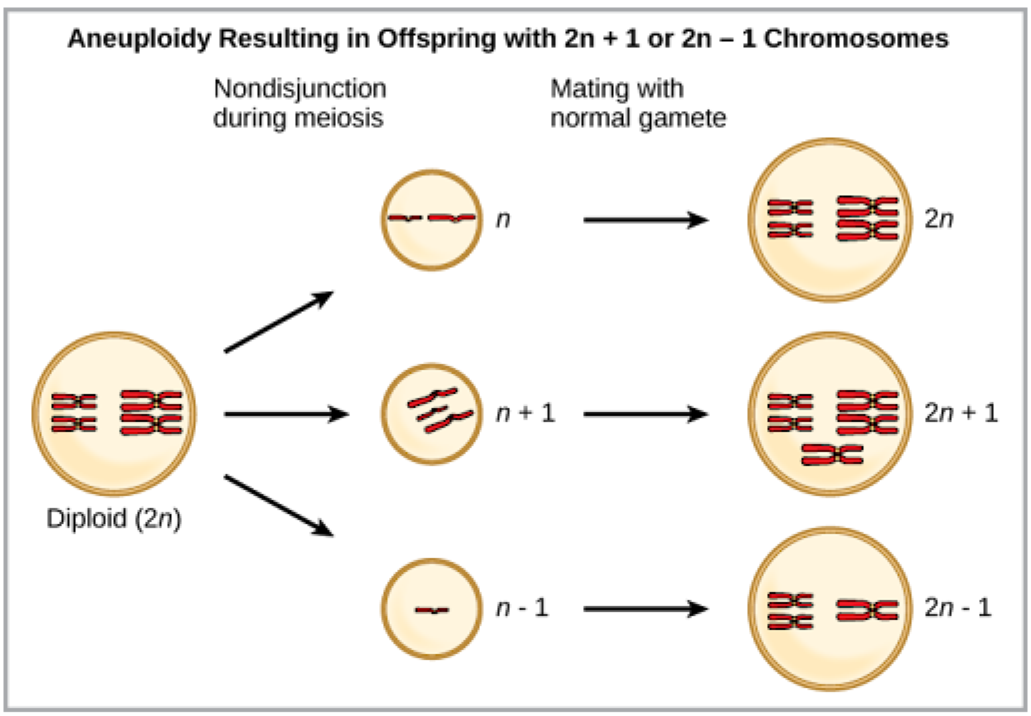

Figure 4. *Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have 2n+1 or 2n−1 chromosomes*

In **Figure 4**, which is most likely to survive, offspring with 2n+1 chromosomes or offspring with 2n-1 chromosomes?

Answer:

Loss of genetic material is almost always lethal, so offspring with 2n+1 chromosomes are more likely to survive.

Polyploidy is a condition in which a cell or organism has an extra set, or sets, of chromosomes. Scientists have identified two main types of polyploidy that can lead to reproductive isolation of an individual in the polyploidy state. Reproductive isolation is the inability to interbreed. In some cases, a polyploid individual will have two or more complete sets of chromosomes from its own species in a condition that we call **autopolyploidy** (**Figure 5**). The prefix "auto-" means "self," so the term means multiple chromosomes from one's own species. Polyploidy results from an error in meiosis in which all of the chromosomes move into one cell instead of separating.

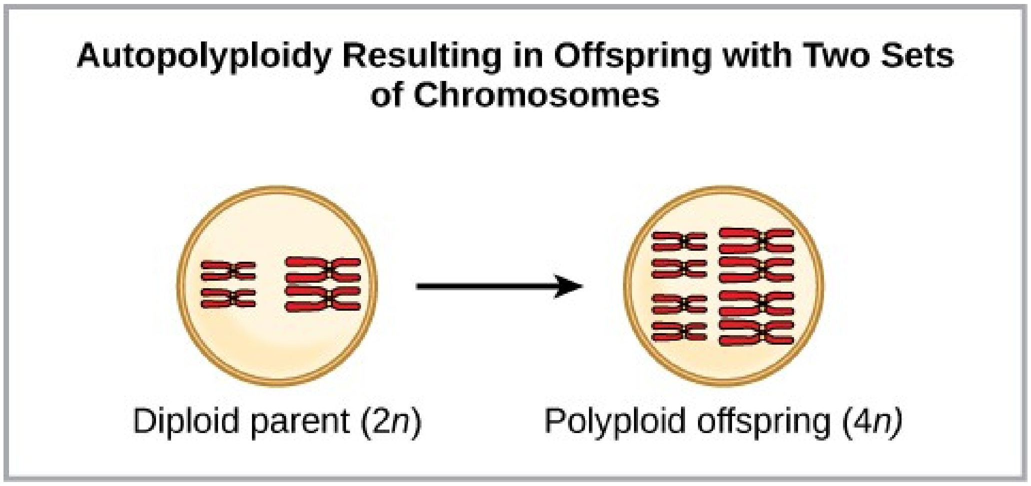

Figure 5. *Autopolyploidy results when mitosis is not followed by cytokinesis.*

For example, if a plant species with $2n = 6$ produces autopolyploid gametes that are also diploid ($2n = 6$, when they should be $n = 3$), the gametes now have twice as many chromosomes as they should have. These new gametes will be incompatible with the normal gametes that this plant species produces. However, they could either self-pollinate or reproduce with other autopolyploid plants with gametes having the same diploid number. In this way, sympatric speciation can occur quickly by forming offspring with $4n$ that we call a tetraploid. These individuals would immediately be able to reproduce only with those of this new kind and not those of the ancestral species.

The other form of polyploidy occurs when individuals of two different species reproduce to form a viable offspring called an **allopolyploid**. The prefix "allo-" means "other" (recall from allopatric): therefore, an allopolyploid occurs when gametes from two different species combine. **Figure 6** illustrates one possible way an allopolyploid can form. Notice how it takes two generations, or two reproductive acts, before the viable fertile hybrid results.

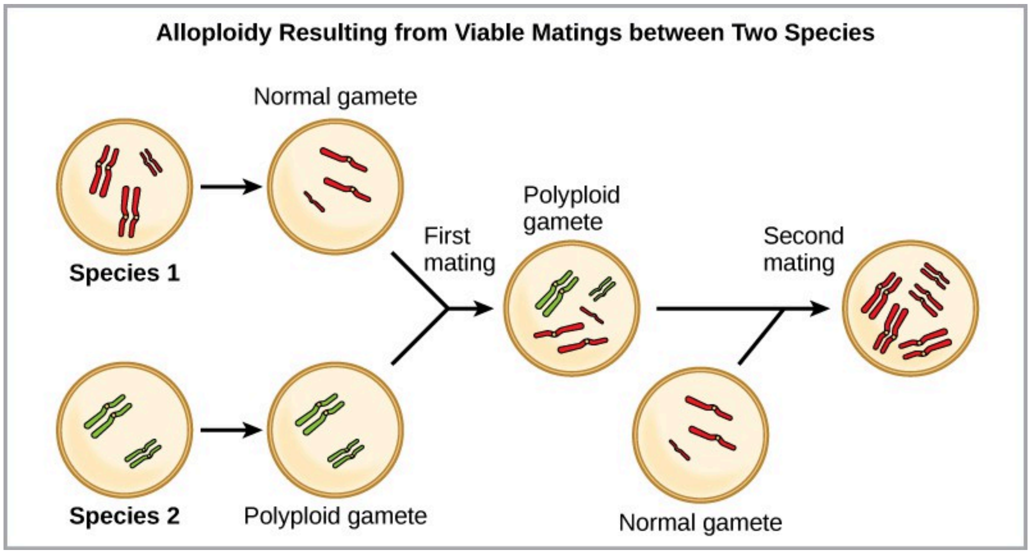

Figure 6. *Alloploidy results when two species mate to produce viable offspring. In the example shown, a normal gamete from one species fuses with a polyploidy gamete from another. Two matings are necessary to produce viable offspring.*

The cultivated forms of wheat, cotton, and tobacco plants are all allopolyploids. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. (Animals with any of the types of chromosomal aberrations that we describe here are unlikely to survive and produce normal offspring.) Scientists have discovered more than half of all plant species studied relate back to a species that evolved through polyploidy. With such a high rate of polyploidy in plants, some scientists hypothesize that this mechanism takes place more as an adaptation than as an error.

Reproductive Isolation

Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction: if individuals of the two populations were brought together, mating would be less likely, but if mating occurred, offspring would be nonviable or infertile. Many types of diverging characters may affect the **reproductive isolation**, the ability to interbreed, of the two populations.

Reproductive isolation can occur in various ways. Scientists organize them into two groups: prezygotic barriers and postzygotic barriers. A zygote is a fertilized egg: the first cell of the development of an organism that reproduces sexually. Therefore, a **prezygotic barrier** is a mechanism that blocks reproduction from taking place; this includes barriers that prevent fertilization when organisms attempt reproduction. A **postzygotic barrier** occurs after zygote formation; this includes organisms that don’t survive the embryonic stage and those that are born sterile.

Some types of prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually. Differences in breeding schedules, which we call **temporal isolation**, can act as a form of reproductive isolation. For example, two frog species inhabit the same area, but one reproduces from January to March; whereas, the other reproduces from March to May (**Figure 7**).

Figure 7. These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii. (credit a: modification of work by Mark R. Jennings, USFWS; credit b: modification of work by Alessandro Catenazzi)

In some cases, populations of a species move or are moved to a new habitat and take up residence in a place that no longer overlaps with the same species' other populations. We call this situation **habitat isolation**. Reproduction with the parent species ceases, and a new group exists that is now reproductively and genetically independent. For example, a cricket population that was divided after a flood could no longer interact with each other. Over time, natural selection forces, mutation, and genetic drift will likely result in the two groups diverging (**Figure 8**).

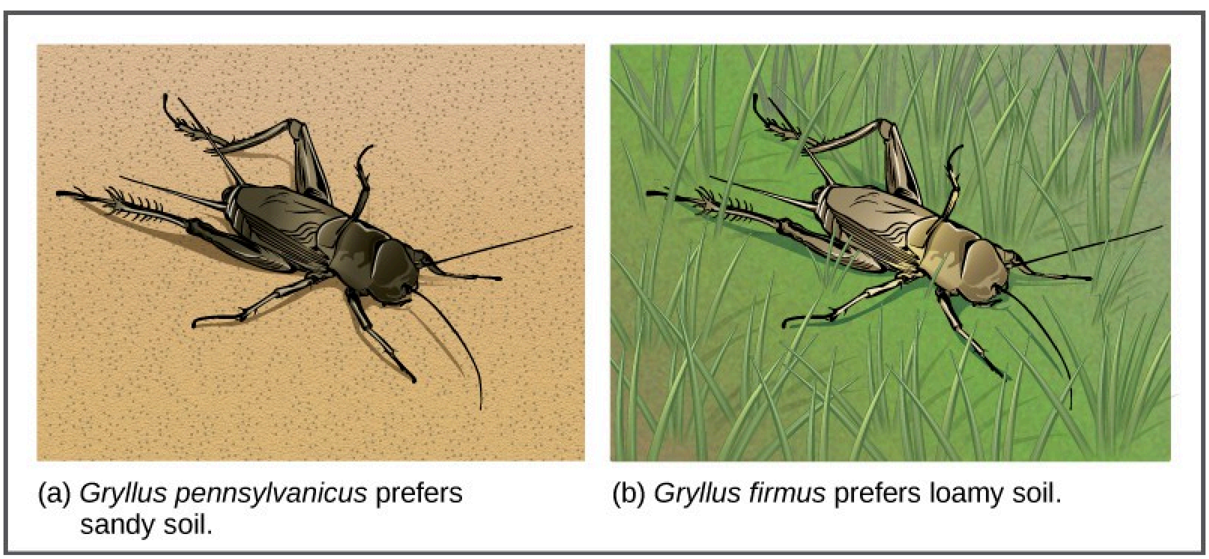

Figure 8. *Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) Gryllus pennsylvanicus prefers sandy soil, and the cricket (b) Gryllus firmus prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.*

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction. For example, male fireflies use specific light patterns to attract females. Various species of fireflies display their lights differently. If a male of one species tried to attract the female of another, she would not recognize the light pattern and would not mate with the male.

Other prezygotic barriers work when differences in their gamete cells (eggs and sperm) prevent fertilization from taking place; this is called a **gametic barrier**. Similarly, in some cases, closely related organisms try to mate, but their reproductive structures simply do not fit together. For example, damselfly males of different species have differently shaped reproductive organs. If one species tries to mate with the female of another, their body parts simply do not fit together. (**Figure 9**).

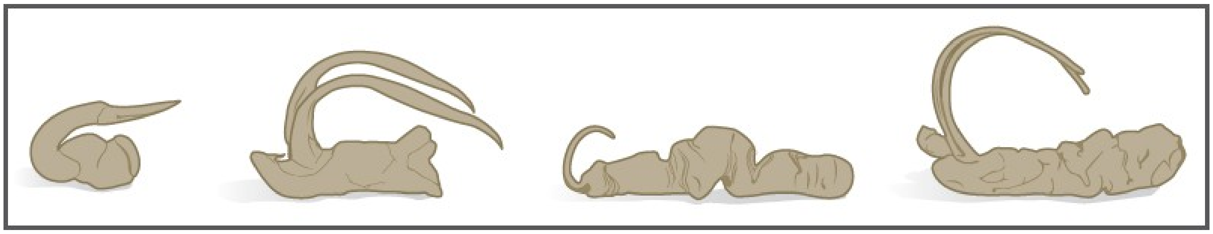

Figure 9. *The shape of the male reproductive organ varies among male damselfly species, and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.*

In plants, certain structures aimed to attract one type of pollinator simultaneously prevent a different pollinator from accessing the pollen. The tunnel through which an animal must access nectar can vary widely in length and diameter, which prevents the plant from being cross-pollinated with a different species (**Figure 10**).

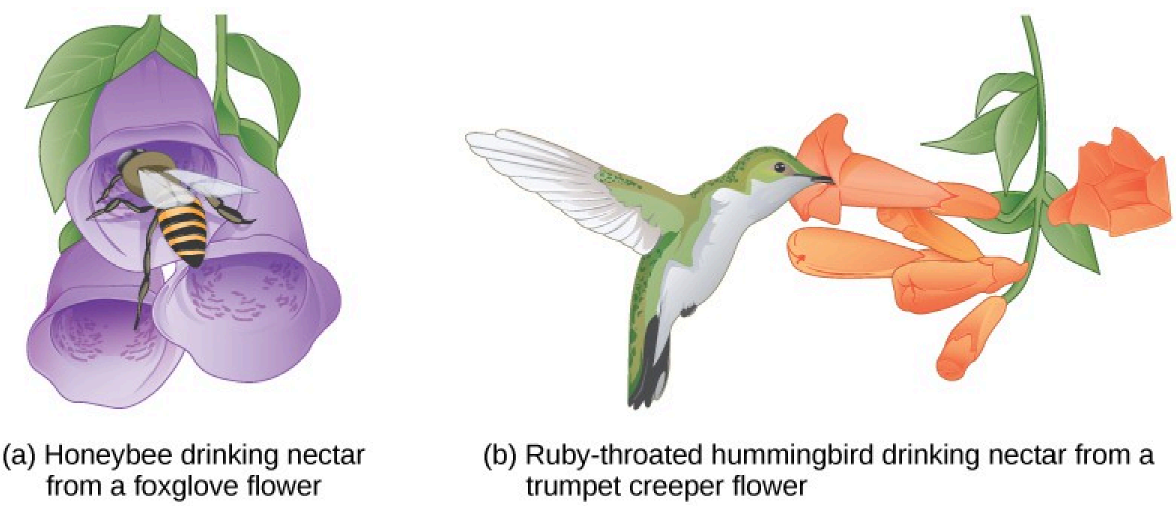

Figure 10. *Some flowers have evolved to attract certain pollinators. The (a) wide foxglove flower is adapted for pollination by bees, while the (b) long, tube-shaped trumpet creeper flower is adapted for pollination by humming birds.*

When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction. Hybrid individuals in many cases cannot form normally in the womb and simply do not survive past the embryonic stages. This is called **hybrid inviability** because the hybrid organisms simply are not viable.

In another postzygotic situation, reproduction leads to the birth and growth of a hybrid that is sterile and unable to reproduce offspring of their own; this is called hybrid sterility.

As the collection of real life examples in the next video demonstrates, not all barriers are physical.

An interactive H5P element has been excluded from this version of the text. You can view it online here: https://rotel.pressbooks.pub/understanding-organisms/?p=250#h5p-49

Habitat Influence on Speciation

Sympatric speciation may also take place in ways other than polyploidy. For example, consider a species of fish that lives in a lake. As the population grows, competition for food also grows. Under pressure to find food, suppose that a group of these fish had the genetic flexibility to discover and feed off another resource that was unused by the other fish. What if this new food source was found at a different depth of the lake? Over time, those feeding on the second food source would interact more with each other than the other fish; therefore, they would breed together as well. Offspring of these fish would likely behave as their parents: feeding and living in the same area and keeping separate from the original population. If this group of fish continued to remain separate from the first population, eventually sympatric speciation might occur as more genetic differences accumulated between them.

This scenario does play out in nature, as do others that lead to reproductive isolation. One such place is Lake Victoria in Africa, famous for its sympatric speciation of cichlid fish. Researchers have found hundreds of sympatric speciation events in these fish, which have not only happened in great number but also over a short period of time. **Figure 11** shows this type of speciation among a cichlid fish population in Nicaragua. In this locale, two types of cichlids live in the same geographic location but have come to have different morphologies that allow them to eat various food sources.

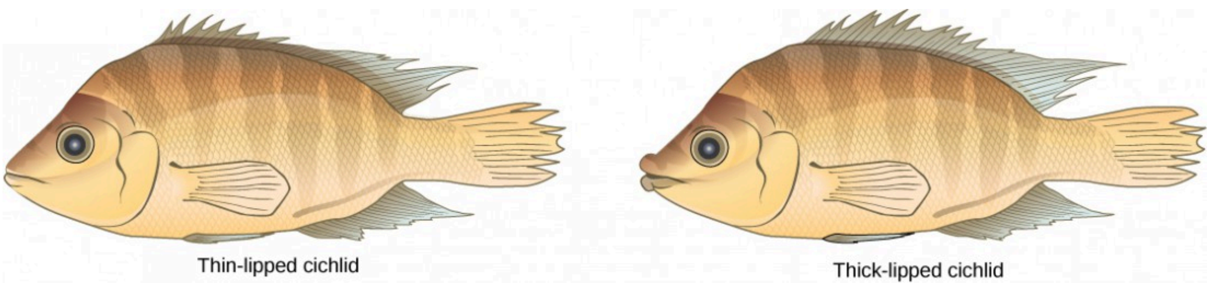

Figure 11. *Cichlid fish from Lake Apoyeque, Nicaragua, show evidence of sympatric speciation. Lake Apoyeque, a crater lake, is 1800 years old, but genetic evidence indicates that the lake was populated only 100 years ago by a single population of cichlid fish. Nevertheless, two populations with distinct morphologies and diets now exist in the lake, and scientists believe these populations may be in an early stage of speciation.*

Did I Get It?

An interactive H5P element has been excluded from this version of the text. You can view it online here: https://rotel.pressbooks.pub/understanding-organisms/?p=250#h5p-50

Phylogenetic Trees

Section Goals

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

- Discuss the structure and purpose of a phylogenetic tree
- Identify the types of evidence used to construct phylogenetic trees
- Recognize the practical applications phylogenetic trees

This bee and *Echinacea* flower (**Figure 1**) could not look more different, yet they are related, as are all living organisms on Earth. By following pathways of similarities and changes—both visible and genetic—scientists seek to map the evolutionary past of how life developed from single-celled organisms to the tremendous collection of creatures that have germinated, crawled, floated, swum, flown, and walked on this planet.

Figure 1. *The life of a bee is very different from the life of a flower, but the two organisms are related. Both are members of the domain Eukarya and have cells containing many similar organelles, genes, and proteins. (credit: photo by Li Yan via Unsplash)*

In scientific terms, phylogeny is the evolutionary history and relationship of an organism or group of organisms. A **phylogeny** describes the organism's relationships, such as from which organisms it may have evolved or to which species it is most closely related. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different.

Scientists use a tool called a phylogenetic tree to show the evolutionary pathways and connections among organisms. A **phylogenetic tree** is a diagram used to reflect evolutionary relationships among organisms or groups of organisms. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past since one cannot go back to confirm the proposed relationships. In other words, we can construct a "tree of life" to illustrate when different organisms evolved and to show the relationships among different organisms (**Figure 2**).

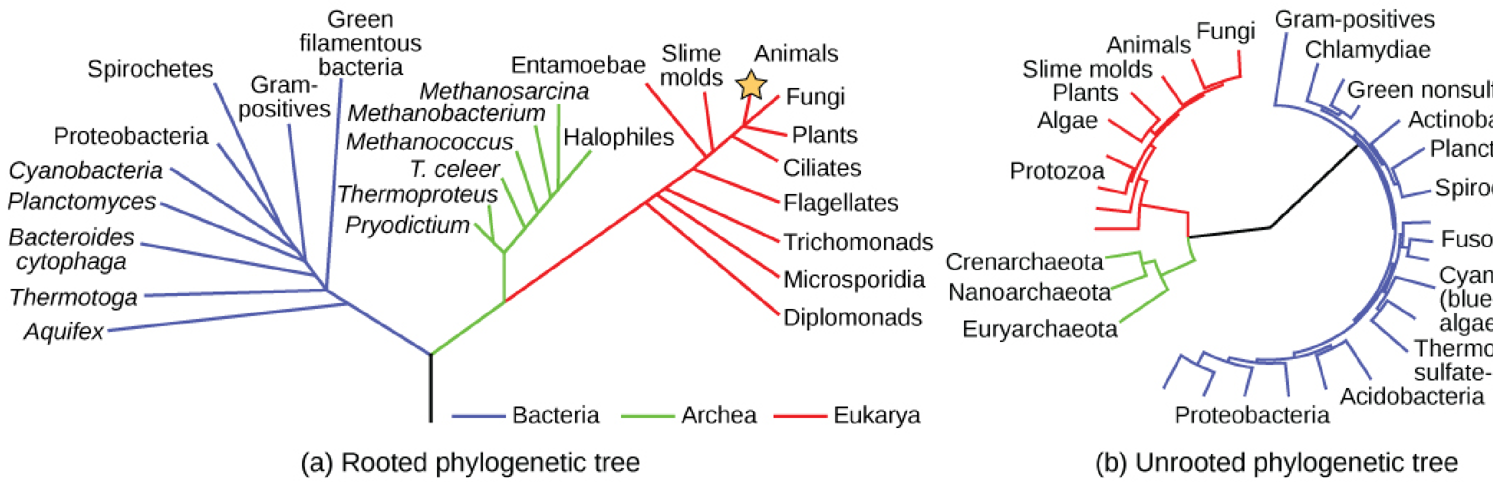

Figure 2. *Both of these phylogenetic trees shows the relationship of the three domains of life—Bacteria, Archaea, ar Eukarya—but the (a) rooted tree attempts to identify when various species diverged from a common ancestor while t unrooted tree does not.*

Unlike a taxonomic classification diagram, we can read a phylogenetic tree like a map of evolutionary history. Many phylogenetic trees have a single lineage at the base representing a common ancestor. Scientists call such trees **rooted**, which means there is a single ancestral lineage (typically drawn from the bottom or left) to which all organisms represented in the diagram relate. Notice in the rooted phylogenetic tree in **Figure 2** that the three domains— Bacteria, Archaea, and Eukarya—diverge from a single point and branch off. The small branch that plants and animals (including humans) occupy in this diagram shows how recent and miniscule these groups are compared with other organisms. Unrooted trees do not show a common ancestor but do show relationships among species.

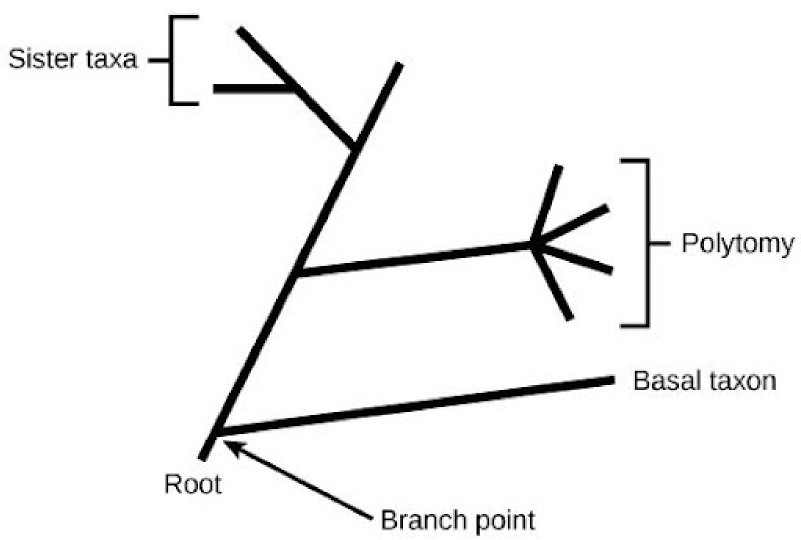

Figure 3. *The root of a phylogenetic tree indicates that an ancestral lineage gave rise to all organisms on the tree. A branch point indicates where two lineages diverged. A lineage that evolved early and remains unbranched is a basal taxon. When two lineages stem from the same branch point, they are sister taxa. A branch with more than two lineages is a*

polytomy.

In a rooted tree, the branching indicates evolutionary relationships (**Figure 3**). The point where a split occurs, called a **node**, represents where a single lineage evolved into a distinct new one. A lineage that evolved early from the root and remains unbranched is called a **basal taxon**. When two lineages stem from the same node, they are called **sister taxa**. A branch with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all of the relationships. It is important to note that although sister taxa and polytomy do share an ancestor, it does not mean that the groups of organisms split or evolved from each other. Organisms in two taxa may have split apart at a specific branch point, but neither taxon gave rise to the other.

The diagrams above can serve as a pathway to understanding evolutionary history. We can trace the pathway from the origin of life to any individual species by navigating through the evolutionary branches between the two points. Also, by starting with a single species and tracing back towards the "trunk" of the tree, one can discover species' ancestors, as well as where lineages share a common ancestry. In addition, we can use the tree to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that rotation at branch points does not change the information. For example, if a branch point rotated and the taxon order changed, this would not alter the information because each taxon's evolution from the branch point was independent of the other.

Many disciplines within the study of biology contribute to understanding how past and present life evolved over time. These disciplines together contribute to building, updating, and maintaining the "tree of life." **Systematics** is the field that scientists use to organize and classify organisms based on evolutionary relationships. Researchers may use data from fossils, from studying the body part structures, or molecules that an organism uses, and DNA analysis. By combining data from many sources, scientists can construct an organism's phylogeny. Since phylogenetic trees are hypotheses, they will continue to change as researchers discover new types of life and learn new information.

Limitations of Phylogenetic Trees

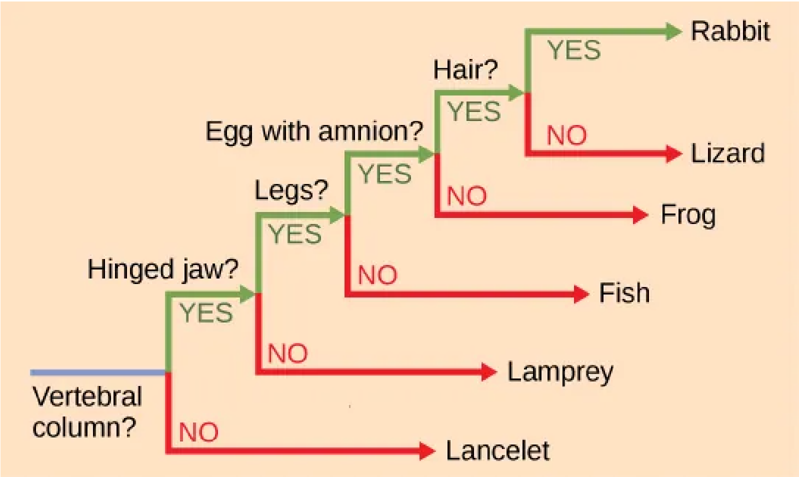

Figure 4. *This ladder-like phylogenetic tree of vertebrates is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups based on the characteristics they*

share.

It may be easy to assume that more closely related organisms look more alike, and while this is often the case, it is not always true. If two closely related lineages evolved under significantly varied surroundings, the two groups can appear more different from other groups that are not as closely related. For example, the phylogenetic tree in **Figure 4** shows that lizards and rabbits both have amniotic eggs, whereas frogs do not. Yet lizards and frogs appear more similar than lizards and rabbits.

Another aspect of phylogenetic trees is that unless otherwise indicated, the branches may not account for length of time, only the evolutionary order. In other words, a branch's length does not mean more time passed, nor does a short branch mean less time passed— unless specified on the diagram. For example, in **Figure 4**, the tree does not indicate how much time passed between the evolution of amniotic eggs and hair. What the tree does show is the order in which things took place. Again using **Figure 4**, the tree shows that the oldest trait is the vertebral column, followed by hinged jaws, and so forth. Remember that any phylogenetic tree is a part of the greater whole, and like a real tree, it does not grow in only one direction after a new branch develops. Thus, for the organisms in **Figure 4**, just because a vertebral column evolved does not mean that invertebrate evolution ceased. It only means that a new branch formed. Also, groups that are not closely related but evolve under similar conditions may appear more phenotypically similar to each other than to a close relative.

Head to this website to see interactive exercises that allow you to explore the evolutionary relationships among species.

Why Does Phylogeny Matter?

There are many reasons why understanding phylogeny is important to everyday life in human society. In addition to enhancing our understanding of the evolutionary history of species, our own included, phylogenetic analysis has numerous practical applications.

For botanists, phylogeny acts as a guide to discovering new plants that can be used to benefit people. Think of all the ways humans use plants—food, medicine, and clothing are a few examples. If a plant contains a compound that is effective in treating cancer, scientists might want to examine all of the compounds for other useful drugs.

A research team in China identified a DNA segment that they thought to be common to some medicinal plants in the family Fabaceae (the legume family) (**Figure 5**). They worked to identify which species had this segment. After testing plant species in this family, the team found a DNA marker (a known location on a chromosome that enabled them to identify the species) present. Then, using the DNA to uncover phylogenetic relationships, the team could identify whether a newly discovered plant was in this family and assess its potential medicinal properties.

Figure 5. *Dalbergia sissoo (D. sissoo) is in the Fabaceae, or legume family. Scientists found that D. sissoo shares a DNA marker with species within the Fabaceae family that have antifungal properties. Subsequently, researchers found that D. sissoo had fungicidal activity, supporting the idea that DNA markers are useful to screen plants with potential medicinal properties.*

Phylogenetics also helps us understand the evolution and transmission of disease. A 2010 study

Harris, S.R. et al. 2010. Evolution of MRSA during hospital transmission and intercontinental spread. Science 327:469–474.

of MRSA (methicillin-resistant *Staphylococcus aureus*), an antibiotic-resistant pathogenic bacterium, traced the origin and spread of the strain throughout the past 40 years. The study uncovered the timing and patterns in which the resistant strain moved from its point of origin in Europe to centers of infection and evolution in South America, Asia, North America, and Australasia. The study suggested that introductions of the bacteria to new populations occurred very few times, perhaps only once, and then spread from that limited number of individuals. This is in contrast to the possibility that many individuals carried the bacteria from one place to another. This result suggests that public health officials should concentrate on quickly identifying the contacts of individuals infected with a new strain of bacteria to control its spread.

Yet another area of usefulness for phylogenetic analysis is in conservation. Biologists have argued that it is important to protect species throughout a phylogenetic tree rather than just those from one branch of the tree. Doing this will preserve more of the variation produced by evolution. For example, conservation efforts should focus on a single species without sister species rather than another species that has a cluster of close sister species that recently evolved. If the single evolutionarily distinct species goes extinct, a disproportionate amount of variation from the tree will be lost compared to one species in the cluster of closely related species. A study published in 2007

Isaac NJ, Turvey ST, Collen B, Waterman C, Baillie JE (2007) Mammals on the EDGE: Conservation Priorities Based on Threat and Phylogeny. PLoS ONE 2(3): e296. doi:10.1371/journal.pone.0000296

made recommendations for the conservation of mammal species worldwide based on how evolutionarily distinct and at risk of extinction they are. The study found that their recommendations differed from priorities based on simply the level of extinction threat to the species. The study recommended protecting some threatened and valued large mammals such as the orangutans, the giant and lesser pandas, and the African and Asian elephants. But they also found that some much lesser-known species should be protected based on how evolutionary distinct they are. These include a number of rodents, bats, shrews and hedgehogs. In addition, there are some critically endangered species that did not rate as very important in evolutionary distinctiveness including species of deer mice and gerbils. While many criteria affect conservation decisions, preserving phylogenetic diversity provides an objective way to protect the full range of diversity generated by evolution.

Reconstructing Evolutionary Relationships

Section Goals

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

- Distinguish between ancestral and derived characters
- Make inferences and predictions based on the patterns depicted in phylogenies

- Explain the principle of parsimony as it relates to phylogenies

How do scientists construct phylogenetic trees? After they sort the homologous and analogous traits, scientists often organize the homologous traits using **cladistics**. This system sorts organisms into clades: groups of organisms that descended from a single ancestor. For example, in **Figure 1**, all the organisms in the orange region evolved from a single ancestor that had amniotic eggs. Consequently, these organisms also have amniotic eggs and make a single clade, or a **monophyletic group**. Clades must include all descendants from a branch point.

The monophyletic group is the "ideal" type of cladogram because it will contain the ancestor and every single descendant species. There are no missing species and no gaps. Every piece of the puzzle is present.

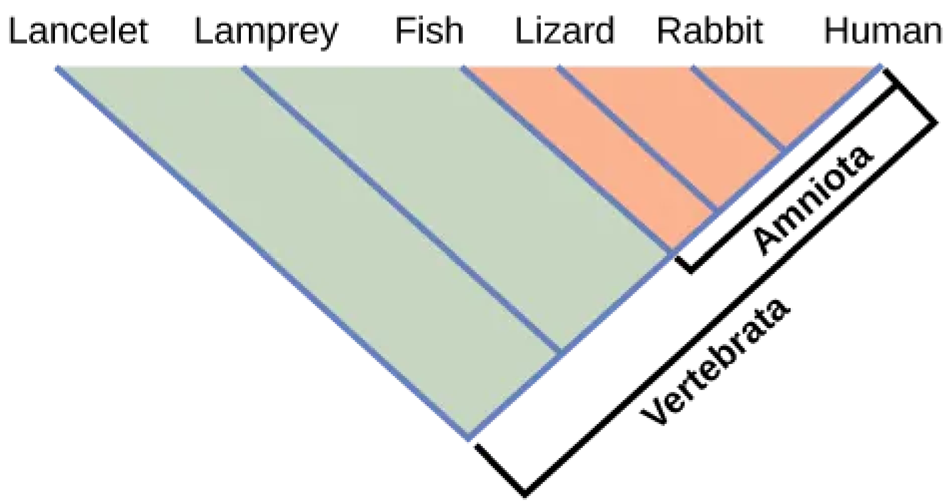

Figure 1. *Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.*

Which animals in this figure belong to a clade that includes animals with hair? Which evolved first, hair or the amniotic egg?

Answer:

The largest clade encompasses the entire tree.

Clades can vary in size depending on which branch point one references. The important factor is that all organisms in the clade or monophyletic group stem from a single point on the tree. You can remember this because monophyletic breaks down into "mono," meaning one, and "phyletic," meaning evolutionary relationship. **Figure 2** shows various clade examples. Notice how each clade comes from a single point; whereas, the non-clade groups show branches that do not share a single point.

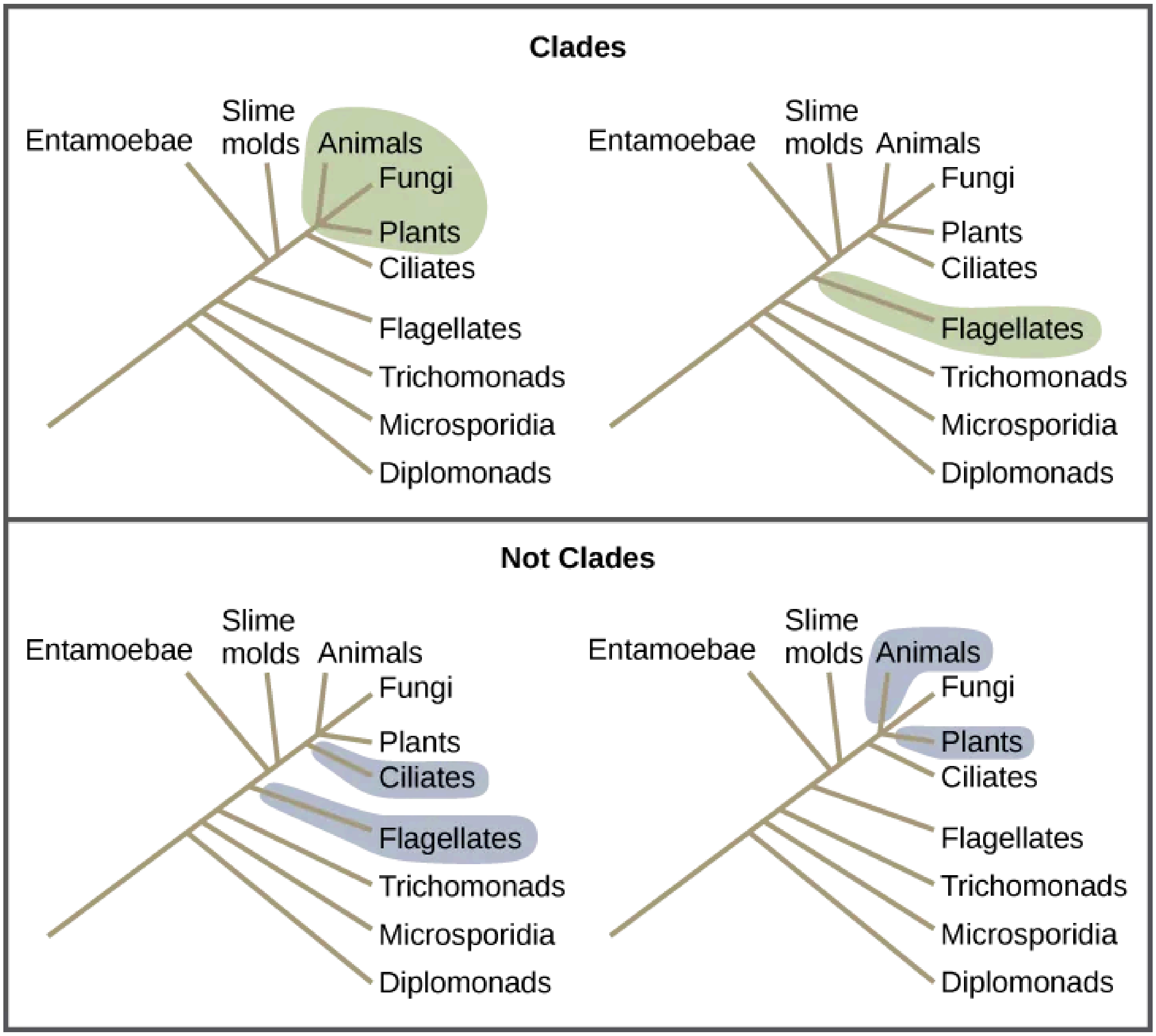

Figure 2. *All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.*

What is the largest clade in this diagram?

Answer:

Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair because the Amniota clade is larger than the clade that encompasses animals with hair.

Shared Characteristics

Organisms evolve from common ancestors and then diversify. Scientists use the phrase "descent with modification" because even though related organisms have many of the same characteristics and genetic codes, changes occur. This pattern repeats as one goes through the phylogenetic tree of life:

1. A change in an organism's genetic makeup leads to a new trait that becomes prevalent in the group.
2. Many organisms descend from this point and have this trait.
3. New variations continue to arise: some are adaptive and persist, leading to new traits.
4. With new traits, a new branch point is determined (go back to step 1 and repeat).

If a characteristic is found in the ancestor of a group, it is considered a **shared ancestral character** because all of the organisms in the taxon or clade have that trait. The vertebra in **Figure 1** is a shared ancestral character. Now consider the amniotic egg characteristic in the same figure. Only some of the organisms in **Figure 1** have this trait, and to those that do, it is called a **shared derived character** because this trait was derived at some point but does not include all of the ancestors in the tree.

The tricky aspect of shared ancestral and shared derived characters is that these terms are relative. We can consider the same trait one or the other depending on the particular diagram that we use. Returning to **Figure 1**, note that the amniotic egg is a shared ancestral character for lizards, rabbits, and humans while having hair is a shared derived character only for humans and rabbits. For the Amniotes as a group, however, the amniotic egg is a shared derived character that is not seen in fish. These terms help scientists distinguish between clades in building phylogenetic trees.

Did I Get It?

An interactive H5P element has been excluded from this version of the text. You can view it online here: https://rotel.pressbooks.pub/understanding-organisms/?p=254#h5p-52

Choosing the Right Relationships

Organizing the evolutionary relationships of all life on Earth is difficult. Scientists must span enormous blocks of time and work with information from long-extinct organisms. Trying to decipher the proper connections, especially given the presence of homologies and analogies, makes the task of building an accurate tree of life extraordinarily difficult. Add to that advancing DNA technology, which now provides large quantities of genetic sequences for researchers to use and analyze. Taxonomy, the branch of science concerned with the classification of organisms, is a subjective discipline in some ways: many organisms have more than one connection to each other, so each taxonomist will decide the order of connections. These relationships can change as more data is gathered and technology changes to highlight previously unknown information.

To aid in the tremendous task of describing phylogenies accurately, scientists often use the concept of **maximum parsimony**, which means that events occurred in the simplest, most obvious way. For example, if a group of people entered a forest preserve to hike, based on the principle of maximum parsimony, one could predict that most would hike on established trails rather than forge new ones.

For scientists deciphering evolutionary pathways, the same idea is used: the pathway of evolution probably includes the fewest major events that coincide with the evidence at hand. Starting with all of the homologous traits in a group of organisms, scientists look for the most obvious and simple order of evolutionary events that led to the occurrence of those traits.

In the following example, notice two evolutionary trees were created, representing Hypothesis 1 and

Hypothesis 2 (**Figure 3**). Notice that Hypothesis 1 shows 6 novel changes indicated by the red bars. Hypothesis 2 shows 7 changes. Based on maximum parsimony, the better hypothesis to describe the relationship between these species would be Hypothesis 1.

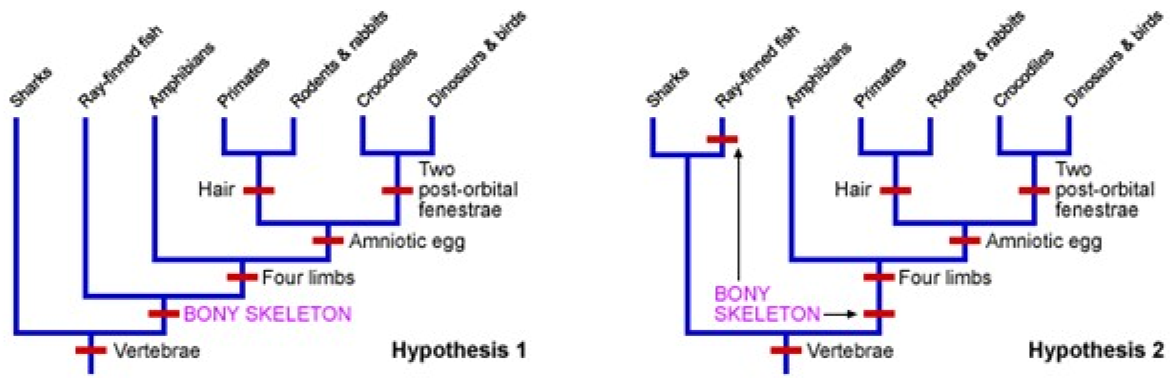

Figure 3. *Two hypotheses are shown visually for the relationship between 7 groups of organisms. Because the evolutionary tree on the left uses fewer changes, we would choose this as the best hypothesis to explain the relationship between these animals.*

Head to the Using parsimony page from *Understanding* Evolution to learn how this principle is used to construct phylogenetic trees.

These tools and concepts are only a few of the strategies scientists use to tackle the task of revealing the evolutionary history of life on Earth. Recently, newer technologies have uncovered surprising discoveries with unexpected relationships, such as the fact that people seem to be more closely related to fungi than fungi are to plants. Sounds unbelievable? As the information about DNA sequences grows, scientists will become closer to mapping the evolutionary history of all life on Earth.

Did I Get It?

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