GENERAL BIOLOGY I AND II



Tara Jo Holmberg
CT State Northwestern

LibreTexts™

Northwestern Connecticut Community College

General Biology I and II

Tara Jo Holmberg

This text is disseminated via the Open Education Resource (OER) LibreTexts Project (https://LibreTexts.org) and like the thousands of other texts available within this powerful platform, it is freely available for reading, printing, and "consuming."

The LibreTexts mission is to bring together students, faculty, and scholars in a collaborative effort to provide an accessible, and comprehensive platform that empowers our community to develop, curate, adapt, and adopt openly licensed resources and technologies; through these efforts we can reduce the financial burden born from traditional educational resource costs, ensuring education is more accessible for students and communities worldwide.

Most, but not all, pages in the library have licenses that may allow individuals to make changes, save, and print this book. Carefully consult the applicable license(s) before pursuing such effects. Instructors can adopt existing LibreTexts texts or Remix them to quickly build course-specific resources to meet the needs of their students. Unlike traditional textbooks, LibreTexts' web based origins allow powerful integration of advanced features and new technologies to support learning.



LibreTexts is the adaptable, user-friendly non-profit open education resource platform that educators trust for creating, customizing, and sharing accessible, interactive textbooks, adaptive homework, and ancillary materials. We collaborate with individuals and organizations to champion open education initiatives, support institutional publishing programs, drive curriculum development projects, and more.

The LibreTexts libraries are Powered by NICE CXone Expert and was supported by the Department of Education Open Textbook Pilot Project, the California Education Learning Lab, the UC Davis Office of the Provost, the UC Davis Library, the California State University Affordable Learning Solutions Program, and Merlot. This material is based upon work supported by the National Science Foundation under Grant No. 1246120, 1525057, and 1413739.

Any opinions, findings, and conclusions or recommendations expressed in this material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation nor the US Department of Education.

Have questions or comments? For information about adoptions or adaptions contact info@LibreTexts.org or visit our main website at https://LibreTexts.org.

This text was compiled on 05/03/2026

TABLE OF CONTENTS

Licensing

1: Unit I- Biology, Science, and the Chemistry of Life

- 1.1: The Study of Life
  - 1.1.1: Themes and Concepts of Biology
  - 1.1.2: The Nature of Science
  - 1.1.3: The Role of Science in Society
  - 1.E: The Study of Life (Exercises)
  - 1.G: Unit 1.1 Glossary
- 1.2: The Chemical Foundation of Life
  - 1.2.1: Prelude to The Chemical Foundation of Life
  - 1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
  - 1.2.3: Water
  - 1.2.4: Carbon
  - 1.2.E: The Chemical Foundation of Life (Exercises)
- 1.3: Biological Macromolecules
  - 1.3.1: Prelude to Biological Macromolecules
  - 1.3.2: Synthesis of Biological Macromolecules
  - 1.3.3: Carbohydrates
  - 1.3.4: Lipids
  - 1.3.5: Proteins
  - 1.3.6: Nucleic Acids
  - 1.3.E: Biological Macromolecules (Exercises)

2: Unit II- The Cell

- 2.1: Cell Structure
  - 2.1.1: Prelude to Cell Structure
  - 2.1.2: Studying Cells
  - 2.1.3: Prokaryotic Cells
  - 2.1.4: Eukaryotic Cells
  - 2.1.5: The Endomembrane System and Proteins
  - 2.1.6: The Cytoskeleton
  - 2.1.7: Connections between Cells and Cellular Activities
  - 2.1.E: Cell Structure (Exercises)
- 2.2: Structure and Function of Plasma Membranes
  - 2.2.1: Prelude to Structure and Function of Plasma Membranes
  - 2.2.2: Components and Structure
  - 2.2.3: Passive Transport
  - 2.2.4: Active Transport
  - 2.2.5: Bulk Transport
  - 2.2.E: Structure and Function of Plasma Membranes (Exercises)
- 2.3: Metabolism
  - 2.3.1: Prelude to Metabolism

- 2.3.2: Energy and Metabolism
- 2.3.3: Potential, Kinetic, Free, and Activation Energy
- 2.3.4: The Laws of Thermodynamics
- 2.3.5: ATP- Adenosine Triphosphate
- 2.3.6: Enzymes
- 2.3.E: Metabolism (Exercises)

- 2.4: Cellular Respiration
  - 2.4.1: Prelude to Cellular Respiration
  - 2.4.2: Energy in Living Systems
  - 2.4.3: Glycolysis
  - 2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
  - 2.4.5: Oxidative Phosphorylation
  - 2.4.6: Metabolism without Oxygen
  - 2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
  - 2.4.E: Cellular Respiration (Exercises)
- 2.5: Photosynthesis
  - 2.5.1: Prelude to Photosynthesis
  - 2.5.2: Overview of Photosynthesis
  - 2.5.3: The Light-Dependent Reactions of Photosynthesis
  - 2.5.4: Using Light Energy to Make Organic Molecules
  - 2.5.E: Photosynthesis (Exercises)
- 2.6: Cell Communication
  - 2.6.1: Prelude to Cell Communication
  - 2.6.2: Signaling Molecules and Cellular Receptors
  - 2.6.3: Propagation of the Signal
  - 2.6.4: Response to the Signal
  - 2.6.5: Signaling in Single-Celled Organisms
  - 2.6.E: Cell Communication (Exercises)
- 2.7: Cell Reproduction
  - 2.7.1: Preface
  - 2.7.2: Cell Division
  - 2.7.3: The Cell Cycle
  - 2.7.4: Control of the Cell Cycle
  - 2.7.5: Cancer and the Cell Cycle
  - 2.7.6: Prokaryotic Cell Division
  - 2.7.E: Cell Reproduction (Exercises)

3: Unit III- Genetics

- 3.1: Meiosis and Sexual Reproduction
  - 3.1.1: Prelude to Meiosis and Sexual Reproduction
  - 3.1.2: The Process of Meiosis
  - 3.1.3: Sexual Reproduction
  - 3.1.E: Meiosis and Sexual Reproduction (Exercises)
- 3.2: Mendel's Experiments and Heredity
  - 3.2.1: Prelude to Mendel's Experiments and Heredity
  - 3.2.2: Mendel’s Experiments and the Laws of Probability
  - 3.2.3: Characteristics and Traits

- 3.2.4: Laws of Inheritance
- 3.2.E: Mendel's Experiments and Heredity (Exercises)
- 3.3: Modern Understandings of Inheritance
  - 3.3.1: Prelude to Modern Understandings of Inheritance
  - 3.3.2: Chromosomal Theory and Genetic Linkage
  - 3.3.3: Chromosomal Basis of Inherited Disorders
  - 3.3.E: Modern Understandings of Inheritance (Exercises)
- 3.4: DNA Structure and Function
  - 3.4.1: Prelude to DNA Structure and Function
  - 3.4.2: Historical Basis of Modern Understanding
  - 3.4.3: DNA Structure and Sequencing
  - 3.4.4: Basics of DNA Replication
  - 3.4.5: DNA Replication in Prokaryotes
  - 3.4.6: DNA Replication in Eukaryotes
  - 3.4.7: DNA Repair
  - 3.4.E: DNA Structure and Function (Exercises)
- 3.5: Genes Expression
  - 3.5.1: Prelude to Genes and Proteins
  - 3.5.2: The Genetic Code
  - 3.5.3: Prokaryotic Transcription
  - 3.5.4: Eukaryotic Transcription
  - 3.5.5: RNA Processing in Eukaryotes
  - 3.5.6: Ribosomes and Protein Synthesis
  - 3.5.E: Genes and Proteins (Exercises)
- 3.6: Gene Regulation
  - 3.6.1: Prelude to Gene Expression
  - 3.6.2: Regulation of Gene Expression
  - 3.6.3: Prokaryotic Gene Regulation
  - 3.6.4: Eukaryotic Epigenetic Gene Regulation
  - 3.6.5: Eukaryotic Transcription Gene Regulation
  - 3.6.6: Eukaryotic Post-transcriptional Gene Regulation
  - 3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
  - 3.6.8: Cancer and Gene Regulation
  - 3.6.E: Gene Expression (Exercises)
- 3.7: Biotechnology and Genomics
  - 3.7.1: Prelude
  - 3.7.2: Biotechnology
  - 3.7.3: Mapping Genomes
  - 3.7.4: Whole-Genome Sequencing
  - 3.7.5: Applying Genomics
  - 3.7.6: Genomics and Proteomics
  - 3.7.E: Biotechnology and Genomics (Exercises)

4: Unit IV- Evolutionary Processes

- 4.1: Evolution - History, Evidence, and Mechanisms
  - 4.1.1: Understanding Evolution
  - 4.1.2: Evidence of Evolution

- 4.1.3: Natural Selection and Adaptive Evolution
- 4.1.4: Additional Mechanisms of Evolution
- 4.2: The Origin of Species
  - 4.2.1: Species Defined
  - 4.2.2: Speciation
  - 4.2.3: Rates of Speciation and Extinction
- 4.3: Genes Within Populations
  - 4.3.1: Evolution of Genomes
  - 4.3.2: Evolution in Populations
- 4.4: Systematics, Phylogeny and Comparative Biology
  - 4.4.1: Systematics and Classification
  - 4.4.2: Phylogeny and Cladistics

5: Unit V- Biological Diversity

- 5.1: The Origin and Diversity of Life
  - 5.1.1: Deep Time
  - 5.1.2: Origins of Life
  - 5.1.3: Evidence for Early Life
  - 5.1.4: Eukaryotic Origins
- 5.2: Acellular Entities - Viruses, Prions, and Viroids
- 5.3: Prokaryotes - Bacteria and Archaea
  - 5.3.E: Prokaryotes - Bacteria and Archaea (Exercises)
- 5.4: Protists
  - 5.4.E: Protists (Exercises)
- 5.5: Fungi
  - 5.5.E: Fungi (Exercises)
- 5.6: Introduction to Animal Diversity
  - 5.6.1: Introduction
  - 5.6.2: The Evolutionary History of the Animal Kingdom
  - 5.6.3: Features of the Animal Kingdom
  - 5.6.4: Features Used to Classify Animals
  - 5.6.5: Animal Phylogeny
  - 5.6.E: Introduction to Animal Diversity (Exercises)
- 5.7: Invertebrates
  - 5.7.1: Prelude to Invertebrates
  - 5.7.2: Phylum Porifera
  - 5.7.3: Phylum Cnidaria
  - 5.7.4: Superphylum Lophotrochozoa
  - 5.7.5: Superphylum Ecdysozoa
  - 5.7.6: Superphylum Deuterostomia
  - 5.7.E: Invertebrates (Exercises)
- 5.8: Vertebrates
  - 5.8.1: Prelude to Vertebrates
  - 5.8.2: Chordates
  - 5.8.3: Fishes
  - 5.8.4: Amphibians

- 5.8.5: Reptiles
- 5.8.6: Birds
- 5.8.7: Mammals
- 5.8.8: The Evolution of Primates
- 5.8.E: Vertebrates (Exercises)

- 5.9: Plantae
  - 5.9.1: Kingdom Plantae - Evolution and Phylogeny
  - 5.9.2: Kingdom Plantae - Adaptations
  - 5.9.E1: Seedless Plants (Exercises)
  - 5.9.E2: Seed Plants (Exercises)
- 5.2.E: Viruses (Exercises)

6: Unit VI- Ecology

- 6.1: Ecosystems and the Biosphere
  - 6.1.1: Ecology of Ecosystems
  - 6.1.2: Energy Flow through Ecosystems
  - 6.1.3: Terrestrial Biomes
  - 6.1.4: Aquatic Biomes
  - 6.1.5: Biogeochemical Cycles
  - 6.1.6: Biogeography
  - 6.1.S: Chapter Resources
- 6.2: Biodiversity and HIPPPOC
  - 6.2.1: Introduction to Biodiversity
  - 6.2.2: Importance of Biodiversity
  - 6.2.3: The Biodiversity Crisis - HIPPPOC
  - 6.2.4: Preserving Biodiversity
  - 6.2.S: Chapter Resources
- 6.3: Climate Change
  - 6.3.1: Introduction to Climate Change
  - 6.3.2: Anthropogenic Climate Change
  - 6.3.3: Current and Future Climate Change Impacts
  - 6.3.4: Climate Strategies

Index

Glossary

Detailed Licensing

Licensing

*A detailed breakdown of this resource's licensing can be found in **Back Matter/Detailed Licensing**.*

SECTION OVERVIEW

1: Unit I- Biology, Science, and the Chemistry of Life

Our opening unit introduces students to the sciences, including the scientific method and the fundamental concepts of chemistry and physics that provide a framework within which learners comprehend biological processes.

1.1: The Study of Life

- 1.1.1: Themes and Concepts of Biology
- 1.1.2: The Nature of Science
- 1.1.3: The Role of Science in Society
- 1.E: The Study of Life (Exercises)
- 1.G: Unit 1.1 Glossary

1.2: The Chemical Foundation of Life

- 1.2.1: Prelude to The Chemical Foundation of Life
- 1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
- 1.2.3: Water
- 1.2.4: Carbon
- 1.2.E: The Chemical Foundation of Life (Exercises)

1.3: Biological Macromolecules

- 1.3.1: Prelude to Biological Macromolecules
- 1.3.2: Synthesis of Biological Macromolecules
- 1.3.3: Carbohydrates
- 1.3.4: Lipids
- 1.3.5: Proteins
- 1.3.6: Nucleic Acids
- 1.3.E: Biological Macromolecules (Exercises)

Contributors

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 1: Unit I- Biology, Science, and the Chemistry of Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

1.1: The Study of Life

1.1.1: Themes and Concepts of Biology
1.1.2: The Nature of Science
1.1.3: The Role of Science in Society
1.E: The Study of Life (Exercises)
1.G: Unit 1.1 Glossary

This page titled 1.1: The Study of Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

Themes and Concepts of Biology

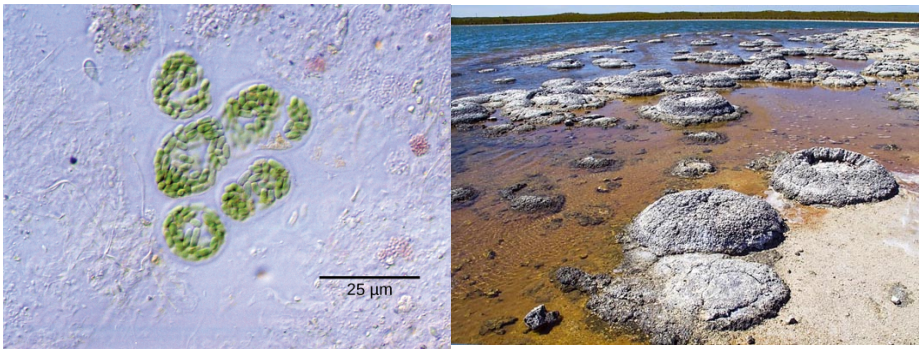
- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities and Resources are embedded.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to Unit 1.1.2, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify and describe the properties of life
- Describe the levels of organization among living things
- Identify the shared characteristics of the natural sciences
- Identify examples of different subdisciplines in biology

What is Biology?

In simple terms, biology is the study of living organisms and their interactions with one another and their environments. This is a very broad definition 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 1.1.1.1).



(a) (b)

Figure 1.1.1.1: Formerly called blue-green algae, these (a) cyanobacteria, shown here at 300x magnification 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 the layering of 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 are discussed every day. For example, recent news topics include *Escherichia coli* (Figure 1.1.1.2) 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.

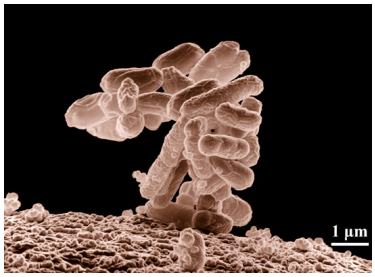


Figure 1.1.1.2: Escherichia coli (*E. coli*) bacteria, seen in this scanning electron micrograph, are normal residents of our digestive tracts that aid in the absorption of vitamin K and other nutrients. However, virulent strains are sometimes responsible for disease outbreaks. (credit: Eric Erbe, digital colorization by Christopher Pooley, both of USDA, ARS, EMU)

Optional Resource

Find an example of up-to-date news on biology at Science Daily here: https://www.sciencedaily.com/news/plants_animals/biology/

Biology is the science that studies life, but what exactly is life? This 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 three questions:

1. What are the shared properties that make something “alive”?
2. And once we know something is alive, how do we find meaningful levels of organization in its structure?
3. And, finally, 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.

Video





Watch this 1.5-minute video as multiple scientists and professors describe what biology means to them. Question after watching: What does biology mean to you?

Properties of Life

All living organisms share several key characteristics or functions: order, sensitivity or response to the environment, reproduction, adaptation, growth and development, regulation, homeostasis, energy processing, and evolution. When viewed together, these are nine characteristics that can serve to define life. However, different scientists have used varying definitions to classify matter as living (**biotic**) or non-living (**abiotic**). Some use seven or fewer of these characteristics, some use all nine. One of the most concise definitions of life is from the National Aeronautics and Space Administration "*Life is a self-sustaining chemical system capable of Darwinian evolution*" (NASA, 2022).

Order

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 1.1.1.1), similar cells form tissues. Tissues, in turn, collaborate to create organs (body structures with a distinct function). Organs work together to form organ systems.



Figure 1.1.1.1: A toad represents a highly organized structure consisting of cells, tissues, organs, and organ systems. (credit: “Ivengo”/Wikimedia Commons)

Sensitivity or Response to Stimuli

Organisms respond to diverse stimuli. For example, plants can bend toward a source of light (**phototaxis**), climb on fences and walls, or respond to touch (Figure 1.1.1.2). Even tiny bacteria can move toward or away from chemicals (**chemotaxis**) or light.



Figure 1.1.1.2: 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)

Video



Watch this 1-minute video to see how plants respond to a stimulus (sunlight) and what that means for their success. Question after watching: What are other types of stimuli that the plant encounters?

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, such as eggs and sperm, that will form new individuals. When reproduction occurs, genes containing DNA are 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.

Growth and Development

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 will grow up to exhibit many of the same characteristics as its parents (Figure 1.1.1.3).



Figure 1.1.1.3: Although no two look alike, these kittens have inherited genes from both parents and share many of the same characteristics. (credit: Rocky Mountain Feline Rescue)

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

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 1.1.1.4), 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.



Figure 1.1.1.4: 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. (credit: “longhorndave”/Flickr)

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; others use chemical energy in molecules they take in as food (Figure 1.1.1.5).

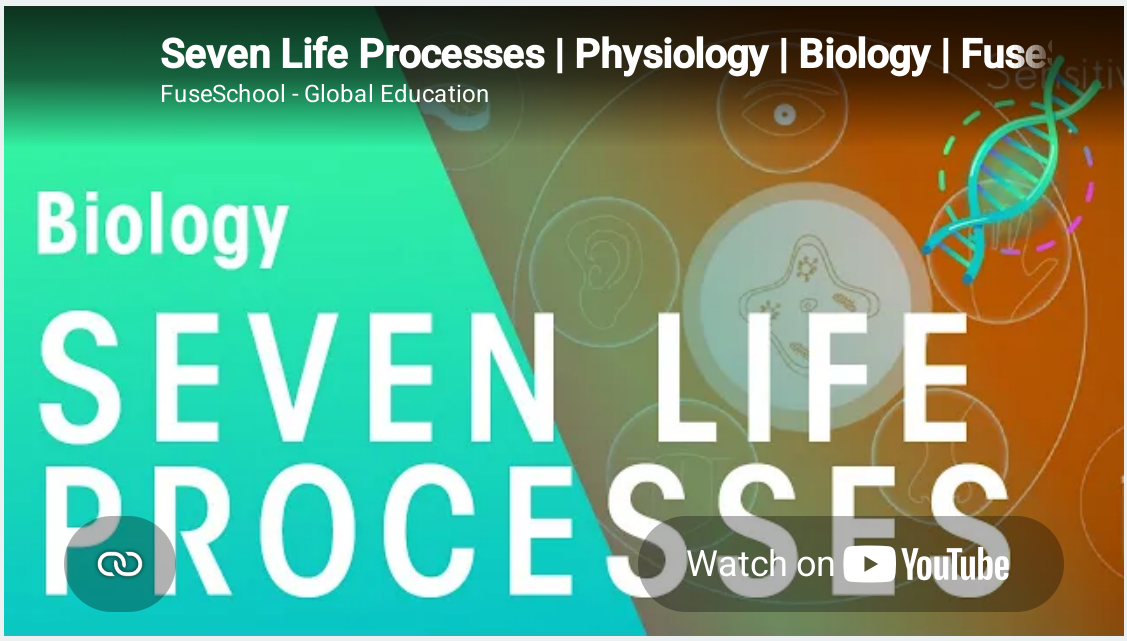


Figure 1.1.1.5: The California condor (*Gymnogyps californianus*) uses chemical energy derived from food to power flight. California condors are an endangered species; this bird has a wing tag that helps biologists identify the individual. (credit: Pacific Southwest Region U.S. Fish and Wildlife Service)

Evolution

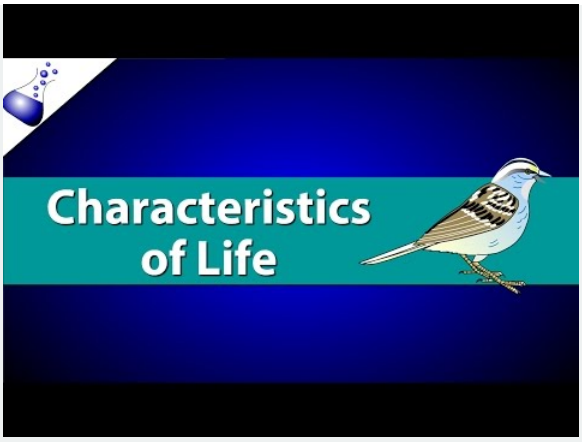
All organisms evolve. We will investigate the theory of evolution and its mechanisms thoroughly in Unit 2.

Videos


Seven Life Processes | Physiology | Biology | Fuse
FuseSchool - Global Education
Biology
SEVEN LIFE
PROCESSES
Watch on YouTube


Biology
SEVEN LIFE
PROCESSES


Characteristics of Life
RicochetScience
Characteristics
of Life
Watch on YouTube



Use these two videos to help you synthesize the ideas from above about the processes of life.
Question after watching: Which features help scientists separate the biotic from the abiotic?

Levels of Organization of Living Things

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 molecules that are biologically important 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 1.1.1.6), which contains the instructions for the structure and functioning of all living organisms.

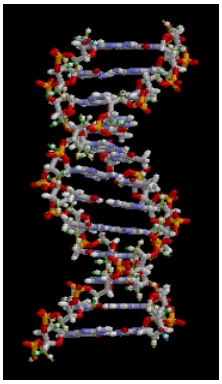


Figure 1.1.1.6: All molecules, including this DNA molecule, are composed of atoms. (credit: “brian0918”/Wikimedia Commons)

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; 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 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. The forest itself is an **ecosystem**. 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, the **biosphere** is the collection of all ecosystems, and it represents the zones of life on earth (Figure 1.1.1.7). It includes land, water, and even the atmosphere to a certain extent.

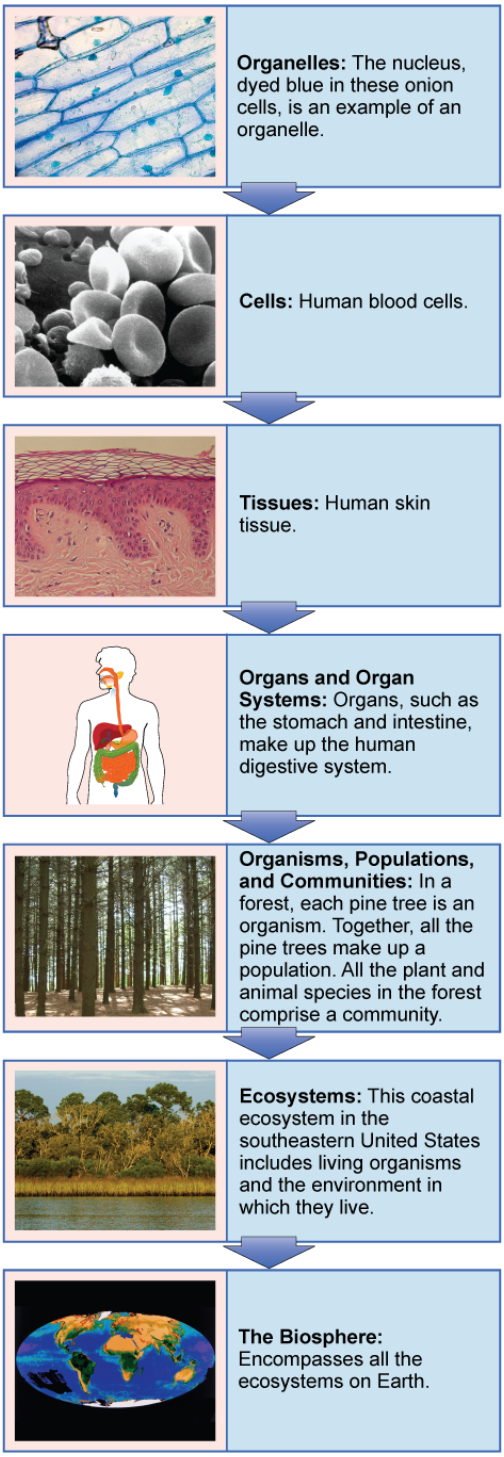
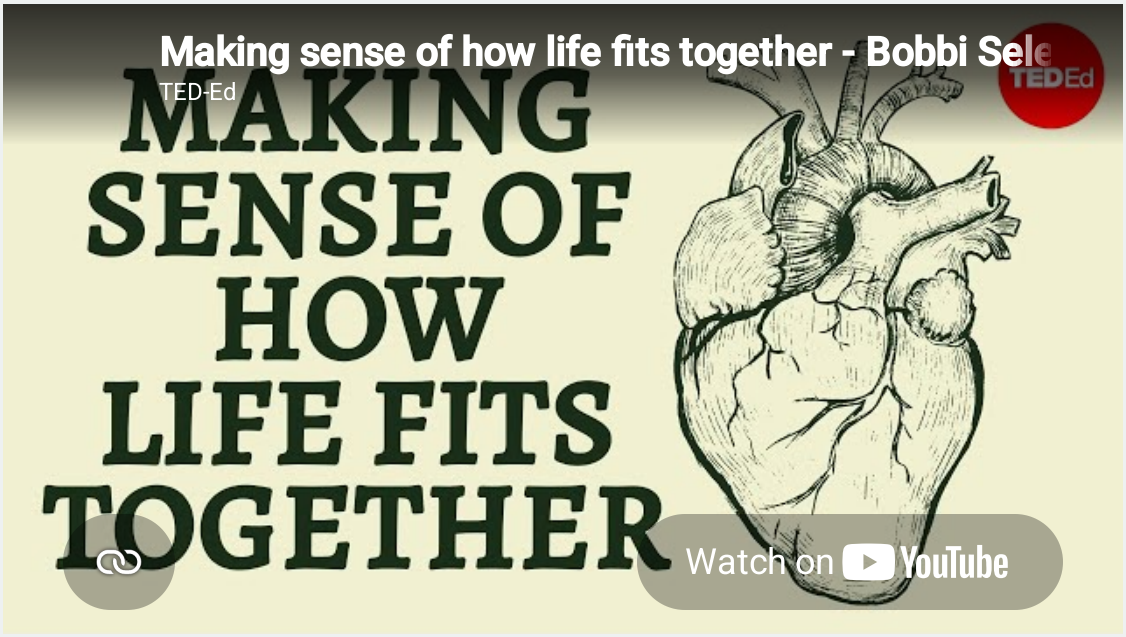
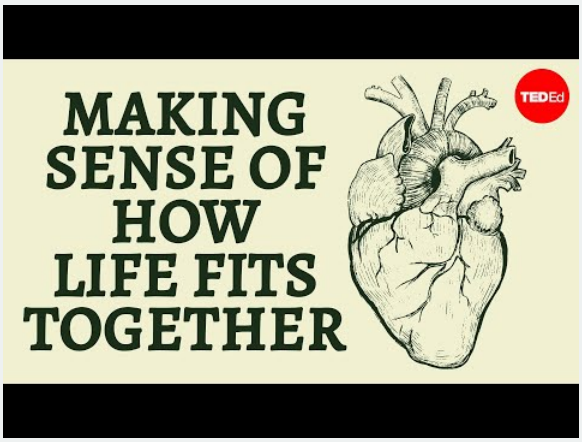


Figure 1.1.1.7: The biological levels of organization of living things are shown. From a single organelle to the entire biosphere, living organisms are parts of a highly structured hierarchy. (credit “organelles”: modification of work by Umberto Salvagnin; credit “cells”: modification of work by Bruce 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”: modification of work by "Crystal"/Flickr; credit “ecosystems”: modification of work by US Fish and Wildlife Service Headquarters; credit “biosphere”: modification of work by NASA)

Video





Discover the many different levels of organization of life in this 5-minute video.
Question after watching: Many scientists specialize in a level of organization. If you were to study only one section of biological organization, which would you choose and why

Optional Activity 1.1.1.1

Which of the following statements is false? Refer to the text above for the correct answer.

A. Tissues exist within organs which exist within organ systems.
B. Communities exist within populations which exist within ecosystems.
C. Organelles exist within cells which exist within tissues.
D. Communities exist within ecosystems which exist in the biosphere.

Answer

B. Communities exist within populations which exist within ecosystems. This is an incorrect answer as populations ar least inclusive, then communities, then ecosystems.

The Diversity of Life

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 during which new species arise from older species. Evolutionary biologists study the evolution of living things in everything from the microscopic world to ecosystems.

The evolution of various life forms on Earth can be summarized in a phylogenetic tree (Figure 1.1.1.8). A phylogenetic tree is a diagram showing the evolutionary relationships among biological species based on similarities and differences in genetic or physical traits or both. A phylogenetic tree is composed of nodes and branches. The internal nodes represent ancestors and are points in evolution when, based on scientific evidence, an ancestor is thought to have diverged to form two new species. The length of each branch is proportional to the time elapsed since the split.

We will investigate the diversity of life further in Unit 3.

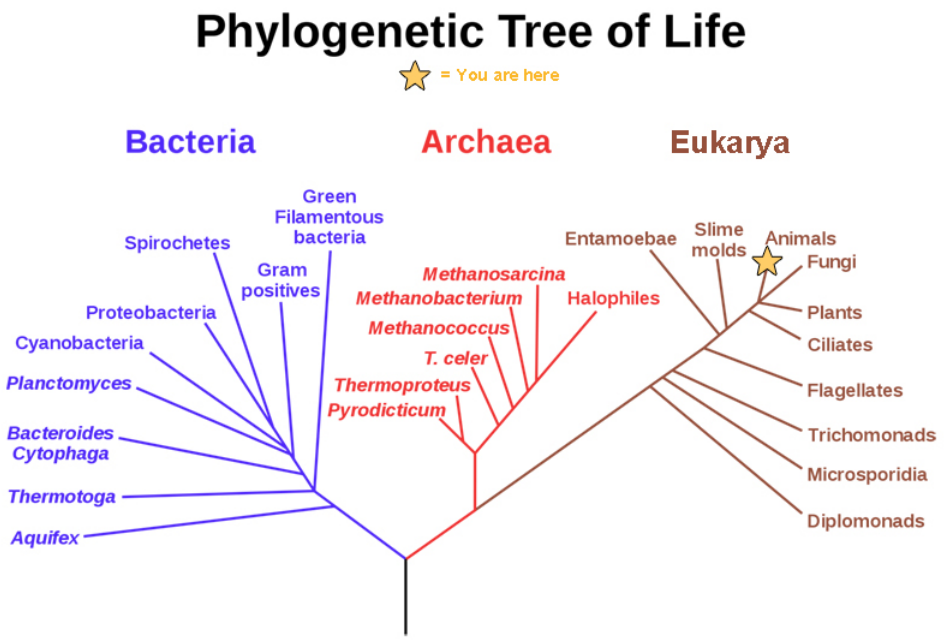


Figure 1.1.1.8: This phylogenetic tree was constructed by microbiologist Carl Woese using data obtained from sequencing ribosomal RNA genes. The tree shows the separation of living organisms into three domains: Bacteria, Archaea, and Eukarya. Bacteria and Archaea are prokaryotes, single-celled organisms lacking intracellular organelles. (credit: Eric Gaba; NASA Astrobiology Institute)

Evolution Connection: Carl Woese and the Phylogenetic Tree

In the past, biologists grouped living organisms into five kingdoms: animals, plants, fungi, protists, and bacteria. The organizational scheme was based mainly on physical features, as opposed to physiology, biochemistry, or molecular biology, all of which are used by modern systematics. The pioneering work of American microbiologist Carl Woese in the early 1970s has shown, however, that life on Earth has evolved along three lineages, now called domains—Bacteria, Archaea, and Eukarya. The first two are prokaryotic cells with microbes that lack membrane-enclosed nuclei and organelles. The third domain contains the eukaryotes and includes unicellular microorganisms together with the four original kingdoms (excluding bacteria). Woese defined Archaea as a new domain, and this resulted in a new taxonomic tree (Figure 1.1.1.8). Many organisms belonging to the Archaea domain live under extreme conditions and are called extremophiles. To construct his tree, Woese used genetic relationships rather than similarities based on morphology (shape).

Woese's tree was constructed from comparative sequencing of the genes that are universally distributed, present in every organism, and conserved (meaning that these genes have remained essentially unchanged throughout evolution). Woese's approach was revolutionary because comparisons of physical features are insufficient to differentiate between the prokaryotes that appear fairly similar in spite of their tremendous biochemical diversity and genetic variability (Figure 1.1.1.9). The

comparison of homologous DNA and RNA sequences provided Woese with a sensitive device that revealed the extensive variability of prokaryotes, and which justified the separation of the prokaryotes into two domains: bacteria and archaea.

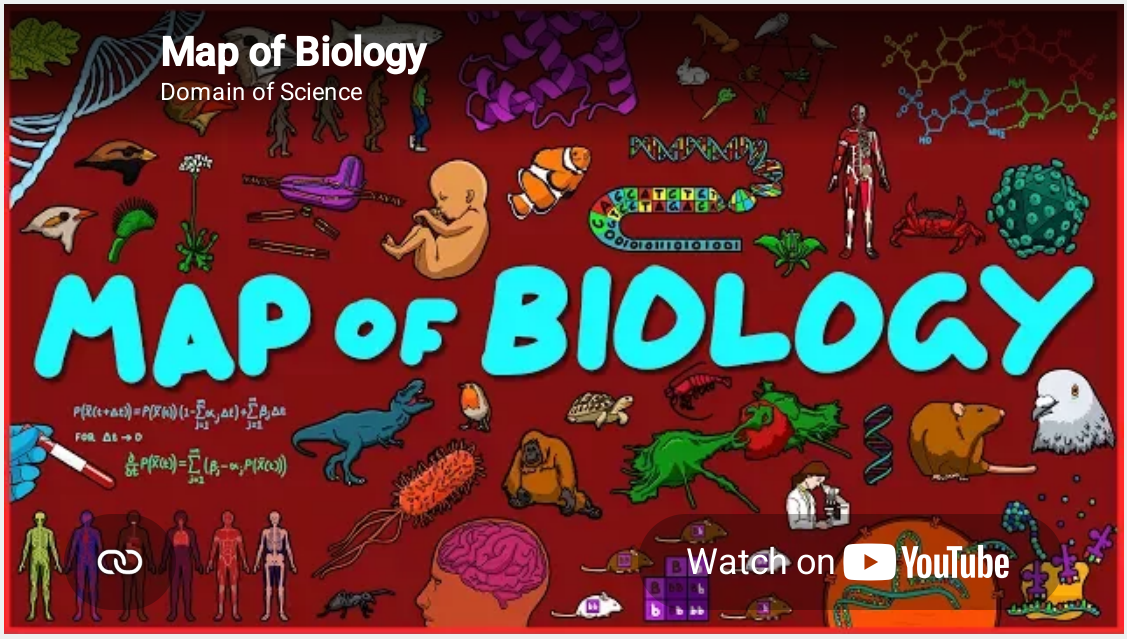


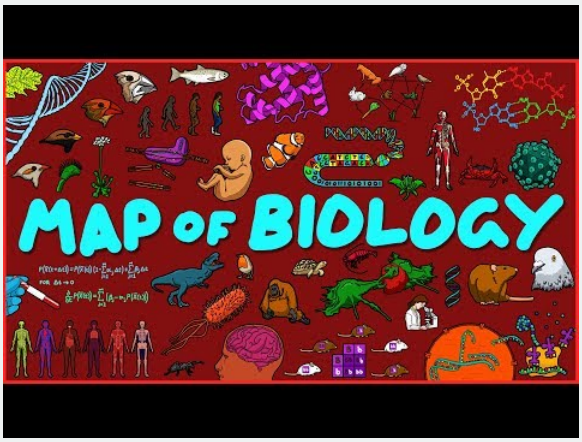
Figure 1.1.1.9: These images represent different domains. The (a) bacteria in this micrograph belong to Domain Bacteria, while the (b) extremophiles (not visible) living in this hot vent belong to Domain Archaea. Both the (c) sunflower and (d) lion are part of Domain Eukarya. (credit a: modification of work by Drew March; credit b: modification of work by Steve Jurvetson; credit c: modification of work by Michael Arrighi; credit d: modification of work by Leszek Leszcynski)

Branches of Biological Study

The scope of biology is broad and therefore contains many branches and subdisciplines. Biologists may pursue one of those subdisciplines and work in a more focused field. For instance, molecular biology and biochemistry study biological processes at the molecular and chemical level, including interactions among molecules such as DNA, RNA, and proteins, as well as the way they are regulated. Microbiology, the study of microorganisms, is the study of the structure and function of single-celled organisms. It is quite a broad branch on its own, and depending on the subject of study, there are also microbial physiologists, ecologists, and geneticists, among others.

Video





This 9-minute video describes many of the fields of biology.
Question after watching: Which of the fields are new to you?

This page titled 1.1.1: Themes and Concepts of Biology is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **1.2: Themes and Concepts of Biology** is licensed CC BY 4.0.
- **1.1: The Science of Biology** by OpenStax is licensed CC BY 4.0.

The Nature of Science

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2.5 hours.
- Optional Activities and Resources are embedded.
- To navigate to to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Use strategies of scientific inquiry to evaluate information, problems, and the validity of science;
- Model the scientific method;
- Compare inductive reasoning with deductive reasoning;
- Compare and contrast observational and descriptive studies;

The Process of Science

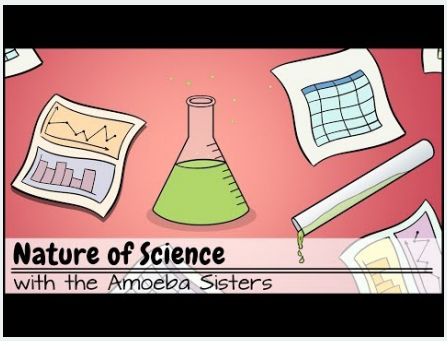
Biology is a science, but what exactly is science? What does the study of biology share with other scientific disciplines? **Science** (from the Latin *scientia*, meaning "knowledge") can be defined as a process that uses evidence, logic, and creativity to discover and explain natural and physical phenomenon while avoiding bias. The **scientific method** is a method of research with defined steps that include experiments and careful observation.

The steps of the scientific method will be examined in detail later, but one of the most important aspects of this method is the testing of hypotheses by means of repeatable experiments. A **hypothesis** is a suggested explanation for an event, which can be tested. Although using the scientific method is inherent to science, it is inadequate in determining what science is. It is relatively easy to apply the scientific method to disciplines such as physics and chemistry, but for disciplines like paleontology and geology, the scientific method is adapted to the field of study.

These areas of study are still sciences, however. Consider paleontology—even though one cannot perform repeatable experiments, hypotheses may still be supported. For instance, a paleontologist can hypothesize that an ancient organism existed based on finding a fossil. Further hypotheses could be made about various characteristics of this fossil, and these hypotheses may be found to be correct or false through continued support or contradictions from other findings. A hypothesis may become a theory with time and evidence. A **theory** is a well-tested and confirmed explanation for observations or phenomena. Science may be better defined as fields of study that attempt to comprehend the physical and natural underpinnings of the universe.

Video





This 10-minute video provides an overview of the process of science.
Question after watching: "What additional characteristics/steps has this video proposed is important in the scientific process that was not mentioned in the text above?"

Natural Sciences

What would you expect to see in a museum of natural sciences? Frogs? Plants? Dinosaur skeletons? Exhibits about how the brain functions? A planetarium? Gems and minerals? Or, maybe all of the above? Science includes such diverse fields as astronomy, biology, computer sciences, geology, logic, physics, chemistry, and mathematics (Figure 1.1.2.1). However, those fields of science related to the physical world and its phenomena and processes are considered **natural sciences**. Thus, a museum of natural sciences might contain any of the items listed above.

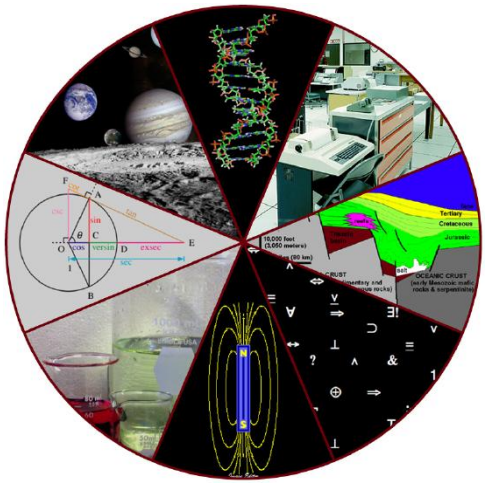
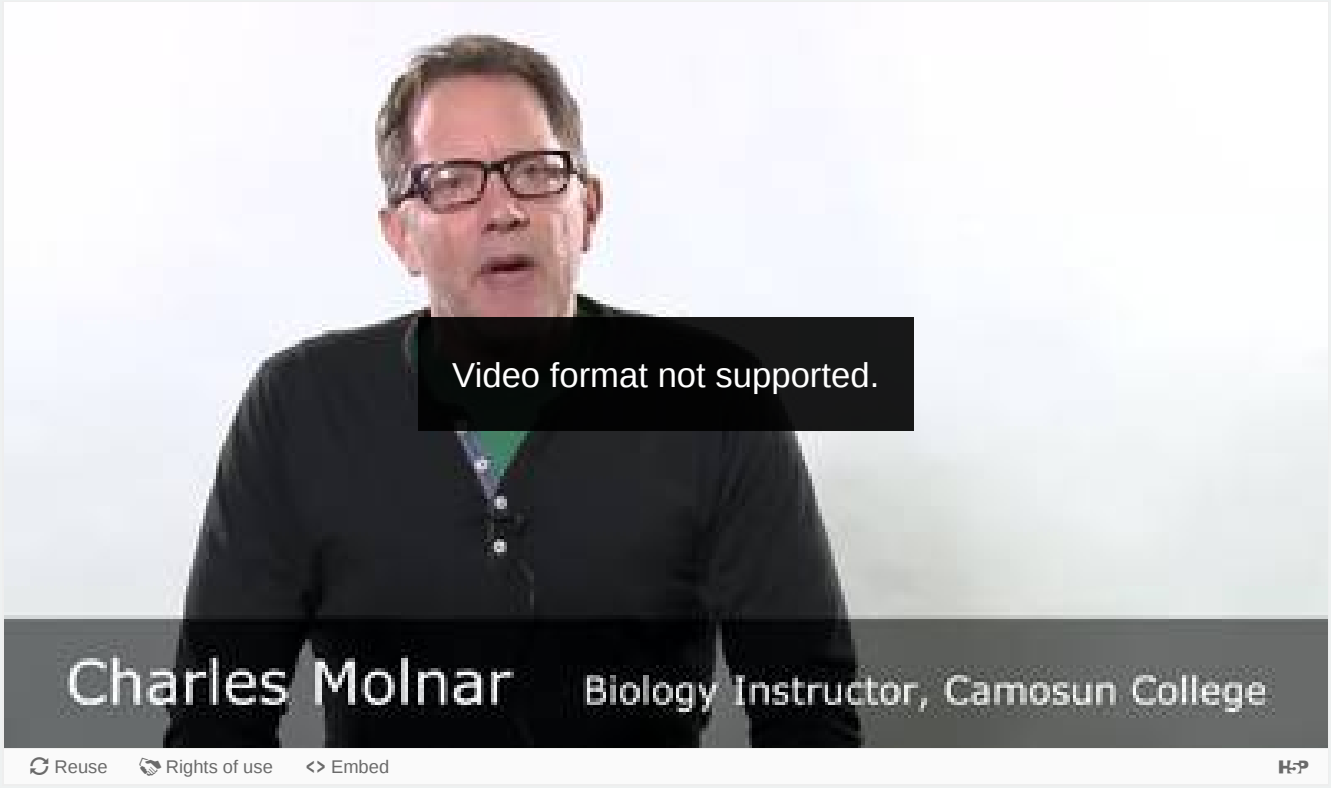


Figure 1.1.2.1: The diversity of scientific fields includes astronomy, biology, computer science, geology, logic, physics, chemistry, mathematics, and many other fields. (credit: “Image Editor”/Flickr)

There is no complete agreement when it comes to defining what the natural sciences include, however. For some experts, the natural sciences are astronomy, biology, chemistry, earth science, and physics. Other scholars choose to divide natural sciences into **life sciences**, which study living things and include biology, and **physical sciences**, which study nonliving matter and include astronomy, geology, physics, and chemistry. Some disciplines such as biophysics and biochemistry build on both life and physical sciences and are **interdisciplinary**. Natural sciences often rely on the use of **quantitative**, or numeric, data although some may use **qualitative**, or non-numeric, data to support findings.

Not surprisingly, the natural science of biology has many branches or **subdisciplines**. Cell biologists study cell structure and function, while biologists who study anatomy investigate the structure of an entire organism. Those biologists studying physiology, however, focus on the internal functioning of an organism. Some areas of biology focus on only particular types of living things. For example, botanists explore plants, while zoologists specialize in animals.

Video



This 5-minute video provides the purpose of the scientific method.
Question after watching: "Charles Molnar describes many ways in which human biases can influence how we observe or interpret the world around us. What steps do scientists put in place to try to remove these human biases from the process of learning about the world so that the final findings are as objective as possible?"

History of Biological Science

Although modern biology is a relatively recent development, sciences related to and included within it have been studied since ancient times. Natural philosophy was studied as early as the ancient civilizations of Mesopotamia, Egypt, the Indian subcontinent, and China. However, the origins of modern biology and its approach to the study of nature are most often traced back to ancient Greece. (Biology is derived from the Greek word "bio" meaning "life" and the suffix "ology" meaning "study of.")

The scientific method was used in ancient times, but it was first documented by England's Sir Francis Bacon (1561–1626), who set up the first methodology for scientific inquiry. The scientific method is not exclusively used by biologists but can be applied to almost all fields of study as a logical, rational problem-solving method. Natural history observations and advances in microscopy have also had a profound impact on biological thinking. In the early 19th century, a number of biologists pointed to the central importance of the cell and in 1838, Schleiden and Schwann began promoting the now universal ideas of the cell theory. Jean-Baptiste Lamarck was the first to present a coherent theory of evolution, although it was the British naturalist Charles Darwin who spread the theory of natural selection throughout the scientific community. In 1953, the discovery of the double-helical structure of DNA marked the transition to the era of molecular genetics.

Video

https://bio.libretexts.org/@go/page/94548



Learn about Karl Popper and falsifiable hypotheses in this 11-minute video.
Question after watching: How does the idea of falsification change how you may have learned about science in the past?

Scientific Reasoning

One thing is common to all forms of science: an ultimate goal "to know." Curiosity and inquiry are the driving forces for the development of science. Scientists seek to understand the world and the way it operates. To do this, they use two methods of logical thinking: inductive reasoning and deductive reasoning (Figure 1.1.2.2).

Inductive reasoning is a form of logical thinking that uses related observations to arrive at a general conclusion. This type of reasoning is common in descriptive science. A life scientist such as a biologist makes observations and records them. These data can be qualitative or quantitative, and the raw data can be supplemented with drawings, pictures, photos, or videos. From many observations, the scientist can infer conclusions (inductions) based on evidence. Inductive reasoning involves formulating generalizations inferred from careful observation and the analysis of a large amount of data. Brain studies provide an example. In this type of research, many live brains are observed while people are doing a specific activity, such as viewing images of food. The part of the brain that "lights up" during this activity is then predicted to be the part controlling the response to the selected stimulus, in this case, images of food. Then, researchers can stimulate that part of the brain to see if similar responses result.

Deductive reasoning or deduction is the type of logic used in hypothesis-based science. In deductive reason, the pattern of thinking moves in the opposite direction as compared to inductive reasoning. Deductive reasoning is a form of logical thinking that uses a general principle or law to forecast specific results. From those general principles, a scientist can extrapolate and predict the specific results that would be valid as long as the general principles are valid. Studies in climate change can illustrate this type of reasoning. For example, scientists may predict that if the climate becomes warmer in a particular region, then the distribution of plants and animals should change. These predictions have been made and tested, and many such changes have been found, such as the modification of arable areas for agriculture, with change based on temperature averages.

Two Types of Reasoning

Inductive reasoning: from a number of observations, a general conclusion is drawn.	**Deductive reasoning:** from a general premise, specific results are predicted.
Observations • Members of a species are not all the same. • Individuals compete for resources. • Species are generally adapted to their environment.	**General premise** Individuals most adapted to their environment are more likely to survive and pass their traits on to the next generation.
↓	↓
Conclusion Individuals most adapted to their environment are more likely to survive and pass their traits to the next generation.	**Predicted results** If the average temperature in an ecosystem increases due to climate change, individuals better adapted to warmer temperatures will outcompete those that are not.

Figure 1.1.2.2: Inductive vs Deductive Reasoning

? Optional Activity 1.1.2.1

Decide if each of the following is an example of inductive or deductive reasoning.

1. All flying birds and insects have wings. Birds and insects flap their wings as they move through the air. Therefore, wings enable flight.
2. Insects generally survive mild winters better than harsh ones. Therefore, insect pests will become more problematic if global temperatures increase.
3. Chromosomes, the carriers of DNA, separate into daughter cells during cell division. Therefore, DNA is the genetic material.
4. Animals as diverse as humans, insects, and wolves all exhibit social behavior. Therefore, social behavior must have an evolutionary advantage.

Answer

1: inductive; 2: deductive; 3: deductive; 4: inductive.

Video





Many students confuse deductive reasoning with inductive reasoning, and vice versa. Learn the difference in this 3-minute video.
Question after watching: Reflect on incidents/events in your life where you applied deductive and inductive reasoning. Describe them and why they are instances of inductive and deductive reasoning.

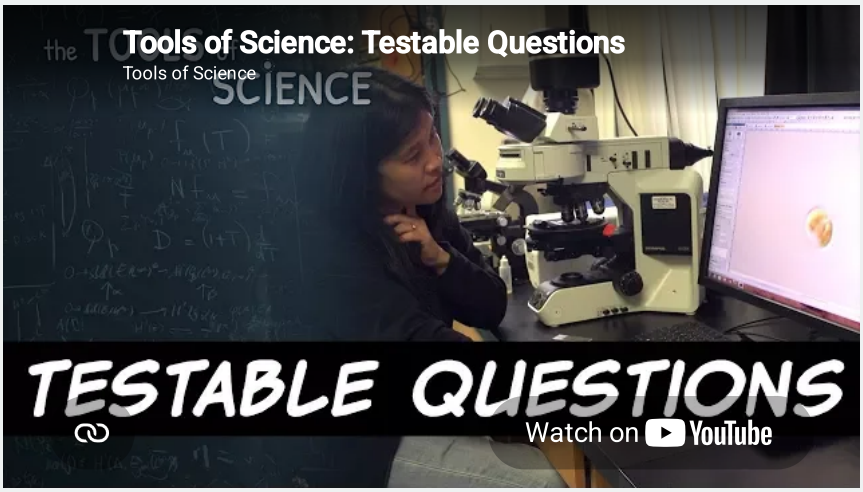
Both types of logical thinking are related to the two main pathways of scientific study: **descriptive science** and **hypothesis-based science**. Descriptive (or discovery) science, which is usually inductive, aims to observe, explore, and discover. Hypothesis-based science, which is usually deductive, begins with a specific question or problem and a potential answer or solution that can be tested. In hypothesis-based science, specific results are predicted from a general premise.

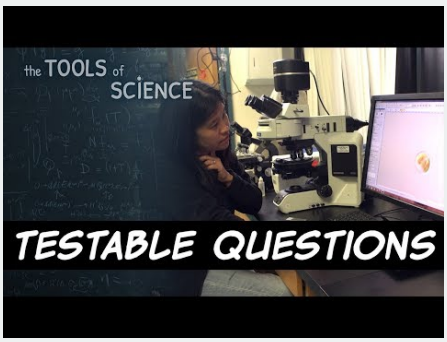
The boundary between descriptive science and hypothesis-based science is often blurred, and most scientific endeavors combine both approaches. Inductive and deductive reasoning are often used in tandem to advance scientific knowledge. The fuzzy boundary becomes apparent when thinking about how easily observation can lead to specific questions. For example, a gentleman in the 1940s observed that the burr seeds that stuck to his clothes and his dog's fur had a tiny hook structure. On closer inspection, he discovered that the burrs' gripping device was more reliable than a zipper. He eventually developed a company and produced the hook-and-loop fastener popularly known today as Velcro. Descriptive science and hypothesis-based science are in continuous dialogue.

The Scientific Method

Biologists study the living world by posing questions about it and seeking science-based responses. This approach is common to other sciences as well and is often referred to as the scientific method. The scientific process typically starts with an observation (often a problem to be solved) that leads to a question. Let's think about a simple problem that starts with an observation and apply the scientific method to solve the problem. One Monday morning, a student arrives at class and quickly discovers that the classroom is too warm. That is an observation that also describes a problem: the classroom is too warm. The student then asks a question: "Why is the classroom so warm?"

Video





Learn about the 5 criteria that a testable question should meet in this 7.5-minute video.

? Optional Activity 1.1.2.2

Read the following questions. Does the statement lend itself to investigation using the scientific method? In other words, is the hypothesis falsifiable (can be proven false)?

1. Is macaroni and cheese tastier than broccoli soup?
2. Are hummingbirds attracted to the color red?
3. Is the moon made out of green cheese?
4. Is plagiarism dishonest?

a. Questions 1 and 2 are subjective and cannot be disproven using scientific method. Questions 3 and 4 can be tested using scientific method.
b. Questions 3 and 4 are subjective and cannot be disproven using scientific method. Questions 1 and 2 can be tested using scientific method.
c. Questions 1 and 3 are subjective and cannot be disproven using scientific method. Questions 2 and 4 can be tested using scientific method.
d. Questions 1 and 4 are subjective and cannot be disproven using scientific method. Questions 2 and 3 can be tested using scientific method.

Answer

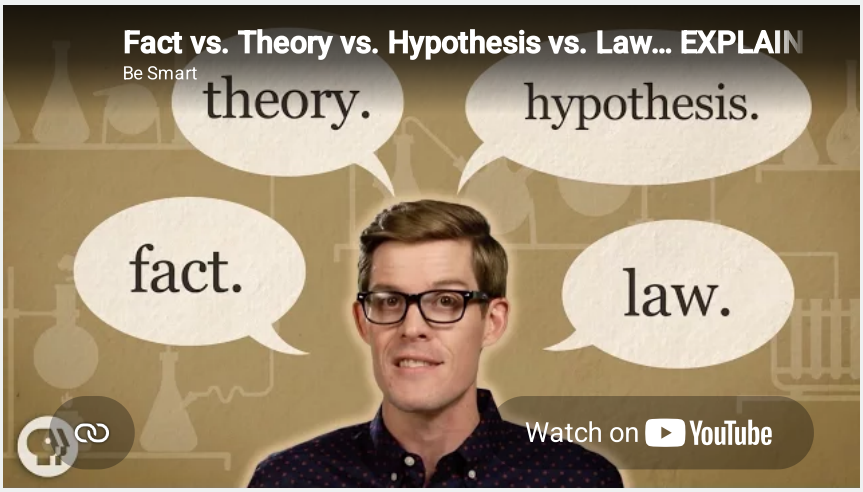
d. Questions 1 and 4 are subjective and cannot be disproven using scientific method. Questions 2 and 3 can be tested using scientific method.

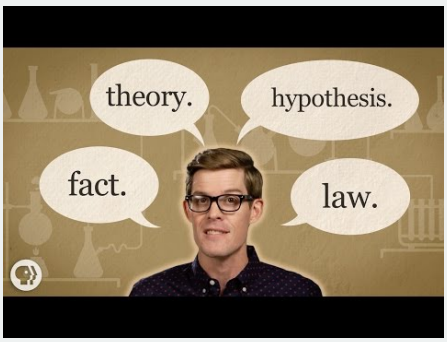
Proposing a Hypothesis

Recall that a hypothesis is a suggested explanation that can be tested. To solve a problem, several hypotheses may be proposed. For example, one hypothesis might be, “The classroom is warm because no one turned on the air conditioning.” But there could be other responses to the question, and therefore other hypotheses may be proposed. A second hypothesis might be, “The classroom is warm because there is a power failure, and so the air conditioning doesn’t work.”

Once a hypothesis has been selected, the student can make a **prediction**. A prediction is similar to a hypothesis but it typically has the format “If . . . then . . . .” For example, the prediction for the first hypothesis might be, “*If* the student turns on the air conditioning, *then* the classroom will no longer be too warm.”

Video





In this 7-minute video, learn the difference between a fact, a theory, a hypothesis, and a scientific law.
Question BEFORE and AFTER watching: How would you define hypothesis and theory?

Testing a Hypothesis

A valid hypothesis must be testable. It should also be **falsifiable**, meaning that it can be disproven by experimental results. Importantly, science does not claim to "prove" anything because scientific understandings are always subject to modification with further information. This step—openness to disproving ideas—is what distinguishes sciences from non-sciences. The presence of the supernatural, for instance, is neither testable nor falsifiable. To test a hypothesis, a researcher will conduct one or more experiments designed to eliminate one or more of the hypotheses. Each experiment will have one or more variables and one or more controls. A **variable** is any part of the experiment that can vary or change during the experiment. The **control group** contains all of the same conditions experimental group EXCEPT for the variable being tested. Therefore, if the results of the **experimental group** differ from the control group, the difference must be due to the manipulation, rather than some outside factor. Identify the variables and controls in the examples from the section above.

Revisit the hypotheses from the section above:

1. The classroom is warm because no one turned on the air conditioning.
2. The classroom is warm because there is a power failure, and so the air conditioning doesn't work.

To test the first hypothesis, the student would find out if the air conditioning is on. If the air conditioning is turned on but does not work, there should be another reason, and this hypothesis should be rejected. To test the second hypothesis, the student could check if the lights in the classroom are functional. If so, there is no power failure and this hypothesis should be rejected. Each hypothesis should be tested by carrying out appropriate experiments. Be aware that rejecting one hypothesis does not determine whether or not the other hypotheses can be accepted; it simply eliminates one hypothesis that is not valid (Figure 1.1.2.4). Using the scientific method, the hypotheses that are inconsistent with experimental data are rejected.

While this "warm classroom" example is based on observational results, other hypotheses and experiments might have clearer controls. For instance, a student might attend class on Monday and realize she had difficulty concentrating on the lecture. One observation to explain this occurrence might be, "When I eat breakfast before class, I am better able to pay attention." The student could then design an experiment with a control to test this hypothesis, including keeping all details of their morning the same but eating breakfast one day versus another to see how their attention holds in class.

The scientific method may seem too rigid and structured (Figure 1.1.2.3). It is important to keep in mind that, although scientists often follow this sequence, there is flexibility. In fact, the scientific process is much more complex in practice. Sometimes an experiment leads to conclusions that favor a change in approach; often, an experiment brings entirely new scientific questions to the puzzle. Many times, science does not operate in a linear fashion; instead, scientists continually draw inferences and make generalizations, finding patterns as their research proceeds. Scientific reasoning is more complex than the scientific method alone suggests. Notice, too, that the scientific method can be applied to solving problems that aren't necessarily scientific in nature.

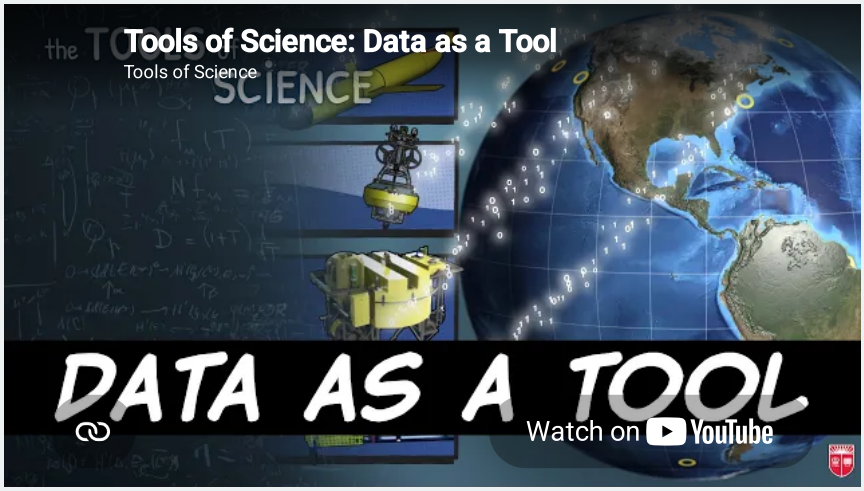
Video





In this 5-minute video, explore how scientists designed and implemented a sampling and data collection plan to answer scientific questions. Questions after watching: What are important things to consider when selecting samples?

Video





In this 6-minute video, explore why data is critically important to the scientific process, what makes good data, and how to use data correctly. Question after watching: What is the distinction and/or relationship between variables and data?

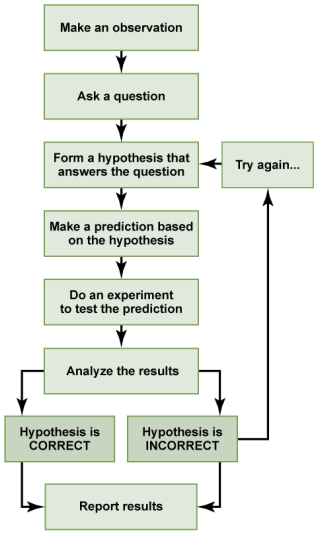


Figure 1.1.2.3: The traditional view of the scientific method.

? Optional Activity 1.1.2.3

In the example below, the scientific method is used to solve an everyday problem. Order the scientific method steps (numbered items) with the process of solving the everyday problem (lettered items). Based on the results of the experiment, is the hypothesis correct? If it is incorrect, propose some alternative hypotheses.

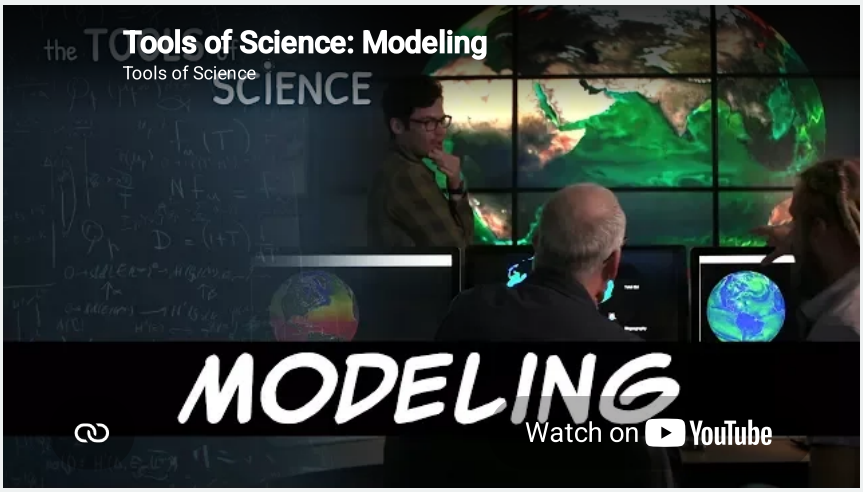
1. Observation
2. Question
3. Hypothesis (answer)
4. Prediction
5. Experiment
6. Result

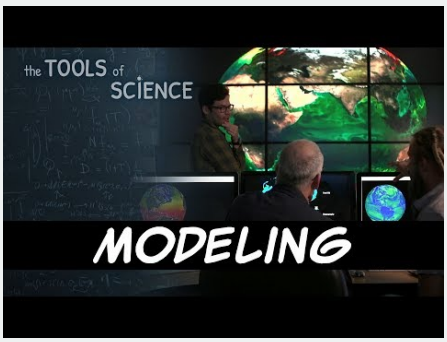
A. There is something wrong with the electrical outlet.
B. If something is wrong with the outlet, my coffeemaker also won't work when plugged into it.
C. My toaster doesn't toast my bread.
D. I plug my coffee maker into the outlet.
E. My coffeemaker works.
F. Why doesn't my toaster work?

Answer

1: C; 2: F; 3: A; 4: B; 5: D; 6: E. The original hypothesis is incorrect, as the coffeemaker works when plugged into the outlet. Alternative hypotheses include that the toaster might be broken or that the toaster wasn't turned on.

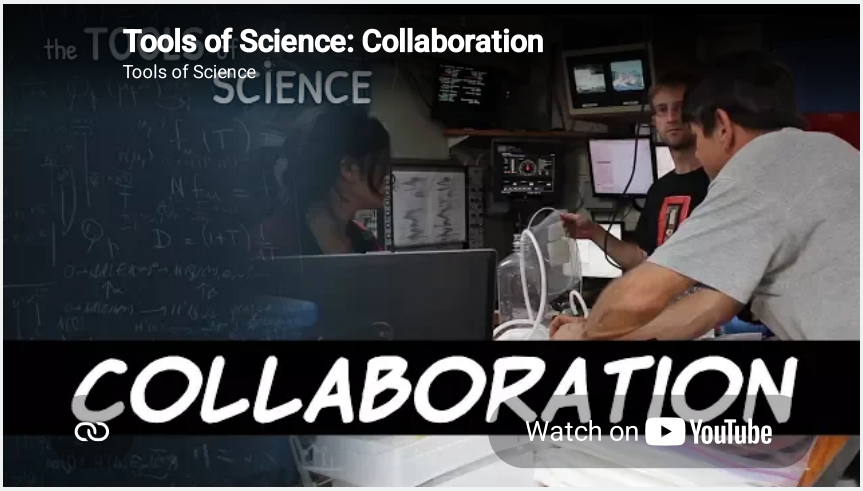
Video





In this 6-minute video, the critical importance of mathematical models to the scientific process is explored.
Question: Why is modeling such a fundamentally important tool?

Video





Discover why collaboration among scientists with different backgrounds and expertise is essential for strong science investigations in this 6.5-minute video.
Question after watching: The research expedition includes several research teams. Why is that?

Video





See how science REALLY works in this 5-minute video.
Question after watching: Why do they use the pinball game analogy for describing how science works?

Optional Resource

Find a more realistic, but more complex, diagram of the scientific method from the University of California - Berkeley here: https://undsci.berkeley.edu/lessons/pdfs/complex_flow_handout.pdf

Pseudoscience

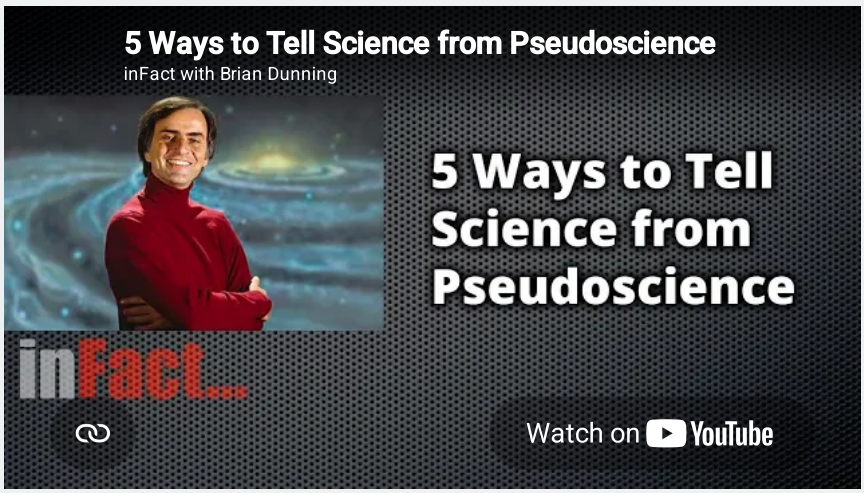
Pseudoscience is a claim, belief, or practice that is presented as scientific but does not adhere to the standards and methods of science. True science is based on repeated evidence-gathering and testing of falsifiable hypotheses. Pseudoscience does not adhere to these criteria. Pseudoscience is often known as fringe or alternative science. It usually lacks the carefully-controlled and thoughtfully-interpreted experiments which provide the foundation of the natural sciences and which contribute to their advancement. In addition to phrenology, some other examples of pseudoscience include astrology, extrasensory perception (ESP), reflexology, reincarnation, and Scientology

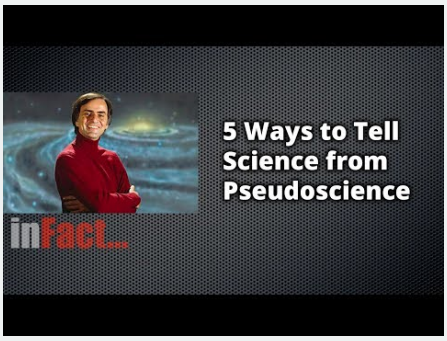
Characteristics of Pseudoscience

Whether a field is actually science or just pseudoscience is not always clear. However, pseudoscience generally exhibits certain common characteristics. Indicators of pseudoscience include:

- *The use of vague, exaggerated, or untestable claims:* Many claims made by pseudoscience cannot be tested with evidence. As a result, they cannot be falsified, even if they are not true.
- *An over-reliance on confirmation rather than refutation:* Any incident that appears to justify a pseudoscience claim is treated as proof of the claim. Claims are assumed true until proven otherwise, and the burden of disproof is placed on skeptics of the claim.
- *A lack of openness to testing by other experts:* Practitioners of pseudoscience avoid subjecting their ideas to peer review. They may refuse to share their data and justify the need for secrecy with claims of proprietary or privacy.
- *An absence of progress in advancing knowledge:* In pseudoscience, ideas are not subjected to repeated testing followed by rejection or refinement, as hypotheses are in true science. Ideas in pseudoscience may remain unchanged for hundreds — or even thousands — of years. In fact, the older an idea is, the more it tends to be trusted in pseudoscience.
- *Personalization of issues:* Proponents of pseudoscience adopt beliefs that have little or no rational basis, so they may try to confirm their beliefs by treating critics as enemies. Instead of arguing to support their own beliefs, they attack the motives and character of their critics.
- *The use of misleading language:* Followers of pseudoscience may use scientific-sounding terms to make their ideas sound more convincing. For example, they may use the formal name dihydrogen monoxide to refer to plain old water.

Video





This 3.5-minute video reviews what is considered pseudoscience.
Question after watching: What are some instances of pseudoscience that you have seen or heard recently?

Persistence of Pseudoscience

Despite failing to meet scientific standards, many pseudosciences survive. Some pseudosciences remain very popular with large numbers of believers. A good example is astrology.

Astrology claims to study the movements and relative positions of celestial objects as a means for divining information about human affairs and terrestrial events. Many ancient cultures attached importance to astronomical events, and some developed elaborate systems for predicting terrestrial events from celestial observations. Throughout most of its history in the West, astrology was actually considered a scholarly tradition and was common in academic circles. With the advent of modern Western sciences and the process of scientific inquiry, however, astrology was called into question. It was challenged on both theoretical and experimental grounds. Eventually, astrology was shown to have no scientific validity or explanatory power.

Today, astrology is considered a pseudoscience, yet it continues to have many devotees. Many people know their astrological sign, and some are familiar with the supposed personality traits associated with their "sign". Astrological readings and horoscopes are readily available online and in print media, and a lot of people read them, even if only occasionally. Some believe that astrology is scientific. Studies suggest that the persistent popularity of pseudosciences such as astrology is due to misunderstandings of

scientific principles and methodology. Alternatively, some are not convinced by scientific arguments that go against their personal beliefs and this, in the end, can do real harm to themselves or others.

Dangers of Pseudoscience

Belief in astrology is unlikely to cause a person harm, but belief in some other pseudosciences might — especially in healthcare-related areas. Treatments that seem scientific but are not may be ineffective, expensive, and even dangerous to patients. Seeking out pseudoscientific treatments may also delay or preclude patients from seeking scientifically-based medical treatments that have been tested and found safe and effective. In short, following pseudoscience instead of established health care practices may be harmful.

Scientific Hoaxes, Frauds, and Fallacies

Pseudoscience is not the only way that science may be misused. Scientific **hoaxes,** frauds, and fallacies may misdirect the pursuit of science, put patients at risk, or mislead and confuse the public. An example of each of these misuses of science and its negative effects is described below.

The Vaccine-Autism Fraud

While it is not true, you may have heard that certain vaccines put the health of young children at risk. This persistent idea is not supported by scientific evidence or accepted by the vast majority of experts in the field. It stems largely from an elaborate medical research fraud that was reported in a 1998 article published in the respected British medical journal, *The Lancet*. The main author of the article was a British physician named Andrew Wakefield. In the article, Wakefield and his colleagues described case histories of only 12 children, most of whom were reported to have developed autism soon after the administration of the MMR (measles, mumps, rubella) vaccine.

There were a whole host of problems with this study, including falsification of research, ethics violations, and experimental design problems. The paper has been retracted (a very big deal in the science community), most of the co-authors have retracted their authorship, and Wakefield lost his medical license. It also later emerged that Wakefield had received research funding from a group of people who were suing vaccine manufacturers. Thousands of follow-up studies have failed to show any association between the MMR vaccine and autism. Unfortunately, by then, the damage had already been done. Parents afraid that their children would develop autism had refrained from having them vaccinated. British MMR vaccination rates fell from nearly 100 percent to 80 percent in the years following the study. The consensus of medical experts today is that Wakefield's fraud put hundreds of thousands of children at risk because of the lower vaccination rates and also diverted research efforts and funding away from finding the true cause of autism.

Correlation-Causation Fallacy

Many statistical tests used in scientific research calculate correlations between variables. **Correlation** refers to how closely related two data sets are, which may be a useful starting point for further investigation. Correlation, however, is also one of the most misused types of evidence, primarily because of the logical fallacy that correlation implies causation. In reality, just because two variables are correlated does not *necessarily* mean that either variable causes the other.

A few simple examples, illustrated by the graphs below, can be used to demonstrate the correlation-causation fallacy. Assume a study found that both per capita consumption of mozzarella cheese and the number of Civil Engineering doctorates awarded are correlated; that is, rates of both events increase together Figure 1.1.2.4. If correlation really did imply causation, then you could conclude from the second example that the increase in age of Miss America causes an increase in murders of a specific type or vice versa Figure 1.1.2.5.

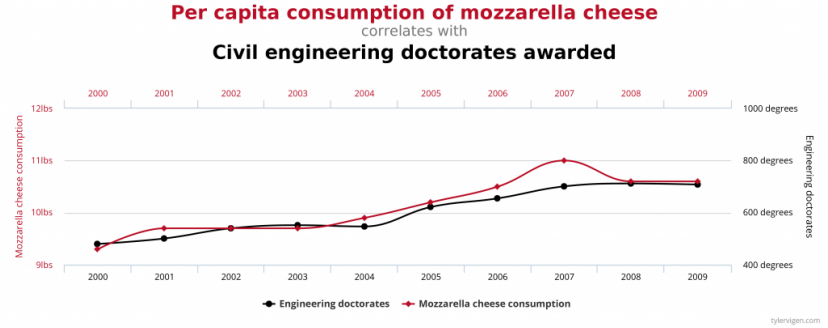


Figure 1.1.2.4 Spurious Correlations [Causation Fallacy] – Consumption of mozzarella cheese and awarded Doctorates

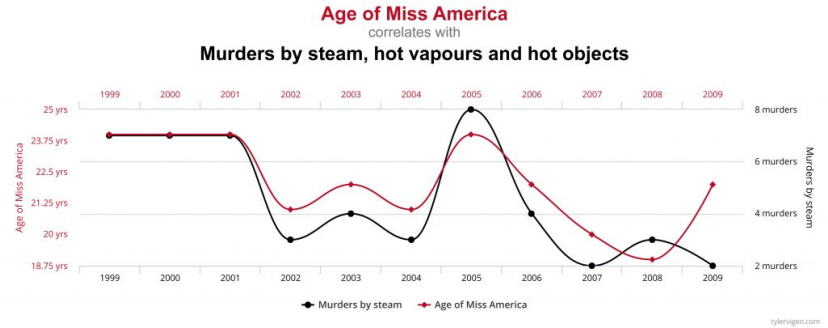


Figure 1.1.2.5: Spurious Correlations (Causation Fallacy)- Miss America and Murder

https://bio.libretexts.org/@go/page/94548

Video





Watch this 4-minute video to learn how to spot a misleading graph.
Question after watching: How can graphs present an opinion?

HRT and CHD

An actual example of the correlation-causation fallacy occurred during the latter half of the 20th century. Numerous studies showed that women taking hormone replacement therapy (HRT) to treat menopausal symptoms also had a lower-than-average incidence of coronary heart disease (CHD). This correlation was misinterpreted as evidence that HRT protects women against CHD. Subsequent studies that controlled other factors related to CHD disproved this presumed causal connection. The studies found that women taking HRT were more likely to come from higher socio-economic groups, with better-than-average diets and exercise regimens. Rather than HRT causing lower CHD incidence, these studies concluded that HRT and lower CHD were both effects of higher socio-economic status and related lifestyle factors.

Video





How statistics can be misleading
Question after watching:
What types of motivation could be at play when people or organizations present statistics?

Finally, read through this "Rough Guide to Spotting Bad Science" infographic from Compound Interest:

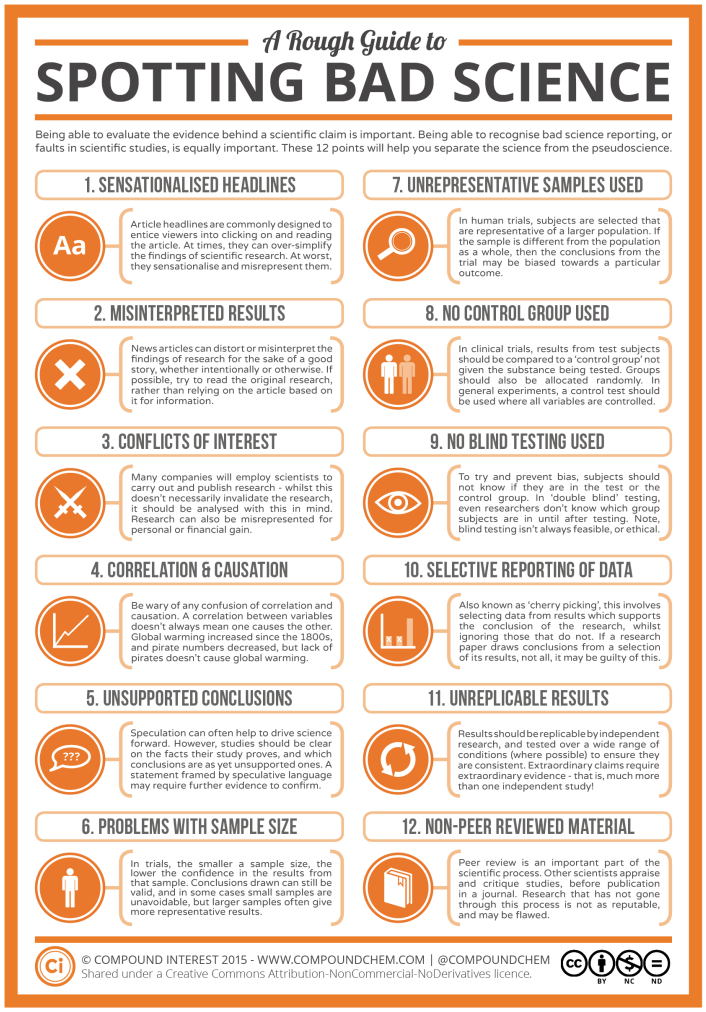


Figure 1.1.2.6: A Rough Guide to Spotting Bad Science.

This page titled 1.1.2: The Nature of Science is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **1.1: The Science of Biology** by OpenStax is licensed CC BY 4.0.

The Role of Science in Society

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 45 minutes.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to the next Chapter, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Appreciate the importance of science in culture and society;
- Compare and contrast basic and applied science;
- Explain how scientists disseminate their work.

Science and Culture

From the United Nations Educational, Scientific and Cultural Organization (UNESCO):

> *"Science is the greatest collective endeavor. It contributes to ensuring a longer and healthier life, monitors our health, provides medicine to cure our diseases, alleviates aches and pains, helps us to provide water for our basic needs – including our food, provides energy and makes life more fun, including sports, music, entertainment and the latest communication technology. Last but not least, it nourishes our spirit.*
>
> *Science generates solutions for everyday life and helps us to answer the great mysteries of the universe. In other words, science is one of the most important channels of knowledge. It has a specific role, as well as a variety of functions for the benefit of our society: creating new knowledge, improving education, and increasing the quality of our lives.*
>
> *Science must respond to societal needs and global challenges. Public understanding and engagement with science, and citizen participation including through the popularization of science are essential to equip citizens to make informed personal and professional choices. Governments need to make decisions based on quality scientific information on issues such as health and agriculture, and parliaments need to legislate on societal issues which necessitate the latest scientific knowledge. National governments need to understand the science behind major global challenges such as climate change, ocean health, biodiversity loss and freshwater security.*
>
> *To face sustainable development challenges, governments and citizens alike must understand the language of science and must become scientifically literate. On the other hand, scientists must understand the problems policy-makers face and endeavor to make the results of their research relevant and comprehensible to society.*
>
> *Challenges today cut across the traditional boundaries of disciplines and stretch across the lifecycle of innovation -- from research to knowledge development and its application. Science, technology and innovation must drive our pursuit of more equitable and sustainable development"* (2021).

Two Types of Science: Basic Science and Applied Science

The scientific community has been debating for the last few decades about the value of different types of science. Is it valuable to pursue science for the sake of simply gaining knowledge, or does scientific knowledge only have worth if we can apply it to solving a specific problem or to bettering our lives? This question focuses on the differences between two types of science: **basic science** and **applied science**.

Basic science or “pure” science seeks to expand knowledge regardless of the short-term application of that knowledge. It is not focused on developing a product or a service of immediate public or commercial value. The immediate goal of basic science is knowledge for knowledge’s sake, though this does not mean that, in the end, it may not result in a practical application.

In contrast, applied science or “technology,” aims to use science to solve real-world problems, making it possible, for example, to improve a crop yield, find a cure for a particular disease, or save animals threatened by a natural disaster (Figure 1.1.3.1). In applied science, the problem is usually defined for the researcher.



Figure 1.1.3.1: After Hurricane Ike struck the Gulf Coast in 2008, the U.S. Fish and Wildlife Service rescued this brown pelican. Thanks to applied science, scientists knew how to rehabilitate the bird. (credit: FEMA)

Some individuals may perceive applied science as “useful” and basic science as “useless.” A question these people might pose to a scientist advocating knowledge acquisition would be, “What for?” A careful look at the history of science, however, reveals that basic knowledge has resulted in many remarkable applications of great value. Many scientists think that a basic understanding of science is necessary before an application is developed; therefore, applied science relies on the results generated through basic science. Other scientists think that it is time to move on from basic science and instead to find solutions to actual problems. Both approaches are valid. It is true that there are problems that demand immediate attention; however, few solutions would be found without the help of the wide knowledge foundation generated through basic science.

One example of how basic and applied science can work together to solve practical problems occurred after the discovery of DNA structure led to an understanding of the molecular mechanisms governing DNA replication. Strands of DNA, unique in every human, are found in our cells, where they provide the instructions necessary for life. During DNA replication, DNA makes new copies of itself, shortly before a cell divides. Understanding the mechanisms of DNA replication enabled scientists to develop laboratory techniques that are now used to identify genetic diseases, pinpoint individuals who were at a crime scene, and determine paternity. Without basic science, it is unlikely that applied science would exist.

Another example of the link between basic and applied research is the Human Genome Project, a study in which each human chromosome was analyzed and mapped to determine the precise sequence of DNA subunits and the exact location of each gene. (The gene is the basic unit of heredity; an individual’s complete collection of genes is his or her genome). Other less complex organisms have also been studied as part of this project in order to gain a better understanding of human chromosomes. The Human Genome Project relied on basic research carried out with simple organisms and, later, with the human genome (Figure 1.1.3.2). An important end goal eventually became using the data for applied research, seeking cures and early diagnoses for genetically related diseases.

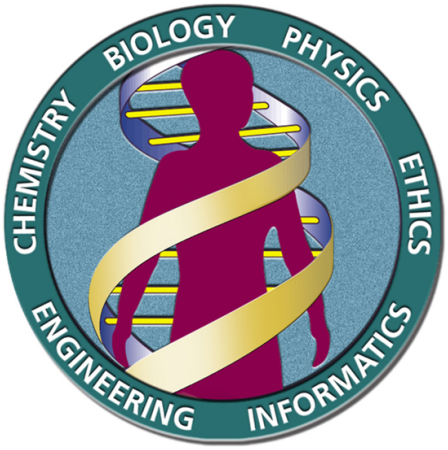


Figure 1.1.3.2: The Human Genome Project was a 13-year collaborative effort among researchers working in several different fields of science. The project, which sequenced the entire human genome, was completed in 2003. (credit: the U.S. Department of Energy Genome Programs (http://genomics.energy.gov))

While research efforts in both basic science and applied science are usually carefully planned, it is important to note that some discoveries are made by **serendipity**, that is, by means of a fortunate accident or a lucky surprise. Penicillin was discovered when biologist Alexander Fleming accidentally left a petri dish of *Staphylococcus* bacteria open. An unwanted mold grew on the dish, killing the bacteria. The mold turned out to be *Penicillium*, and a new antibiotic was discovered. Even in the highly organized world of science, luck—when combined with an observant, curious mind—can lead to unexpected breakthroughs.

Video





Watch this video to see how science is playing a role in understanding Peary caribou in Canada.
Question after watching:
What type of research is this? Basic or applied?

Reporting Scientific Work

Whether scientific research is basic science or applied science, scientists must share their findings in order for other researchers to expand and build upon their discoveries. Collaboration with other scientists—when planning, conducting, and analyzing results—are all important for scientific research. For this reason, important aspects of a scientist's work are communicating with peers and disseminating results to peers. Scientists can share results by presenting them at a scientific meeting or conference, but this approach can reach only the select few who are present. Instead, most scientists present their results in peer-reviewed manuscripts that are published in scientific journals. Peer-reviewed manuscripts are scientific papers that are reviewed by a scientist's colleagues, or peers. These colleagues are qualified individuals, often experts in the same research area, who judge whether or not the scientist's work is suitable for publication. The process of **peer review** helps to ensure that the research described in a scientific paper or grant proposal is original, significant, logical, and thorough. Grant proposals, which are requests for research funding, are also subject to peer review. Scientists publish their work so other scientists can reproduce their experiments under similar or different conditions to expand on the findings. The experimental results must be consistent with the findings of other scientists.

A scientific paper is very different from creative writing. Although creativity is required to design experiments, there are fixed guidelines when it comes to presenting scientific results. First, scientific writing should be concise and accurate. A scientific paper needs to be succinct but detailed enough to allow peers to reproduce the experiments.

The scientific paper consists of several specific sections—introduction, materials and methods, results, and discussion. This structure is sometimes called the "**IMRaD**" format. There are usually acknowledgment and reference sections as well as an abstract (a concise summary) at the beginning of the paper. There might be additional sections depending on the type of paper and the journal where it will be published; for example, some review papers require an outline.

The **introduction** starts with brief, but broad, background information about what is known in the field. A good introduction also gives the rationale of the work; it justifies the work carried out and is where the hypothesis or research question driving the research will be presented. The introduction may also briefly mention the results of the paper. The introduction refers to the published scientific work of others and therefore requires citations following the style of the journal. Using the work or ideas of others without proper citation is considered plagiarism.

The **materials and methods** section includes a complete and accurate description of the substances used, and the method and techniques used by the researchers to gather data. The description should be thorough enough to allow another researcher to repeat the experiment and obtain similar results, but it does not have to be verbose. This section will also include information on how measurements were made and what types of calculations and statistical analyses were used to examine raw data. Although the materials and methods section gives an accurate description of the experiments, it does not discuss them.

Some journals require a **results** section followed by a **discussion** section, but some may combine both. If the journal does not allow the combination of both sections, the results section simply narrates the findings without any further interpretation. The results are

presented by means of tables or graphs, but no duplicate information should be presented. In the discussion section, the researcher will interpret the results, describe how variables may be related, and attempt to explain the observations. It is indispensable to conduct an extensive literature search to put the results in the context of previously published scientific research. Therefore, proper **citations** are included in this section as well.

Finally, a **conclusion** section may be used to summarize the importance of the experimental findings. Most often, the conclusions are included in the discussion. While the scientific paper almost certainly answered one or more scientific questions that were stated, any good research should lead to more questions. Therefore, a well-done scientific paper leaves doors open for the researcher and others to continue and expand on the findings.

Review articles do not follow the IMRAD format because they do not present original scientific findings, or primary literature; instead, they summarize and comment on findings that were published as primary literature and typically include extensive reference sections. They follow specific methods of searching and summarizing the scientific literature, to ensure that their findings are reproducible.

References:

UNESCO. (2021). Science for Society. United Nations Education, Science, and Culture Organization. From: https://en.unesco.org/themes/science-society

---

This page titled 1.1.3: The Role of Science in Society is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **1.1: The Science of Biology** by OpenStax is licensed CC BY 4.0.

1.E: The Study of Life (Exercises)

Review Questions

The first forms of life on Earth were _____.

A. plants
B. microorganisms
C. birds
D. dinosaurs

Answer

B

A suggested and testable explanation for an event is called a _____.

A. hypothesis
B. variable
C. theory
D. control

Answer

A

Which of the following sciences is not considered a natural science?

A. biology
B. astronomy
C. physics
D. computer science

Answer

D

The type of logical thinking that uses related observations to arrive at a general conclusion is called _____.

A. deductive reasoning
B. the scientific method
C. hypothesis-based science
D. inductive reasoning

Answer

D

The process of _____ helps to ensure that a scientist's research is original, significant, logical, and thorough.

A. publication
B. public speaking
C. peer review
D. the scientific method

Answer

C

A person notices that her houseplants that are regularly exposed to music seem to grow more quickly than those in rooms with no music. As a result, she determines that plants grow better when exposed to music. This example most closely resembles which type of reasoning?

A. inductive reasoning
B. deductive reasoning
C. neither, because no hypothesis was made
D. both inductive and deductive reasoning

Answer

A

Free Response

Although the scientific method is used by most of the sciences, it can also be applied to everyday situations. Think about a problem that you may have at home, at school, or with your car, and apply the scientific method to solve it.

Answer

Answers will vary, but should apply the steps of the scientific method. One possibility could be a car which doesn't start. The hypothesis could be that the car doesn't start because the battery is dead. The experiment would be to change the battery or to charge the battery and then check whether the car starts or not. If it starts, the problem was due to the battery, and the hypothesis is accepted.

Give an example of how applied science has had a direct effect on your daily life.

Answer

Answers will vary. One example of how applied science has had a direct effect on daily life is the presence of vaccines. Vaccines to prevent diseases such polio, measles, tetanus, and even influenza affect daily life by contributing to individual and societal health.

Name two topics that are likely to be studied by biologists, and two areas of scientific study that would fall outside the realm of biology.

Answer

Answers will vary. Topics that fall inside the area of biological study include how diseases affect human bodies, how pollution impacts a species' habitat, and how plants respond to their environments. Topics that fall outside of biology (the "study of life") include how metamorphic rock is formed and how planetary orbits function.

Thinking about the topic of cancer, write a basic science question and an applied science question that a researcher interested in this topic might ask

Answer

Answers will vary. Basic science: What evolutionary purpose might cancer serve? Applied science: What strategies might be found to prevent cancer from reproducing at the cellular level?

The smallest unit of biological structure that meets the functional requirements of "living" is the _____.

A. organ
B. organelle

C. cell
D. macromolecule

Answer

C

Viruses are not considered living because they _____.

A. are not made of cells
B. lack cell nuclei
C. do not contain DNA or RNA
D. cannot reproduce

Answer

A

The presence of a membrane-enclosed nucleus is a characteristic of _____.

A. prokaryotic cells
B. eukaryotic cells
C. living organisms
D. bacteria

Answer

B

A group of individuals of the same species living in the same area is called a(n) _____.

A. family
B. community
C. population
D. ecosystem

Answer

C

Which of the following sequences represents the hierarchy of biological organization from the most inclusive to the least complex level?

A. organelle, tissue, biosphere, ecosystem, population
B. organ, organism, tissue, organelle, molecule
C. organism, community, biosphere, molecule, tissue, organ
D. biosphere, ecosystem, community, population, organism

Answer

D

Where in a phylogenetic tree would you expect to find the organism that had evolved most recently?

A. at the base
B. within the branches
C. at the nodes

D. at the branch tips

Answer

D

Free Response

Select two items that biologists agree are necessary in order to consider an organism “alive.” For each, give an example of a non-living object that otherwise fits the definition of “alive.”

Answer

Answers will vary. Layers of sedimentary rock have order but are not alive. Technology is capable of regulation but is not, of itself, alive.

Consider the levels of organization of the biological world, and place each of these items in order from smallest level of organization to most encompassing: skin cell, elephant, water molecule, planet Earth, tropical rainforest, hydrogen atom, wolf pack, liver.

Answer

Smallest level of organization to largest: hydrogen atom, water molecule, skin cell, liver, elephant, wolf pack, tropical rainforest, planet Earth

You go for a long walk on a hot day. Give an example of a way in which homeostasis keeps your body healthy.

Answer

During your walk, you may begin to perspire, which cools your body and helps your body to maintain a constant internal temperature. You might also become thirsty and pause long enough for a cool drink, which will help to restore the water lost during perspiration.

Using examples, explain how biology can be studied from a microscopic approach to a global approach.

Answer

Researchers can approach biology from the smallest to the largest, and everything in between. For instance, an ecologist may study a population of individuals, the population’s community, the community’s ecosystem, and the ecosystem’s part in the biosphere. When studying an individual organism, a biologist could examine the cell and its organelles, the tissues that the cells make up, the organs and their respective organ systems, and the sum total—the organism itself.

This page titled 1.E: The Study of Life (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **1.E: The Study of Life (Exercises)** by OpenStax is licensed CC BY 4.0.

1.G: Unit 1.1 Glossary

Unit 1.2

atom
smallest and most fundamental unit of matter

biochemistry
study of the chemistry of biological organisms

biosphere
collection of all the ecosystems on Earth

botany
study of plants

cell
smallest fundamental unit of structure and function in living things

community
set of populations inhabiting a particular area

ecosystem
all the living things in a particular area together with the abiotic, nonliving parts of that environment

eukaryote
organism with cells that have nuclei and membrane-bound organelles

evolution
process of gradual change during which new species arise from older species and some species become extinct

homeostasis
ability of an organism to maintain constant internal conditions

macromolecule
large molecule, typically formed by the joining of smaller molecules

microbiology
study of the structure and function of microorganisms

molecule
chemical structure consisting of at least two atoms held together by one or more chemical bonds

molecular biology
study of biological processes and their regulation at the molecular level, including interactions among molecules such as DNA, RNA, and proteins

neurobiology
study of the biology of the nervous system

organ
collection of related tissues grouped together performing a common function

organ system
level of organization that consists of functionally related interacting organs

organelle
small structures that exist within cells and carry out cellular functions

organism
individual living entity

paleontology
study of life's history by means of fossils

phylogenetic tree
diagram showing the evolutionary relationships among various biological species based on similarities and differences in genetic or physical traits or both; in essence, a hypothesis concerning evolutionary connections

population
all of the individuals of a species living within a specific area

prokaryote
single-celled organism that lacks organelles and does not have nuclei surrounded by a nuclear membrane

tissue
group of similar cells carrying out related functions

Unit 1.3

zoology
study of animals

abstract
opening section of a scientific paper that summarizes the research and conclusions

applied science
form of science that aims to solve real-world problems

basic science
science that seeks to expand knowledge and understanding regardless of the short-term application of that knowledge

biology
the study of living organisms and their interactions with one another and their environments

conclusion
section of a scientific paper that summarizes the importance of the experimental findings

control
part of an experiment that does not change during the experiment

deductive reasoning

form of logical thinking that uses a general inclusive statement to forecast specific results

descriptive science
(also, discovery science) form of science that aims to observe, explore, and investigate

discussion
section of a scientific paper in which the author interprets experimental results, describes how variables may be related, and attempts to explain the phenomenon in question

falsifiable
able to be disproven by experimental results

hypothesis
suggested explanation for an observation, which can be tested

hypothesis-based science
form of science that begins with a specific question and potential testable answers

inductive reasoning
form of logical thinking that uses related observations to arrive at a general conclusion

introduction
opening section of a scientific paper, which provides background information about what was known in the field prior to the research reported in the paper

life science
field of science, such as biology, that studies living things

materials and methods
section of a scientific paper that includes a complete description of the substances, methods, and techniques used by the researchers to gather data

natural science
field of science that is related to the physical world and its phenomena and processes

peer-reviewed manuscript
scientific paper that is reviewed by a scientist's colleagues who are experts in the field of study

physical science
field of science, such as geology, astronomy, physics, and chemistry, that studies nonliving matter

plagiarism
using other people's work or ideas without proper citation, creating the false impression that those are the author's original ideas

results
section of a scientific paper in which the author narrates the experimental findings and presents relevant figures, pictures, diagrams, graphs, and tables, without any further interpretation

review article
paper that summarizes and comments on findings that were published as primary literature

science
knowledge that covers general truths or the operation of general laws, especially when acquired and tested by the scientific method

scientific method
method of research with defined steps that include observation, formulation of a hypothesis, testing, and confirming or falsifying the hypothesis

serendipity
fortunate accident or a lucky surprise

theory
tested and confirmed explanation for observations or phenomena

variable
part of an experiment that the experimenter can vary or change

Unit 1.4

applied science
process of science to solve real-world problems

basic science
process of science for the sake of gaining knowledge

IMRaD
traditional format of a scientific paper comprised of introduction, materials and methods, results, and discussion

peer review
ensures that research described in a scientific paper or grant proposal is original, significant, logical, and thorough

serendipity
fortunate accident

This page titled 1.G: Unit 1.1 Glossary is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

1.2: The Chemical Foundation of Life

Elements in various combinations comprise all matter, including living things. Some of the most abundant elements in living organisms include carbon, hydrogen, nitrogen, oxygen, sulfur, and phosphorus. These form the nucleic acids, proteins, carbohydrates, and lipids that are the fundamental components of living matter. Biologists must understand these important building blocks and the unique structures of the atoms that make up molecules, allowing for the formation of cells, tissues, organ systems, and entire organisms.

1.2.1: Prelude to The Chemical Foundation of Life

1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

1.2.3: Water

1.2.4: Carbon

1.2.E: The Chemical Foundation of Life (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 1.2: The Chemical Foundation of Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

1.2.1: Prelude to The Chemical Foundation of Life

Elements in various combinations comprise all matter, including living things. Some of the most abundant elements in living organisms include carbon, hydrogen, nitrogen, oxygen, sulfur, and phosphorus. These form the nucleic acids, proteins, carbohydrates, and lipids that are the fundamental components of living matter. Biologists must understand these important building blocks and the unique structures of the atoms that make up molecules, allowing for the formation of cells, tissues, organ systems, and entire organisms.

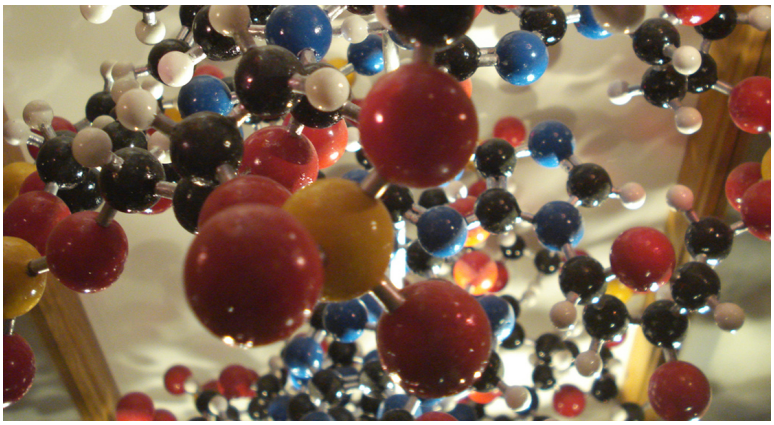


Figure 1.2.1.1: Atoms are the building blocks of molecules found in the universe—air, soil, water, rocks ... and also the cells of all living organisms. In this model of an organic molecule, the atoms of carbon (black), hydrogen (white), nitrogen (blue), oxygen (red), and sulfur (yellow) are shown in proportional atomic size. The silver rods indicate chemical bonds. (credit: modification of work by Christian Guthier)

All biological processes follow the laws of physics and chemistry, so in order to understand how biological systems work, it is important to understand the underlying physics and chemistry. For example, the flow of blood within the circulatory system follows the laws of physics that regulate the modes of fluid flow. The breakdown of the large, complex molecules of food into smaller molecules—and the conversion of these to release energy to be stored in adenosine triphosphate (ATP)—is a series of chemical reactions that follow chemical laws. The properties of water and the formation of hydrogen bonds are key to understanding living processes. Recognizing the properties of acids and bases is important, for example, to our understanding of the digestive process. Therefore, the fundamentals of physics and chemistry are important for gaining insight into biological processes.

This page titled 1.2.1: Prelude to The Chemical Foundation of Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **2.0: Prelude to The Chemical Foundation of Life** by OpenStax is licensed CC BY 4.0.

1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

Learning Objectives

- Define matter and elements
- Describe the interrelationship between protons, neutrons, and electrons
- Compare the ways in which electrons can be donated or shared between atoms
- Explain the ways in which naturally occurring elements combine to create molecules, cells, tissues, organ systems, and organisms

Video



This 18-minute video covers the nature of matter, elements, atomic structure and what those sneaky electrons do. You do not need to know the Lewis dot diagrams for this course but they can be helpful!

At its most fundamental level, life is made up of matter. Matter is any substance that occupies space and has mass. Elements are unique forms of matter with specific chemical and physical properties that cannot be broken down into smaller substances by ordinary chemical reactions. There are 118 elements, but only 92 occur naturally. The remaining elements are synthesized in laboratories and are unstable.

Each element is designated by its chemical symbol, which is a single capital letter or, when the first letter is already "taken" by another element, a combination of two letters. Some elements follow the English term for the element, such as C for carbon and Ca for calcium. Other elements' chemical symbols derive from their Latin names; for example, the symbol for sodium is Na, referring to *natrium*, the Latin word for sodium.

The four elements common to all living organisms are oxygen (O), carbon (C), hydrogen (H), and nitrogen (N). In the non-living world, elements are found in different proportions, and some elements common to living organisms are relatively rare on the earth as a whole, as shown in Table 1.2.2.1. For example, the atmosphere is rich in nitrogen and oxygen but contains little carbon and hydrogen, while the earth's crust, although it contains oxygen and a small amount of hydrogen, has little nitrogen and carbon. In spite of their differences in abundance, all elements and the chemical reactions between them obey the same chemical and physical laws regardless of whether they are a part of the living or non-living world.

Table 1.2.2.1: Approximate Percentage of Elements in Living Organisms (Humans) Compared to the Non-living World

Element	Life (Humans)	Atmosphere	Earth's Crust
Oxygen (O)	65%	21%	46%
Carbon (C)	18%	trace	trace
Hydrogen (H)	10%	trace	0.1%
Nitrogen (N)	3%	78%	trace

The Structure of the Atom

To understand how elements come together, we must first discuss the smallest component or building block of an element, the atom. An atom is the smallest unit of matter that retains all of the chemical properties of an element. For example, one gold atom has all of the properties of gold in that it is a solid metal at room temperature. A gold coin is simply a very large number of gold atoms molded into the shape of a coin and containing small amounts of other elements known as impurities. Gold atoms cannot be broken down into anything smaller while still retaining the properties of gold.

An atom is composed of two regions: the nucleus, which is in the center of the atom and contains protons and neutrons, and the outermost region of the atom which holds its electrons in orbit around the nucleus, as illustrated in Figure 1.2.2.1. Atoms contain protons, electrons, and neutrons, among other subatomic particles. The only exception is hydrogen (H), which is made of one proton and one electron with no neutrons.

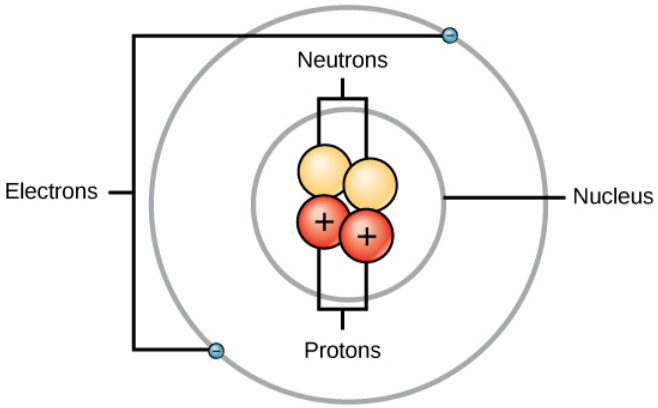


Figure 1.2.2.1: Elements, such as helium, depicted here, are made up of atoms. Atoms are made up of protons and neutrons located within the nucleus, with electrons in orbitals surrounding the nucleus.

Protons and neutrons have approximately the same mass, about 1.67×10^{-24} grams. Scientists arbitrarily define this amount of mass as one atomic mass unit (amu) or one Dalton, as shown in Table 1.2.2.2. Although similar in mass, protons and neutrons differ in their electric charge. A proton is positively charged whereas a neutron is uncharged. Therefore, the number of neutrons in an atom contributes significantly to its mass, but not to its charge. Electrons are much smaller in mass than protons, weighing only 9.11×10^{-28} grams, or about 1/1800 of an atomic mass unit. Hence, they do not contribute much to an element's overall atomic mass. Therefore, when considering atomic mass, it is customary to ignore the mass of any electrons and calculate the atom's mass based on the number of protons and neutrons alone. Although not significant contributors to mass, electrons do contribute greatly to the atom's charge, as each electron has a negative charge equal to the positive charge of a proton. In uncharged, neutral atoms, the number of electrons orbiting the nucleus is equal to the number of protons inside the nucleus. In these atoms, the positive and negative charges cancel each other out, leading to an atom with no net charge.

Accounting for the sizes of protons, neutrons, and electrons, most of the volume of an atom—greater than 99 percent—is, in fact, empty space. With all this empty space, one might ask why so-called solid objects do not just pass through one another. The reason they do not is that the electrons that surround all atoms are negatively charged and negative charges repel each other.

Table 1.2.2.2: Protons, Neutrons, and Electrons

	Charge	Mass (amu)	Location
Proton	+1	1	nucleus
Neutron	0	1	nucleus
Electron	–1	0	orbitals

Atomic Number and Mass

Atoms of each element contain a characteristic number of protons and electrons. The number of protons determines an element's atomic number and is used to distinguish one element from another. The number of neutrons is variable, resulting in isotopes, which are different forms of the same atom that vary only in the number of neutrons they possess. Together, the number of protons and the number of neutrons determine an element's mass number, as illustrated in Figure 1.2.2.2. Note that the small contribution of mass from electrons is disregarded in calculating the mass number. This approximation of mass can be used to easily calculate how many neutrons an element has by simply subtracting the number of protons from the mass number. Since an element's isotopes will have slightly different mass numbers, scientists also determine the atomic mass, which is the calculated mean of the mass number for its naturally occurring isotopes. Often, the resulting number contains a fraction. For example, the atomic mass of chlorine (Cl) is 35.45 because chlorine is composed of several isotopes, some (the majority) with atomic mass 35 (17 protons and 18 neutrons) and some with atomic mass 37 (17 protons and 20 neutrons).

Exercise 1.2.2.1

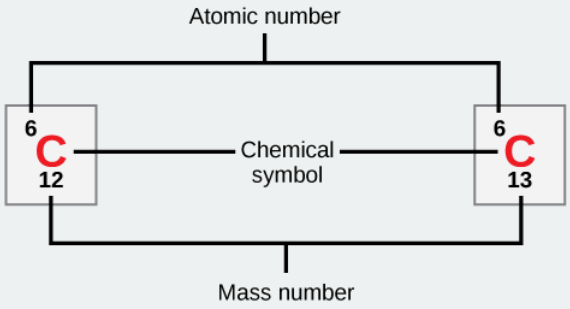


Figure 1.2.2.2: Carbon has an atomic number of six, and two stable isotopes with mass numbers of twelve and thirteen, respectively. Its atomic mass is 12.11.

Figure 1.2.2.2: How many neutrons do carbon-12 and carbon-13 have, respectively?

Answer

Carbon-12 has six neutrons. Carbon-13 has seven neutrons.

Isotopes

Isotopes are different forms of an element that have the same number of protons but a different number of neutrons. Some elements —such as carbon, potassium, and uranium—have naturally occurring isotopes. Carbon-12 contains six protons, six neutrons, and six electrons; therefore, it has a mass number of 12 (six protons and six neutrons). Carbon-14 contains six protons, eight neutrons, and six electrons; its atomic mass is 14 (six protons and eight neutrons). These two alternate forms of carbon are isotopes. Some isotopes may emit neutrons, protons, and electrons, and attain a more stable atomic configuration (lower level of potential energy); these are radioactive isotopes, or radioisotopes. Radioactive decay (carbon-14 losing neutrons to eventually become carbon-12) describes the energy loss that occurs when an unstable atom's nucleus releases radiation.

Evolution Connection: Carbon Dating

Carbon is normally present in the atmosphere in the form of gaseous compounds like carbon dioxide and methane. Carbon-14 (C^{14}) is a naturally occurring radioisotope that is created in the atmosphere from atmospheric N^{14} (nitrogen) by the addition of a neutron and the loss of a proton because of cosmic rays. This is a continuous process, so more C^{14} is always being created. As a living organism incorporates C^{14} initially as carbon dioxide fixed in the process of photosynthesis, the relative amount of C^{14} in

its body is equal to the concentration of C^{14} in the atmosphere. When an organism dies, it is no longer ingesting C^{14}, so the ratio between C^{14} and C^{12} will decline as C^{14} decays gradually to N^{14} by a process called beta decay—the emission of electrons or positrons. This decay gives off energy in a slow process.

After approximately 5,730 years, half of the starting concentration of C^{14} will have been converted back to N^{14}. The time it takes for half of the original concentration of an isotope to decay back to its more stable form is called its half-life. Because the half-life of C^{14} is long, it is used to date formerly living objects such as old bones or wood. Comparing the ratio of the C^{14} concentration found in an object to the amount of C^{14} detected in the atmosphere, the amount of the isotope that has not yet decayed can be determined. On the basis of this amount, the age of the material, such as the pygmy mammoth shown in Figure 1.2.2.3, can be calculated with accuracy if it is not much older than about 50,000 years. Other elements have isotopes with different half lives. For example, K^{40} (potassium-40) has a half-life of 1.25 billion years, and U^{235} (Uranium 235) has a half-life of about 700 million years. Through the use of radiometric dating, scientists can study the age of fossils or other remains of extinct organisms to understand how organisms have evolved from earlier species.



Figure 1.2.2.3: The age of carbon-containing remains less than about 50,000 years old, such as this pygmy mammoth, can be determined using carbon dating. (credit: Bill Faulkner, NPS)

The Periodic Table

The different elements are organized and displayed in the periodic table. Devised by Russian chemist Dmitri Mendeleev (1834–1907) in 1869, the table groups elements that, although unique, share certain chemical properties with other elements. The properties of elements are responsible for their physical state at room temperature: they may be gases, solids, or liquids. Elements also have specific chemical reactivity, the ability to combine and to chemically bond with each other.

In the periodic table, shown in Figure 1.2.2.4, the elements are organized and displayed according to their atomic number and are arranged in a series of rows and columns based on shared chemical and physical properties. In addition to providing the atomic number for each element, the periodic table also displays the element's atomic mass. Looking at carbon, for example, its symbol (C) and name appear, as well as its atomic number of six (in the upper left-hand corner) and its atomic mass of 12.11.

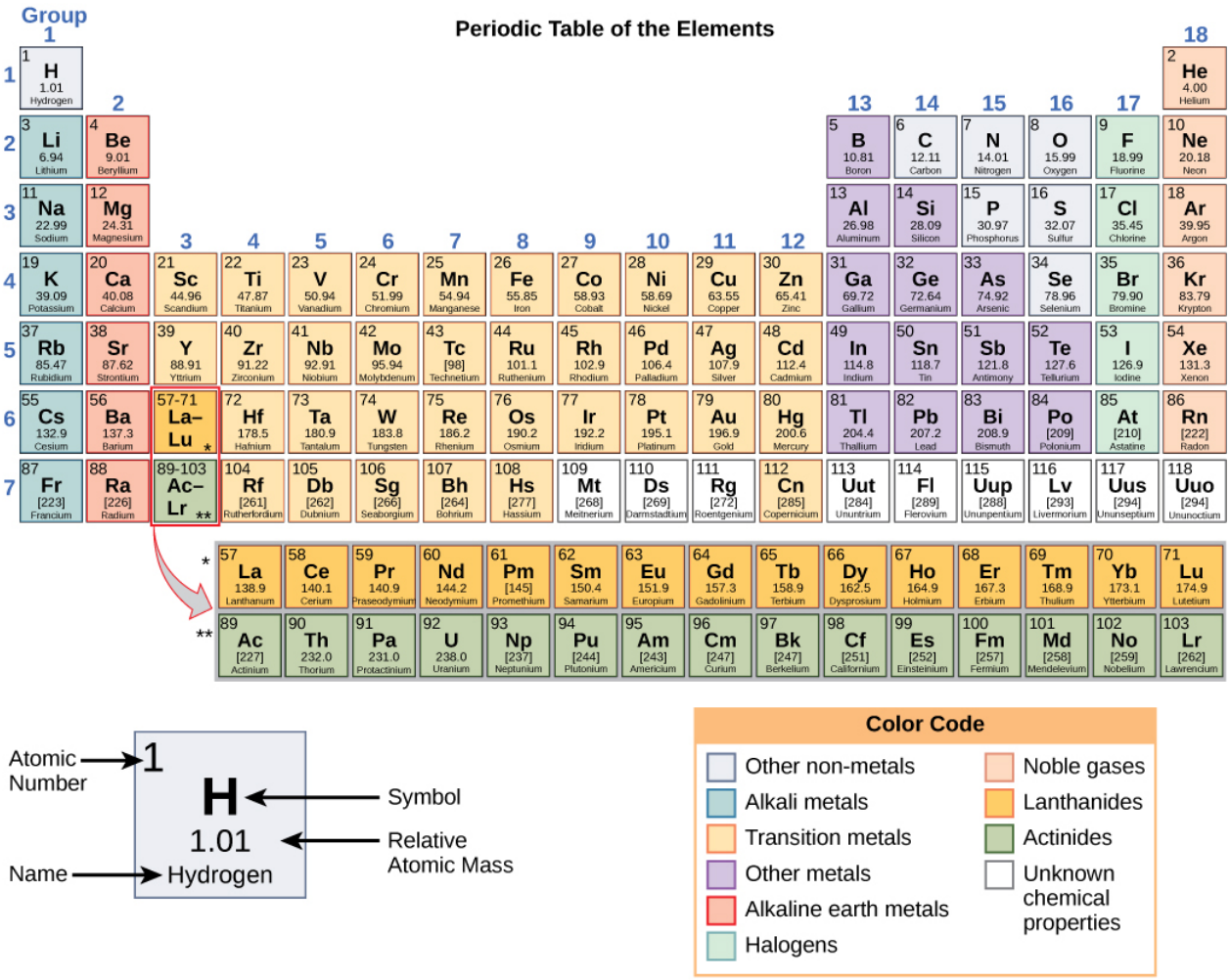


Figure 1.2.2.4: The periodic table shows the atomic mass and atomic number of each element. The atomic number appears above the symbol for the element and the approximate atomic mass appears below it.

The periodic table groups elements according to chemical properties. The differences in chemical reactivity between the elements are based on the number and spatial distribution of an atom's electrons. Atoms that chemically react and bond to each other form molecules. Molecules are simply two or more atoms chemically bonded together. Logically, when two atoms chemically bond to form a molecule, their electrons, which form the outermost region of each atom, come together first as the atoms form a chemical bond.

Electron Shells and the Bohr Model

It should be stressed that there is a connection between the number of protons in an element, the atomic number that distinguishes one element from another, and the number of electrons it has. In all electrically neutral atoms, the number of electrons is the same as the number of protons. Thus, each element, at least when electrically neutral, has a characteristic number of electrons equal to its atomic number.

An early model of the atom was developed in 1913 by Danish scientist Niels Bohr (1885–1962). The Bohr model shows the atom as a central nucleus containing protons and neutrons, with the electrons in circular orbitals at specific distances from the nucleus, as illustrated in Figure 1.2.2.5. These orbits form electron shells or energy levels, which are a way of visualizing the number of electrons in the outermost shells. These energy levels are designated by a number and the symbol "n." For example, 1n represents the first energy level located closest to the nucleus.

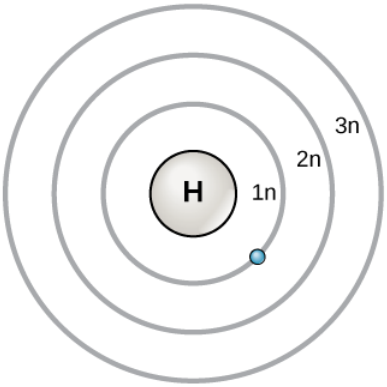


Figure 1.2.2.5: The Bohr model was developed by Niels Bohrs in 1913. In this model, electrons exist within principal shells. An electron normally exists in the lowest energy shell available, which is the one closest to the nucleus. Energy from a photon of light can bump it up to a higher energy shell, but this situation is unstable, and the electron quickly decays back to the ground state. In the process, a photon of light is released

Electrons fill orbitals in a consistent order: they first fill the orbitals closest to the nucleus, then they continue to fill orbitals of increasing energy further from the nucleus. If there are multiple orbitals of equal energy, they will be filled with one electron in each energy level before a second electron is added. The electrons of the outermost energy level determine the energetic stability of the atom and its tendency to form chemical bonds with other atoms to form molecules.

Under standard conditions, atoms fill the inner shells first, often resulting in a variable number of electrons in the outermost shell. The innermost shell has a maximum of two electrons but the next two electron shells can each have a maximum of eight electrons. This is known as the octet rule, which states, with the exception of the innermost shell, that atoms are more stable energetically when they have eight electrons in their valence shell, the outermost electron shell. Examples of some neutral atoms and their electron configurations are shown in Figure 1.2.2.6. Notice that in this figure, helium has a complete outer electron shell, with two electrons filling its first and only shell. Similarly, neon has a complete outer 2n shell containing eight electrons. In contrast, chlorine and sodium have seven and one in their outer shells, respectively, but theoretically they would be more energetically stable if they followed the octet rule and had eight.

Exercise 1.2.2.2

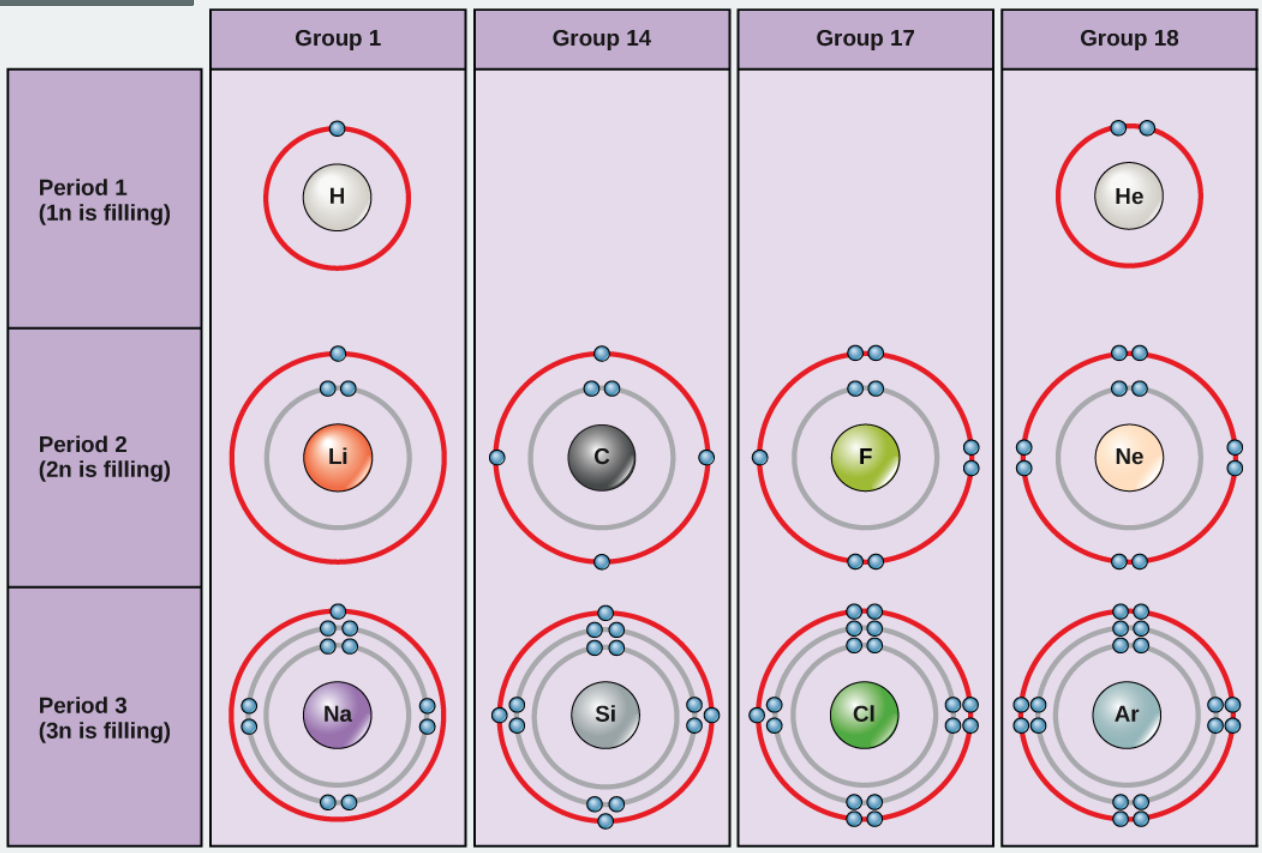


Figure 1.2.2.6: Bohr diagrams indicate how many electrons fill each principal shell. Group 18 elements (helium, neon, and argon are shown) have a full outer, or valence, shell. A full valence shell is the most stable electron configuration. Elements in other groups have partially filled valence shells and gain or lose electrons to achieve a stable electron configuration.

Figure 1.2.2.6: An atom may give, take, or share electrons with another atom to achieve a full valence shell, the most stable electron configuration. Looking at this figure, how many electrons do elements in group 1 need to lose in order to achieve a stable electron configuration? How many electrons do elements in groups 14 and 17 need to gain to achieve a stable configuration?

Answer

Elements in group 1 need to lose one electron to achieve a stable electron configuration. Elements in groups 14 and 17 need to gain four and one electrons, respectively, to achieve a stable configuration.

Understanding that the organization of the periodic table is based on the total number of protons (and electrons) helps us know how electrons are distributed among the outer shell. The periodic table is arranged in columns and rows based on the number of electrons and where these electrons are located. Take a closer look at the some of the elements in the table's far right column in Figure 1.2.2.6. The group 18 atoms helium (He), neon (Ne), and argon (Ar) all have filled outer electron shells, making it unnecessary for them to share electrons with other atoms to attain stability; they are highly stable as single atoms. Their non-reactivity has resulted in their being named the inert gases (or noble gases). Compare this to the group 1 elements in the left-hand column. These elements, including hydrogen (H), lithium (Li), and sodium (Na), all have one electron in their outermost shells. That means that they can achieve a stable configuration and a filled outer shell by donating or sharing one electron with another atom or a molecule such as water. Hydrogen will donate or share its electron to achieve this configuration, while lithium and sodium will donate their electron to become stable. As a result of losing a negatively charged electron, they become positively charged ions. Group 17 elements, including fluorine and chlorine, have seven electrons in their outmost shells, so they tend to fill this shell with an electron from other atoms or molecules, making them negatively charged ions. Group 14 elements, of which carbon is the most important to living systems, have four electrons in their outer shell allowing them to make several covalent

bonds (discussed below) with other atoms. Thus, the columns of the periodic table represent the potential shared state of these elements' outer electron shells that is responsible for their similar chemical characteristics.

Chemical Reactions and Molecules

Video



This 14-minute video discusses atoms forming bonds - why they do it, how they do it and what happens when they do it...including ionic bonds, non-polar covalent bonds, polar covalent bonds and hydrogen bonds.

All elements are most stable when their outermost shell is filled with electrons according to the octet rule. This is because it is energetically favorable for atoms to be in that configuration and it makes them stable. However, since not all elements have enough electrons to fill their outermost shells, atoms form chemical bonds with other atoms thereby obtaining the electrons they need to attain a stable electron configuration. When two or more atoms chemically bond with each other, the resultant chemical structure is a molecule. The familiar water molecule, H_2O, consists of two hydrogen atoms and one oxygen atom; these bond together to form water, as illustrated in Figure 1.2.2.8. Atoms can form molecules by donating, accepting, or sharing electrons to fill their outer shells.

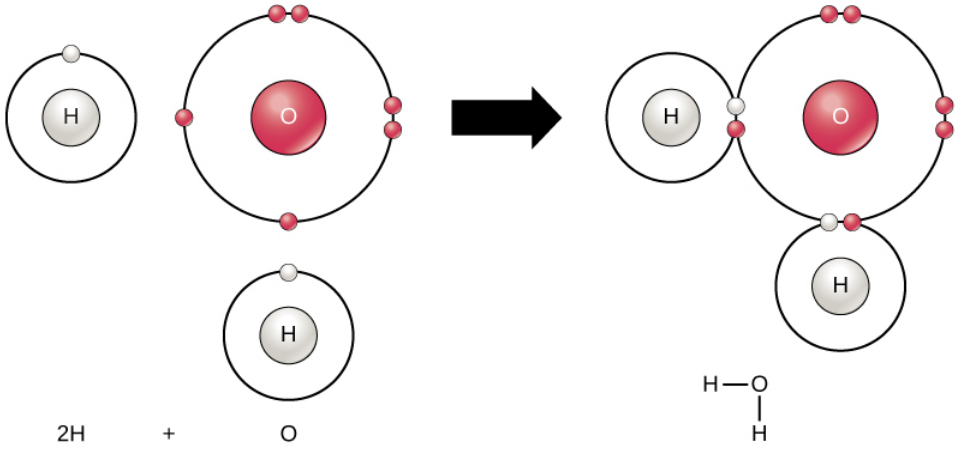
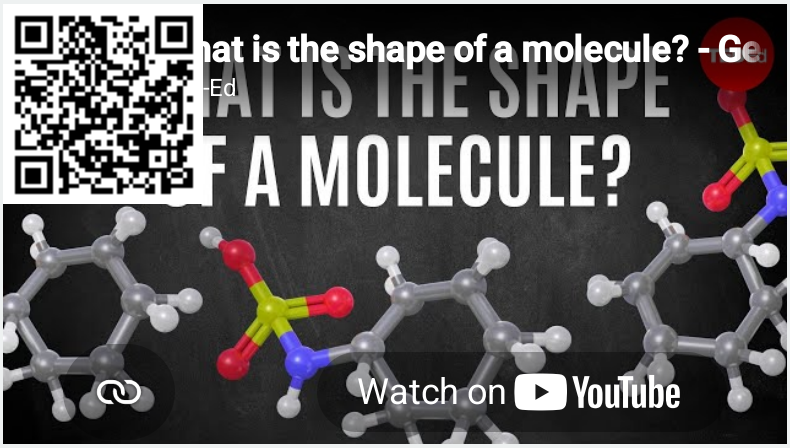


Figure 1.2.2.8: Two or more atoms may bond with each other to form a molecule. When two hydrogens and an oxygen share electrons via covalent bonds, a water molecule is formed.

Video



A molecule is nearly all empty space, apart from the extremely dense nuclei of its atoms and the clouds of electrons that bond them together. When that molecule forms, it arranges itself to maximize attraction of opposite charges and minimize repulsion of unlike (4 minutes).

Chemical reactions occur when two or more atoms bond together to form molecules or when bonded atoms are broken apart. The substances used in the beginning of a chemical reaction are called the reactants (usually found on the left side of a chemical equation), and the substances found at the end of the reaction are known as the products (usually found on the right side of a chemical equation). An arrow is typically drawn between the reactants and products to indicate the direction of the chemical reaction; this direction is not always a "one-way street." For the creation of the water molecule shown above, the chemical equation would be:

$$2\,H + O \rightarrow H_2O$$

An example of a simple chemical reaction is the breaking down of hydrogen peroxide molecules, each of which consists of two hydrogen atoms bonded to two oxygen atoms (H_2O_2). The reactant hydrogen peroxide is broken down into water, containing one oxygen atom bound to two hydrogen atoms (H_2O), and oxygen, which consists of two bonded oxygen atoms (O_2). In the equation below, the reaction includes two hydrogen peroxide molecules and two water molecules. This is an example of a balanced chemical equation, wherein the number of atoms of each element is the same on each side of the equation. According to the law of conservation of matter, the number of atoms before and after a chemical reaction should be equal, such that no atoms are, under normal circumstances, created or destroyed.

$$2\,H_2O_2\ (\text{hydrogen peroxide}) \rightarrow 2\,H_2O\ (\text{water}) + O_2\ (\text{oxygen})$$

Even though all of the reactants and products of this reaction are molecules (each atom remains bonded to at least one other atom), in this reaction only hydrogen peroxide and water are representatives of compounds: they contain atoms of more than one type of element. Molecular oxygen, on the other hand, as shown in Figure 1.2.2.9, consists of two doubly bonded oxygen atoms and is not classified as a compound but as a mononuclear molecule.

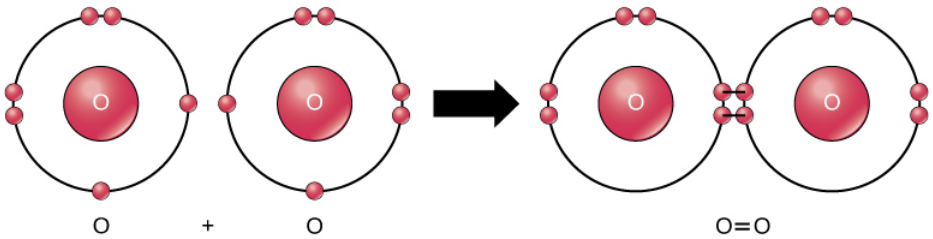


Figure 1.2.2.9: The oxygen atoms in an O_2 molecule are joined by a double bond.

Some chemical reactions, such as the one shown above, can proceed in one direction until the reactants are all used up. The equations that describe these reactions contain a unidirectional arrow and are irreversible. Reversible reactions are those that can go in either direction. In reversible reactions, reactants are turned into products, but when the concentration of product goes beyond a

certain threshold (characteristic of the particular reaction), some of these products will be converted back into reactants; at this point, the designations of products and reactants are reversed. This back and forth continues until a certain relative balance between reactants and products occurs—a state called equilibrium. These situations of reversible reactions are often denoted by a chemical equation with a double headed arrow pointing towards both the reactants and products.

For example, in human blood, excess hydrogen ions (H^+) bind to bicarbonate ions (HCO_3^-) forming an equilibrium state with carbonic acid (H_2CO_3). If carbonic acid were added to this system, some of it would be converted to bicarbonate and hydrogen ions.

$$HCO_3^- + H^+ \leftrightarrow H_2CO_3$$

In biological reactions, however, equilibrium is rarely obtained because the concentrations of the reactants or products or both are constantly changing, often with a product of one reaction being a reactant for another. To return to the example of excess hydrogen ions in the blood, the formation of carbonic acid will be the major direction of the reaction. However, the carbonic acid can also leave the body as carbon dioxide gas (via exhalation) instead of being converted back to bicarbonate ion, thus driving the reaction to the right by the chemical law known as law of mass action. These reactions are important for maintaining the homeostasis of our blood.

$$HCO_3^- + H^+ \leftrightarrow H_2CO_3 \leftrightarrow CO_2 + H_2O$$

Ions and Ionic Bonds

Some atoms are more stable when they gain or lose an electron (or possibly two) and form ions. This fills their outermost electron shell and makes them energetically more stable. Because the number of electrons does not equal the number of protons, each ion has a net charge. Cations are positive ions that are formed by losing electrons. Negative ions are formed by gaining electrons and are called anions. Anions are designated by their elemental name being altered to end in “-ide”: the anion of chlorine is called chloride, and the anion of sulfur is called sulfide, for example.

This movement of electrons from one element to another is referred to as electron transfer. As Figure 1.2.2.10 illustrates, sodium (Na) only has one electron in its outer electron shell. It takes less energy for sodium to donate that one electron than it does to accept seven more electrons to fill the outer shell. If sodium loses an electron, it now has 11 protons, 11 neutrons, and only 10 electrons, leaving it with an overall charge of +1. It is now referred to as a sodium ion. Chlorine (Cl) in its lowest energy state (called the ground state) has seven electrons in its outer shell. Again, it is more energy-efficient for chlorine to gain one electron than to lose seven. Therefore, it tends to gain an electron to create an ion with 17 protons, 17 neutrons, and 18 electrons, giving it a net negative (–1) charge. It is now referred to as a chloride ion. In this example, sodium will donate its one electron to empty its shell, and chlorine will accept that electron to fill its shell. Both ions now satisfy the octet rule and have complete outermost shells. Because the number of electrons is no longer equal to the number of protons, each is now an ion and has a +1 (sodium cation) or –1 (chloride anion) charge. Note that these transactions can normally only take place simultaneously: in order for a sodium atom to lose an electron, it must be in the presence of a suitable recipient like a chlorine atom.

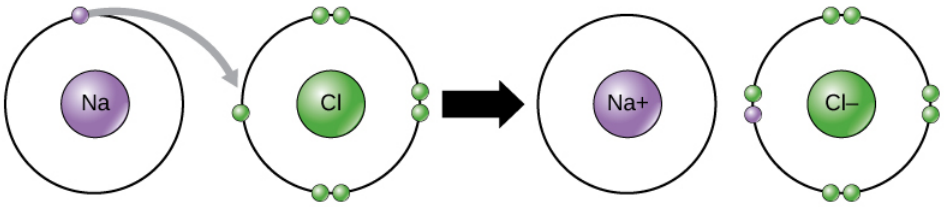


Figure 1.2.2.10: In the formation of an ionic compound, metals lose electrons and nonmetals gain electrons to achieve an octet.

Ionic bonds are formed between ions with opposite charges. For instance, positively charged sodium ions and negatively charged chloride ions bond together to make crystals of sodium chloride, or table salt, creating a crystalline molecule with zero net charge.

Certain salts are referred to in physiology as electrolytes (including sodium, potassium, and calcium), ions necessary for nerve impulse conduction, muscle contractions and water balance. Many sports drinks and dietary supplements provide these ions to replace those lost from the body via sweating during exercise.

Covalent Bonds and Other Bonds and Interactions

Another way the octet rule can be satisfied is by the sharing of electrons between atoms to form covalent bonds. These bonds are stronger and much more common than ionic bonds in the molecules of living organisms. Covalent bonds are commonly found in carbon-based organic molecules, such as our DNA and proteins. Covalent bonds are also found in inorganic molecules like H_2O, CO_2, and O_2. One, two, or three pairs of electrons may be shared, making single, double, and triple bonds, respectively. The more covalent bonds between two atoms, the stronger their connection. Thus, triple bonds are the strongest.

The strength of different levels of covalent bonding is one of the main reasons living organisms have a difficult time in acquiring nitrogen for use in constructing their molecules, even though molecular nitrogen, N_2, is the most abundant gas in the atmosphere. Molecular nitrogen consists of two nitrogen atoms triple bonded to each other and, as with all molecules, the sharing of these three pairs of electrons between the two nitrogen atoms allows for the filling of their outer electron shells, making the molecule more stable than the individual nitrogen atoms. This strong triple bond makes it difficult for living systems to break apart this nitrogen in order to use it as constituents of proteins and DNA.

The formation of water molecules provides an example of covalent bonding. The hydrogen and oxygen atoms that combine to form water molecules are bound together by covalent bonds, as shown in Figure 1.2.2.8. The electron from the hydrogen splits its time between the incomplete outer shell of the hydrogen atoms and the incomplete outer shell of the oxygen atoms. To completely fill the outer shell of oxygen, which has six electrons in its outer shell but which would be more stable with eight, two electrons (one from each hydrogen atom) are needed: hence the well-known formula H_2O. The electrons are shared between the two elements to fill the outer shell of each, making both elements more stable.

Polar Covalent Bonds

There are two types of covalent bonds: polar and nonpolar. In a polar covalent bond, shown in Figure 1.2.2.11, the electrons are unequally shared by the atoms and are attracted more to one nucleus than the other. Because of the unequal distribution of electrons between the atoms of different elements, a slightly positive (δ+) or slightly negative (δ–) charge develops. This partial charge is an important property of water and accounts for many of its characteristics.

Water is a polar molecule, with the hydrogen atoms acquiring a partial positive charge and the oxygen a partial negative charge. This occurs because the nucleus of the oxygen atom is more attractive to the electrons of the hydrogen atoms than the hydrogen nucleus is to the oxygen's electrons. Thus oxygen has a higher electronegativity than hydrogen and the shared electrons spend more time in the vicinity of the oxygen nucleus than they do near the nucleus of the hydrogen atoms, giving the atoms of oxygen and hydrogen slightly negative and positive charges, respectively. Another way of stating this is that the probability of finding a shared electron near an oxygen nucleus is more likely than finding it near a hydrogen nucleus. Either way, the atom's relative electronegativity contributes to the development of partial charges whenever one element is significantly more electronegative than the other, and the charges generated by these polar bonds may then be used for the formation of hydrogen bonds based on the attraction of opposite partial charges. (Hydrogen bonds, which are discussed in detail below, are weak bonds between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules.) Since macromolecules often have atoms within them that differ in electronegativity, polar bonds are often present in organic molecules.

Nonpolar Covalent Bonds

Nonpolar covalent bonds form between two atoms of the same element or between different elements that share electrons equally. For example, molecular oxygen (O_2) is nonpolar because the electrons will be equally distributed between the two oxygen atoms.

Another example of a nonpolar covalent bond is methane (CH_4), also shown in Figure 1.2.2.11. Carbon has four electrons in its outermost shell and needs four more to fill it. It gets these four from four hydrogen atoms, each atom providing one, making a stable outer shell of eight electrons. Carbon and hydrogen do not have the same electronegativity but are similar; thus, nonpolar bonds form. The hydrogen atoms each need one electron for their outermost shell, which is filled when it contains two electrons. These elements share the electrons equally among the carbons and the hydrogen atoms, creating a nonpolar covalent molecule.

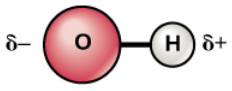
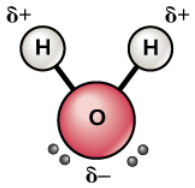
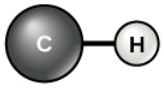
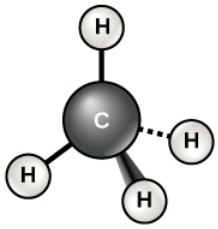
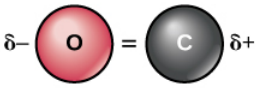
	Bond type	Molecular shape	Molecular type
Water	 Polar covalent	 Bent	Polar
Methane	 Nonpolar covalent	 Tetrahedral	Nonpolar
Carbon dioxide	 Polar covalent	 Linear	Nonpolar

Figure 1.2.2.11: Whether a molecule is polar or nonpolar depends both on bond type and molecular shape. Both water and carbon dioxide have polar covalent bonds, but carbon dioxide is linear, so the partial charges on the molecule cancel each other out.

Hydrogen Bonds and Van Der Waals Interactions

Ionic and covalent bonds between elements require energy to break. Ionic bonds are not as strong as covalent, which determines their behavior in biological systems. However, not all bonds are ionic or covalent bonds. Weaker bonds can also form between molecules. Two weak bonds that occur frequently are hydrogen bonds and van der Waals interactions. Without these two types of bonds, life as we know it would not exist. Hydrogen bonds provide many of the critical, life-sustaining properties of water and also stabilize the structures of proteins and DNA, the building block of cells.

When polar covalent bonds containing hydrogen form, the hydrogen in that bond has a slightly positive charge because hydrogen's electron is pulled more strongly toward the other element and away from the hydrogen. Because the hydrogen is slightly positive, it will be attracted to neighboring negative charges. When this happens, a weak interaction occurs between the $\delta^+$of the hydrogen from one molecule and the δ– charge on the more electronegative atoms of another molecule, usually oxygen or nitrogen, or within the same molecule. This interaction is called a hydrogen bond. This type of bond is common and occurs regularly between water molecules. Individual hydrogen bonds are weak and easily broken; however, they occur in very large numbers in water and in organic polymers, creating a major force in combination. Hydrogen bonds are also responsible for zipping together the DNA double helix.

Like hydrogen bonds, van der Waals interactions are weak attractions or interactions between molecules. Van der Waals attractions can occur between any two or more molecules and are dependent on slight fluctuations of the electron densities, which are not always symmetrical around an atom. For these attractions to happen, the molecules need to be very close to one another. These bonds—along with ionic, covalent, and hydrogen bonds—contribute to the three-dimensional structure of the proteins in our cells that is necessary for their proper function.

Career Connection: Pharmaceutical Chemist

Pharmaceutical chemists are responsible for the development of new drugs and trying to determine the mode of action of both old and new drugs. They are involved in every step of the drug development process. Drugs can be found in the natural

environment or can be synthesized in the laboratory. In many cases, potential drugs found in nature are changed chemically in the laboratory to make them safer and more effective, and sometimes synthetic versions of drugs substitute for the version found in nature.

After the initial discovery or synthesis of a drug, the chemist then develops the drug, perhaps chemically altering it, testing it to see if the drug is toxic, and then designing methods for efficient large-scale production. Then, the process of getting the drug approved for human use begins. In the United States, drug approval is handled by the Food and Drug Administration (FDA) and involves a series of large-scale experiments using human subjects to make sure the drug is not harmful and effectively treats the condition it aims to treat. This process often takes several years and requires the participation of physicians and scientists, in addition to chemists, to complete testing and gain approval.

An example of a drug that was originally discovered in a living organism is Paclitaxel (Taxol), an anti-cancer drug used to treat breast cancer. This drug was discovered in the bark of the pacific yew tree. Another example is aspirin, originally isolated from willow tree bark. Finding drugs often means testing hundreds of samples of plants, fungi, and other forms of life to see if any biologically active compounds are found within them. Sometimes, traditional medicine can give modern medicine clues to where an active compound can be found. For example, the use of willow bark to make medicine has been known for thousands of years, dating back to ancient Egypt. It was not until the late 1800s, however, that the aspirin molecule, known as acetylsalicylic acid, was purified and marketed for human use.

Occasionally, drugs developed for one use are found to have unforeseen effects that allow these drugs to be used in other, unrelated ways. For example, the drug minoxidil (Rogaine) was originally developed to treat high blood pressure. When tested on humans, it was noticed that individuals taking the drug would grow new hair. Eventually the drug was marketed to men and women with baldness to restore lost hair.

The career of the pharmaceutical chemist may involve detective work, experimentation, and drug development, all with the goal of making human beings healthier.

Summary

Matter is anything that occupies space and has mass. It is made up of elements. All of the 92 elements that occur naturally have unique qualities that allow them to combine in various ways to create molecules, which in turn combine to form cells, tissues, organ systems, and organisms. Atoms, which consist of protons, neutrons, and electrons, are the smallest units of an element that retain all of the properties of that element. Electrons can be transferred, shared, or cause charge disparities between atoms to create bonds, including ionic, covalent, and hydrogen bonds, as well as van der Waals interactions.

Glossary

anion
: negative ion that is formed by an atom gaining one or more electrons

atom
: the smallest unit of matter that retains all of the chemical properties of an element

atomic mass
: calculated mean of the mass number for an element’s isotopes

atomic number
: total number of protons in an atom

balanced chemical equation
: statement of a chemical reaction with the number of each type of atom equalized for both the products and reactants

cation
: positive ion that is formed by an atom losing one or more electrons

chemical bond
interaction between two or more of the same or different atoms that results in the formation of molecules

chemical reaction
process leading to the rearrangement of atoms in molecules

chemical reactivity
the ability to combine and to chemically bond with each other

compound
substance composed of molecules consisting of atoms of at least two different elements

covalent bond
type of strong bond formed between two of the same or different elements; forms when electrons are shared between atoms

electrolyte
ion necessary for nerve impulse conduction, muscle contractions and water balance

electron
negatively charged subatomic particle that resides outside of the nucleus in the electron orbital; lacks functional mass and has a negative charge of –1 unit

electron configuration
arrangement of electrons in an atom's electron shell (for example, $1s^2 2s^2 2p^6$)

electron orbital
how electrons are spatially distributed surrounding the nucleus; the area where an electron is most likely to be found

electron transfer
movement of electrons from one element to another; important in creation of ionic bonds

electronegativity
ability of some elements to attract electrons (often of hydrogen atoms), acquiring partial negative charges in molecules and creating partial positive charges on the hydrogen atoms

element
one of 118 unique substances that cannot be broken down into smaller substances; each element has unique properties and a specified number of protons

equilibrium
steady state of relative reactant and product concentration in reversible chemical reactions in a closed system

hydrogen bond
weak bond between slightly positively charged hydrogen atoms to slightly negatively charged atoms in other molecules

inert gas
(also, noble gas) element with filled outer electron shell that is unreactive with other atoms

ion
atom or chemical group that does not contain equal numbers of protons and electrons

ionic bond
chemical bond that forms between ions with opposite charges (cations and anions)

irreversible chemical reaction
chemical reaction where reactants proceed uni-directionally to form products

isotope
one or more forms of an element that have different numbers of neutrons

law of mass action
chemical law stating that the rate of a reaction is proportional to the concentration of the reacting substances

mass number
total number of protons and neutrons in an atom

matter
anything that has mass and occupies space

molecule
two or more atoms chemically bonded together

neutron
uncharged particle that resides in the nucleus of an atom; has a mass of one amu

noble gas
see inert gas

nonpolar covalent bond
type of covalent bond that forms between atoms when electrons are shared equally between them

nucleus
core of an atom; contains protons and neutrons

octet rule
rule that atoms are most stable when they hold eight electrons in their outermost shells

orbital
region surrounding the nucleus; contains electrons

periodic table
organizational chart of elements indicating the atomic number and atomic mass of each element; provides key information about the properties of the elements

polar covalent bond
type of covalent bond that forms as a result of unequal sharing of electrons, resulting in the creation of slightly positive and slightly negative charged regions of the molecule

product
molecule found on the right side of a chemical equation

proton
positively charged particle that resides in the nucleus of an atom; has a mass of one amu and a charge of +1

radioisotope
isotope that emits radiation composed of subatomic particles to form more stable elements

reactant

molecule found on the left side of a chemical equation

reversible chemical reaction

chemical reaction that functions bi-directionally, where products may turn into reactants if their concentration is great enough

valence shell

outermost shell of an atom

van der Waals interaction

very weak interaction between molecules due to temporary charges attracting atoms that are very close together

---

This page titled 1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **2.1: Atoms, Isotopes, Ions, and Molecules - The Building Blocks** by OpenStax is licensed CC BY 4.0.

1.2.3: Water

Learning Objectives

- Describe the properties of water that are critical to maintaining life
- Explain why water is an excellent solvent
- Provide examples of water's cohesive and adhesive properties
- Discuss the role of acids, bases, and buffers in homeostasis

Why do scientists spend time looking for water on other planets? Why is water so important? It is because water is essential to life as we know it. Water is one of the more abundant molecules and the one most critical to life on Earth. Approximately 60–70 percent of the human body is made up of water. Without it, life as we know it simply would not exist.

Properties of Water

The polarity of the water molecule and its resulting hydrogen bonding make water a unique substance with special properties that are intimately tied to the processes of life. Life originally evolved in a watery environment, and most of an organism's cellular chemistry and metabolism occur inside the watery contents of the cell's cytoplasm. Special properties of water are its high heat capacity and heat of vaporization, its ability to dissolve polar molecules, its cohesive and adhesive properties, and its dissociation into ions that leads to the generation of pH. Understanding these characteristics of water helps to elucidate its importance in maintaining life.

Video



This four minute animation describes the properties of water that support life. These properties include solvency, cohesion and adhesion, high surface temperature, high heat capacity, high heat of vaporization, and varying density.

Water's Polarity

One of water's important properties is that it is composed of polar molecules: the hydrogen and oxygen within water molecules (H_2O) form polar covalent bonds. While there is no net charge to a water molecule, the polarity of water creates a slightly positive charge on hydrogen and a slightly negative charge on oxygen, contributing to water's properties of attraction. Water's charges are generated because oxygen is more electronegative than hydrogen, making it more likely that a shared electron would be found near the oxygen nucleus than the hydrogen nucleus, thus generating the partial negative charge near the oxygen.

As a result of water's polarity, each water molecule attracts other water molecules because of the opposite charges between water molecules, forming hydrogen bonds. Water also attracts or is attracted to other polar molecules and ions. A polar substance that interacts readily with or dissolves in water is referred to as hydrophilic (hydro- = "water"; -philic = "loving"). In contrast, non-polar molecules such as oils and fats do not interact well with water, as shown in Figure 1.2.3.1 and separate from it rather than

dissolve in it, as we see in salad dressings containing oil and vinegar (an acidic water solution). These nonpolar compounds are called hydrophobic (hydro- = “water”; -phobic = “fearing”).

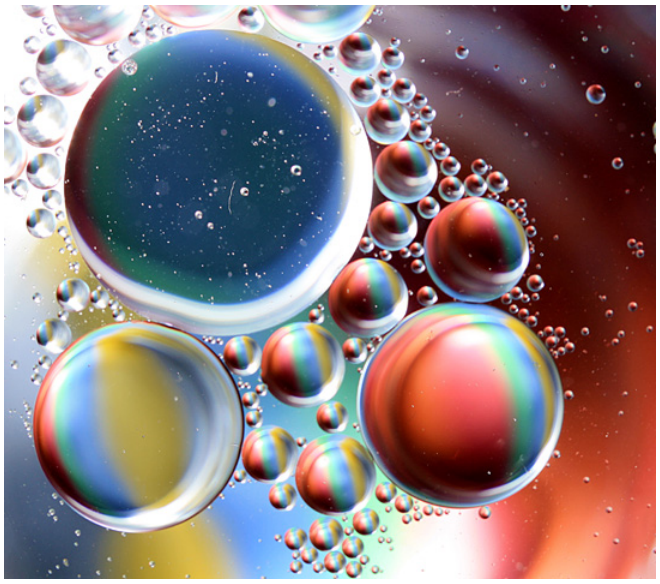


Figure 1.2.3.1: Oil and water do not mix. As this macro image of oil and water shows, oil does not dissolve in water but forms droplets instead. This is due to it being a nonpolar compound. (credit: Gautam Dogra).

Video



In this 5-minute video, you will discover that salt dissolves in water; oil does not. But why?

Water’s States: Gas, Liquid, and Solid

The formation of hydrogen bonds is an important quality of the liquid water that is crucial to life as we know it. As water molecules make hydrogen bonds with each other, water takes on some unique chemical characteristics compared to other liquids and, since living things have a high water content, understanding these chemical features is key to understanding life. In liquid water, hydrogen bonds are constantly formed and broken as the water molecules slide past each other. The breaking of these bonds is caused by the motion (kinetic energy) of the water molecules due to the heat contained in the system. When the heat is raised as water is boiled, the higher kinetic energy of the water molecules causes the hydrogen bonds to break completely and allows water molecules to escape into the air as gas (steam or water vapor). On the other hand, when the temperature of water is reduced and water freezes, the water molecules form a crystalline structure maintained by hydrogen bonding (there is not enough energy to break the hydrogen bonds) that makes ice less dense than liquid water, a phenomenon not seen in the solidification of other liquids.

Water’s lower density in its solid form is due to the way hydrogen bonds are oriented as it freezes: the water molecules are pushed farther apart compared to liquid water. With most other liquids, solidification when the temperature drops includes the lowering of

kinetic energy between molecules, allowing them to pack even more tightly than in liquid form and giving the solid a greater density than the liquid.

The lower density of ice, illustrated and pictured in Figure 1.2.3.2, an anomaly, causes it to float at the surface of liquid water, such as in an iceberg or in the ice cubes in a glass of ice water. In lakes and ponds, ice will form on the surface of the water creating an insulating barrier that protects the animals and plant life in the pond from freezing. Without this layer of insulating ice, plants and animals living in the pond would freeze in the solid block of ice and could not survive. The detrimental effect of freezing on living organisms is caused by the expansion of ice relative to liquid water. The ice crystals that form upon freezing rupture the delicate membranes essential for the function of living cells, irreversibly damaging them. Cells can only survive freezing if the water in them is temporarily replaced by another liquid like glycerol.

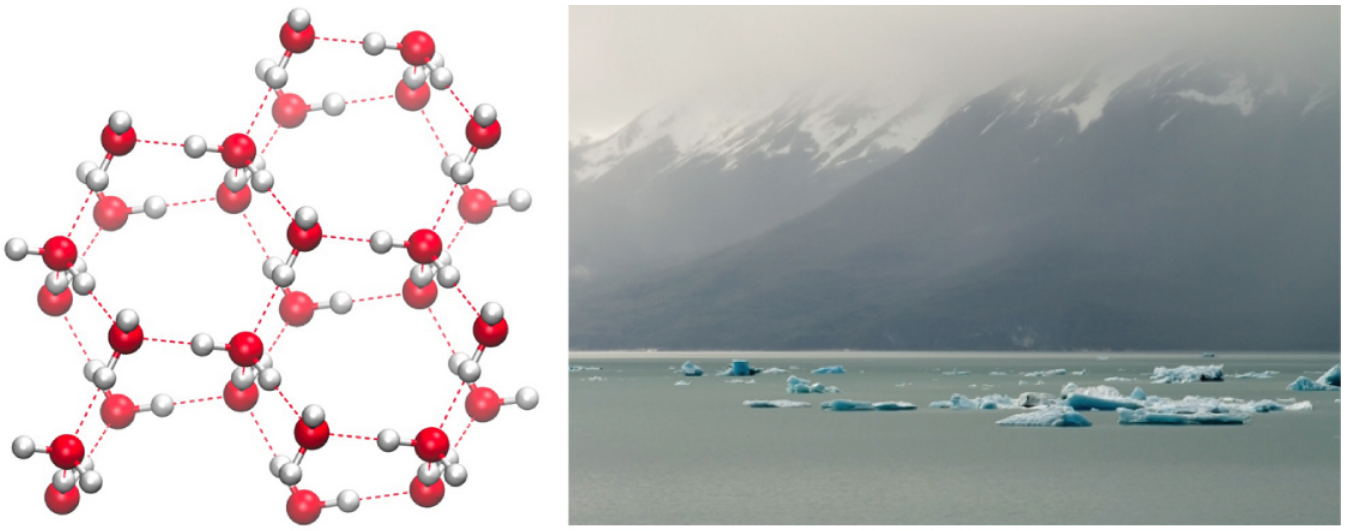


Figure 1.2.3.2: Hydrogen bonding makes ice less dense than liquid water. The (a) lattice structure of ice makes it less dense than the freely flowing molecules of liquid water, enabling it to (b) float on water. (credit a: modification of work by Jane Whitney, image created using Visual Molecular Dynamics (VMD) software[1]; credit b: modification of work by Carlos Ponte)

Water's High Heat Capacity

Water's high heat capacity is a property caused by hydrogen bonding among water molecules. Water has the highest specific heat capacity of any liquids. Specific heat is defined as the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius. For water, this amount is one calorie. It therefore takes water a long time to heat and long time to cool. In fact, the specific heat capacity of water is about five times more than that of sand. This explains why the land cools faster than the sea. Due to its high heat capacity, water is used by warm blooded animals to more evenly disperse heat in their bodies: it acts in a similar manner to a car's cooling system, transporting heat from warm places to cool places, causing the body to maintain a more even temperature.

Water's Heat of Vaporization

Water also has a high heat of vaporization, the amount of energy required to change one gram of a liquid substance to a gas. A considerable amount of heat energy (586 cal) is required to accomplish this change in water. This process occurs on the surface of water. As liquid water heats up, hydrogen bonding makes it difficult to separate the liquid water molecules from each other, which is required for it to enter its gaseous phase (steam). As a result, water acts as a heat sink or heat reservoir and requires much more heat to boil than does a liquid such as ethanol (grain alcohol), whose hydrogen bonding with other ethanol molecules is weaker than water's hydrogen bonding. Eventually, as water reaches its boiling point of 100° Celsius (212° Fahrenheit), the heat is able to break the hydrogen bonds between the water molecules, and the kinetic energy (motion) between the water molecules allows them to escape from the liquid as a gas. Even when below its boiling point, water's individual molecules acquire enough energy from other water molecules such that some surface water molecules can escape and vaporize: this process is known as evaporation.

The fact that hydrogen bonds need to be broken for water to evaporate means that a substantial amount of energy is used in the process. As the water evaporates, energy is taken up by the process, cooling the environment where the evaporation is taking place.

In many living organisms, including in humans, the evaporation of sweat, which is 90 percent water, allows the organism to cool so that homeostasis of body temperature can be maintained.

Water's Solvent Properties

Since water is a polar molecule with slightly positive and slightly negative charges, ions and polar molecules can readily dissolve in it. Therefore, water is referred to as a solvent, a substance capable of dissolving other polar molecules and ionic compounds. The charges associated with these molecules will form hydrogen bonds with water, surrounding the particle with water molecules. This is referred to as a sphere of hydration, or a hydration shell, as illustrated in Figure 1.2.3.3 and serves to keep the particles separated or dispersed in the water.

When ionic compounds are added to water, the individual ions react with the polar regions of the water molecules and their ionic bonds are disrupted in the process of dissociation. Dissociation occurs when atoms or groups of atoms break off from molecules and form ions. Consider table salt (NaCl, or sodium chloride): when NaCl crystals are added to water, the molecules of NaCl dissociate into Na^+ and Cl^- ions, and spheres of hydration form around the ions, illustrated in Figure 1.2.3.3. The positively charged sodium ion is surrounded by the partially negative charge of the water molecule's oxygen. The negatively charged chloride ion is surrounded by the partially positive charge of the hydrogen on the water molecule.

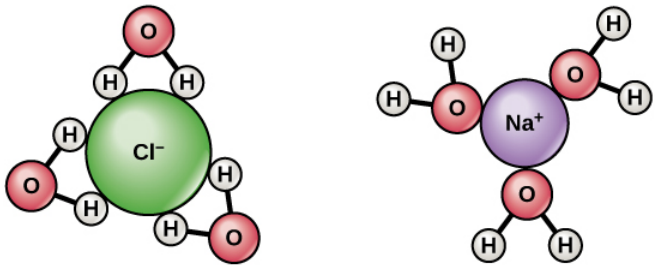


Figure 1.2.3.3: When table salt (NaCl) is mixed in water, spheres of hydration are formed around the ions.

Video



In this 2-minute video, learn the definitions of solutes and solvents and why solutions are so important to life.

Water's Cohesive and Adhesive Properties

Have you ever filled a glass of water to the very top and then slowly added a few more drops? Before it overflows, the water forms a dome-like shape above the rim of the glass. This water can stay above the glass because of the property of cohesion. In cohesion, water molecules are attracted to each other (because of hydrogen bonding), keeping the molecules together at the liquid-gas (water-air) interface, although there is no more room in the glass.

Cohesion allows for the development of surface tension, the capacity of a substance to withstand being ruptured when placed under tension or stress. This is also why water forms droplets when placed on a dry surface rather than being flattened out by gravity. When a small scrap of paper is placed onto the droplet of water, the paper floats on top of the water droplet even though paper is

denser (heavier) than the water. Cohesion and surface tension keep the hydrogen bonds of water molecules intact and support the item floating on the top. It's even possible to "float" a needle on top of a glass of water if it is placed gently without breaking the surface tension, as shown in Figure 1.2.3.4.



Figure 1.2.3.4: The weight of the needle is pulling the surface downward; at the same time, the surface tension is pulling it up, suspending it on the surface of the water and keeping it from sinking. Notice the indentation in the water around the needle. (credit: Cory Zanker)

These cohesive forces are related to water's property of adhesion, or the attraction between water molecules and other molecules. This attraction is sometimes stronger than water's cohesive forces, especially when the water is exposed to charged surfaces such as those found on the inside of thin glass tubes known as capillary tubes. Adhesion is observed when water "climbs" up the tube placed in a glass of water: notice that the water appears to be higher on the sides of the tube than in the middle. This is because the water molecules are attracted to the charged glass walls of the capillary more than they are to each other and therefore adhere to it. This type of adhesion is called capillary action, and is illustrated in Figure 1.2.3.5.

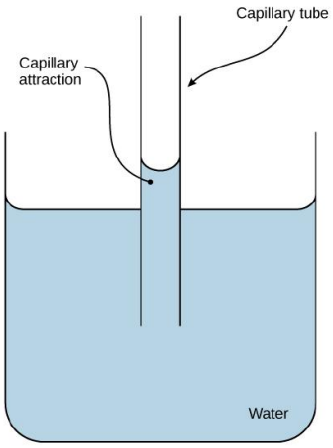


Figure 1.2.3.5: Capillary action in a glass tube is caused by the adhesive forces exerted by the internal surface of the glass exceeding the cohesive forces between the water molecules themselves. (credit: modification of work by Pearson-Scott Foresman, donated to the Wikimedia Foundation)

Why are cohesive and adhesive forces important for life? Cohesive and adhesive forces are important for the transport of water from the roots to the leaves in plants. These forces create a "pull" on the water column. This pull results from the tendency of water molecules being evaporated on the surface of the plant to stay connected to water molecules below them, and so they are pulled along. Plants use this natural phenomenon to help transport water from their roots to their leaves. Without these properties of water, plants would be unable to receive the water and the dissolved minerals they require. In another example, insects such as the water strider, shown in Figure 1.2.3.6, use the surface tension of water to stay afloat on the surface layer of water and even mate there.

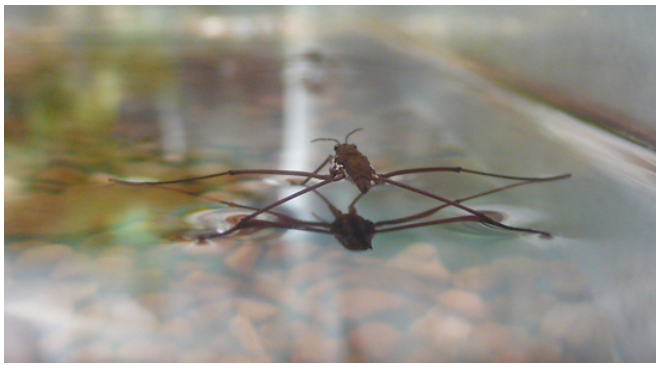


Figure 1.2.3.6: Water's cohesive and adhesive properties allow this water strider (*Gerris* sp.) to stay afloat. (credit: Tim Vickers)

pH, Buffers, Acids, and Bases

Video



This 2-minute video covers a quick explanation of what defines an acid and a base, and how this relates to the pH scale.

The pH of a solution indicates its acidity or alkalinity.

$$H_2O(I) \rightleftharpoons H^+(aq) + O^-(aq)$$

litmus or pH paper, filter paper that has been treated with a natural water-soluble dye so it can be used as a pH indicator, to test how much acid (acidity) or base (alkalinity) exists in a solution. You might have even used some to test whether the water in a swimming pool is properly treated. In both cases, the pH test measures the concentration of hydrogen ions in a given solution.

Hydrogen ions are spontaneously generated in pure water by the dissociation (ionization) of a small percentage of water molecules into equal numbers of hydrogen (H^+) ions and hydroxide (OH^-) ions. While the hydroxide ions are kept in solution by their hydrogen bonding with other water molecules, the hydrogen ions, consisting of naked protons, are immediately attracted to un-ionized water molecules, forming hydronium ions (H_30^+). Still, by convention, scientists refer to hydrogen ions and their concentration as if they were free in this state in liquid water.

The concentration of hydrogen ions dissociating from pure water is 1×10^{-7} moles H^+ ions per liter of water. Moles (mol) are a way to express the amount of a substance (which can be atoms, molecules, ions, etc), with one mole being equal to 6.02×10^{23} particles of the substance. Therefore, 1 mole of water is equal to 6.02×10^{23} water molecules. The pH is calculated as the negative of the base 10 logarithm of this concentration. The log10 of 1×10^{-7} is -7.0, and the negative of this number (indicated by the "p" of "pH") yields a pH of 7.0, which is also known as neutral pH. The pH inside of human cells and blood are examples of two areas of the body where near-neutral pH is maintained.

Video



In this 4-minute video, you will learn that while vinegar may have a powerful smell, it's actually a weak acid? In the chemical economy, acids actively give away their protons while bases actively collect them -- but some more aggressively than others.

Non-neutral pH readings result from dissolving acids or bases in water. Using the negative logarithm to generate positive integers, high concentrations of hydrogen ions yield a low pH number, whereas low levels of hydrogen ions result in a high pH. An acid is a substance that increases the concentration of hydrogen ions (H^+) in a solution, usually by having one of its hydrogen atoms dissociate. A base provides either hydroxide ions (OH^-) or other negatively charged ions that combine with hydrogen ions, reducing their concentration in the solution and thereby raising the pH. In cases where the base releases hydroxide ions, these ions bind to free hydrogen ions, generating new water molecules.

The stronger the acid, the more readily it donates H^+. For example, hydrochloric acid (HCl) completely dissociates into hydrogen and chloride ions and is highly acidic, whereas the acids in tomato juice or vinegar do not completely dissociate and are considered weak acids. Conversely, strong bases are those substances that readily donate OH^- or take up hydrogen ions. Sodium hydroxide (NaOH) and many household cleaners are highly alkaline and give up OH^- rapidly when placed in water, thereby raising the pH. An example of a weak basic solution is seawater, which has a pH near 8.0, close enough to neutral pH that marine organisms adapted to this saline environment are able to thrive in it.

The pH scale is, as previously mentioned, an inverse logarithm and ranges from 0 to 14 (Figure 1.2.3.7). Anything below 7.0 (ranging from 0.0 to 6.9) is acidic, and anything above 7.0 (from 7.1 to 14.0) is alkaline. Extremes in pH in either direction from 7.0 are usually considered inhospitable to life. The pH inside cells (6.8) and the pH in the blood (7.4) are both very close to neutral. However, the environment in the stomach is highly acidic, with a pH of 1 to 2. So how do the cells of the stomach survive in such an acidic environment? How do they homeostatically maintain the near-neutral pH inside them? The answer is that they cannot do it and are constantly dying. New stomach cells are constantly produced to replace dead ones, which are digested by the stomach acids. It is estimated that the lining of the human stomach is completely replaced every seven to ten days.

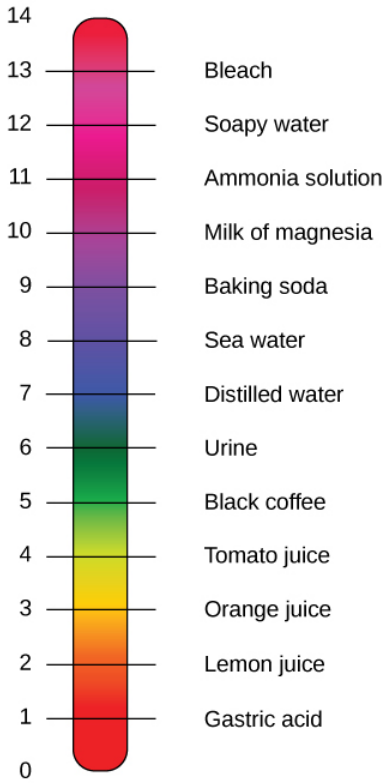


Figure 1.2.3.7: The pH scale measures the concentration of hydrogen ions (H^+) in a solution. (credit: modification of work by Edward Stevens)

So how can organisms whose bodies require a near-neutral pH ingest acidic and basic substances (a human drinking orange juice, for example) and survive? Buffers are the key. Buffers readily absorb excess H^+ or OH^-, keeping the pH of the body carefully maintained in the narrow range required for survival. Maintaining a constant blood pH is critical to a person's well-being. The buffer maintaining the pH of human blood involves carbonic acid (H_2CO_3), bicarbonate ion (HCO_3^-), and carbon dioxide (CO_2). When bicarbonate ions combine with free hydrogen ions and become carbonic acid, hydrogen ions are removed, moderating pH changes. Similarly, as shown in Figure 1.2.3.8, excess carbonic acid can be converted to carbon dioxide gas and exhaled through the lungs. This prevents too many free hydrogen ions from building up in the blood and dangerously reducing the blood's pH. Likewise, if too much OH^- is introduced into the system, carbonic acid will combine with it to create bicarbonate, lowering the pH. Without this buffer system, the body's pH would fluctuate enough to put survival in jeopardy.

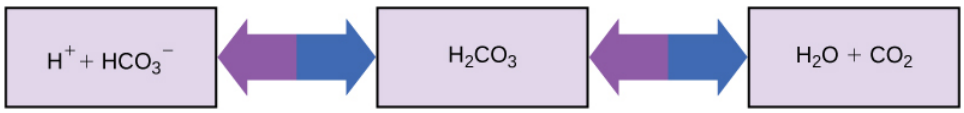
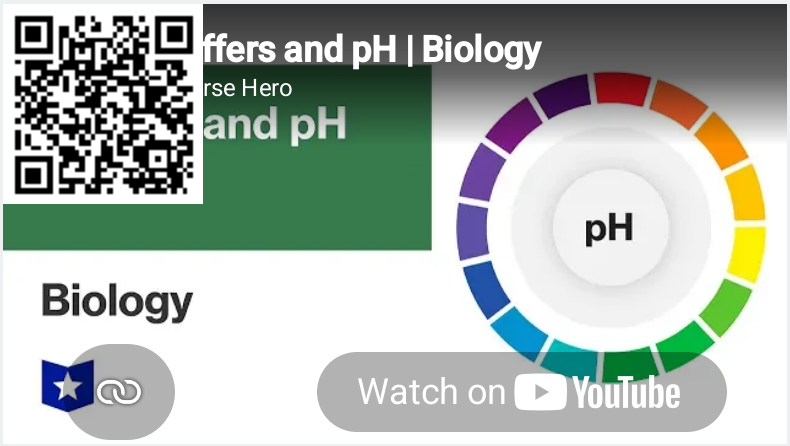


Figure 1.2.3.8: This diagram shows the body's buffering of blood pH levels. The blue arrows show the process of raising pH as more CO_2 is made. The purple arrows indicate the reverse process: the lowering of pH as more bicarbonate is created.

Other examples of buffers are antacids used to combat excess stomach acid. Many of these over-the-counter medications work in the same way as blood buffers, usually with at least one ion capable of absorbing hydrogen and moderating pH, bringing relief to those that suffer "heartburn" after eating. The unique properties of water that contribute to this capacity to balance pH—as well as water's other characteristics—are essential to sustaining life on Earth.

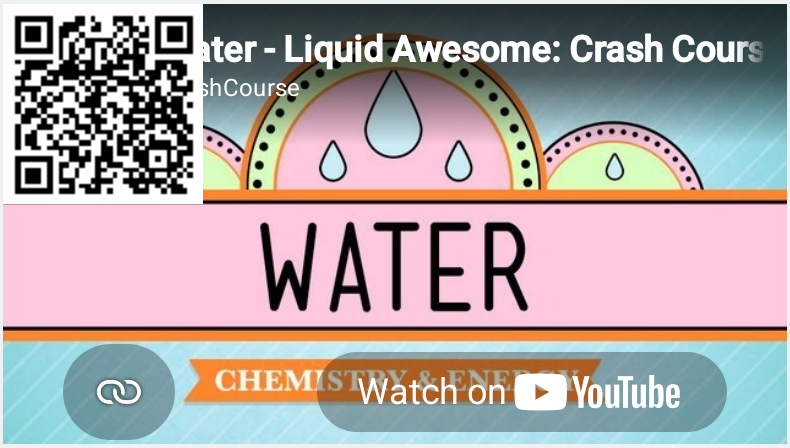
Video



Learn all about buffers and pH in just 3.5 minutes.

Summary

Video



In this 11-minute video, Hank teaches us why water is one of the most fascinating and important substances in the universe.

Water has many properties that are critical to maintaining life. It is a polar molecule, allowing for the formation of hydrogen bonds. Hydrogen bonds allow ions and other polar molecules to dissolve in water. Therefore, water is an excellent solvent. The hydrogen bonds between water molecules cause the water to have a high heat capacity, meaning it takes a lot of added heat to raise its temperature. As the temperature rises, the hydrogen bonds between water continually break and form anew. This allows for the overall temperature to remain stable, although energy is added to the system. Water also exhibits a high heat of vaporization, which is key to how organisms cool themselves by the evaporation of sweat. Water's cohesive forces allow for the property of surface tension, whereas its adhesive properties are seen as water rises inside capillary tubes. The pH value is a measure of hydrogen ion concentration in a solution and is one of many chemical characteristics that is highly regulated in living organisms through homeostasis. Acids and bases can change pH values, but buffers tend to moderate the changes they cause. These properties of water are intimately connected to the biochemical and physical processes performed by living organisms, and life would be very different if these properties were altered, if it could exist at all.

Footnotes

1. 1 W. Humphrey W., A. Dalke, and K. Schulten, "VMD—Visual Molecular Dynamics," *Journal of Molecular Graphics* 14 (1996): 33-38.

2. 2 W. Humphrey W., A. Dalke, and K. Schulten, “VMD—Visual Molecular Dynamics,” *Journal of Molecular Graphics* 14 (1996): 33-38.

Glossary

acid
molecule that donates hydrogen ions and increases the concentration of hydrogen ions in a solution

adhesion
attraction between water molecules and other molecules

base
molecule that donates hydroxide ions or otherwise binds excess hydrogen ions and decreases the concentration of hydrogen ions in a solution

buffer
substance that prevents a change in pH by absorbing or releasing hydrogen or hydroxide ions

calorie
amount of heat required to change the temperature of one gram of water by one degree Celsius

capillary action
occurs because water molecules are attracted to charges on the inner surfaces of narrow tubular structures such as glass tubes, drawing the water molecules to the sides of the tubes

cohesion
intermolecular forces between water molecules caused by the polar nature of water; responsible for surface tension

dissociation
release of an ion from a molecule such that the original molecule now consists of an ion and the charged remains of the original, such as when water dissociates into H^+ and OH^-

evaporation
separation of individual molecules from the surface of a body of water, leaves of a plant, or the skin of an organism

heat of vaporization of water
high amount of energy required for liquid water to turn into water vapor

hydrophilic
describes ions or polar molecules that interact well with other polar molecules such as water

hydrophobic
describes uncharged non-polar molecules that do not interact well with polar molecules such as water

litmus paper
(also, pH paper) filter paper that has been treated with a natural water-soluble dye that changes its color as the pH of the environment changes so it can be used as a pH indicator

pH paper
see litmus paper

pH scale
scale ranging from zero to 14 that is inversely proportional to the concentration of hydrogen ions in a solution

solvent

substance capable of dissolving another substance

specific heat capacity

the amount of heat one gram of a substance must absorb or lose to change its temperature by one degree Celsius

sphere of hydration

when a polar water molecule surrounds charged or polar molecules thus keeping them dissolved and in solution

surface tension

tension at the surface of a body of liquid that prevents the molecules from separating; created by the attractive cohesive forces between the molecules of the liquid

---

This page titled 1.2.3: Water is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **2.2: Water** by OpenStax is licensed CC BY 4.0.

1.2.4: Carbon

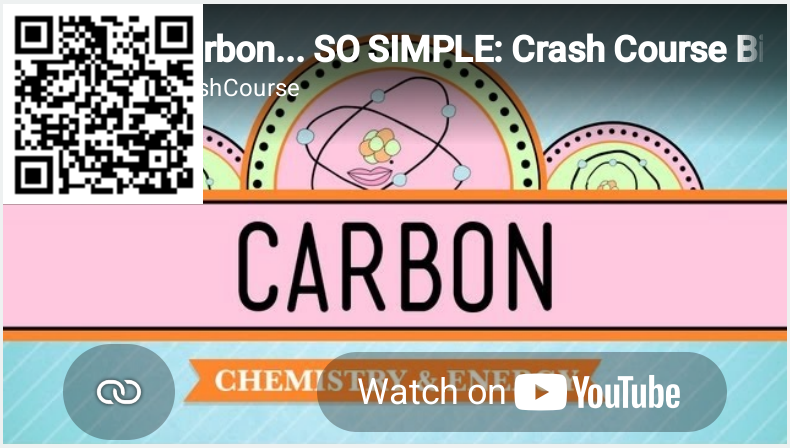
Skills to Develop

- Explain why carbon is important for life
- Describe the role of functional groups in biological molecules

Cells are made of many complex molecules called macromolecules, such as proteins, nucleic acids (RNA and DNA), carbohydrates, and lipids. The macromolecules are a subset of organic molecules (any carbon-containing liquid, solid, or gas) that are especially important for life. The fundamental component for all of these macromolecules is carbon. The carbon atom has unique properties that allow it to form covalent bonds to as many as four different atoms, making this versatile element ideal to serve as the basic structural component, or "backbone," of the macromolecules.

Individual carbon atoms have an incomplete outermost electron shell. With an atomic number of 6 (six electrons and six protons), the first two electrons fill the inner shell, leaving four in the second shell. Therefore, carbon atoms can form up to four covalent bonds with other atoms to satisfy the octet rule. The methane molecule provides an example: it has the chemical formula CH_4. Each of its four hydrogen atoms forms a single covalent bond with the carbon atom by sharing a pair of electrons. This results in a filled outermost shell.

Video



In this 11-minute video, Hank describes the importance of carbon and a bit of chemistry review.

Hydrocarbons

Hydrocarbons are organic molecules consisting entirely of carbon and hydrogen, such as methane (CH_4) described above. We often use hydrocarbons in our daily lives as fuels—like the propane in a gas grill or the butane in a lighter. The many covalent bonds between the atoms in hydrocarbons store a great amount of energy, which is released when these molecules are burned (oxidized). Methane, an excellent fuel, is the simplest hydrocarbon molecule, with a central carbon atom bonded to four different hydrogen atoms, as illustrated in Figure 1.2.4.1. The geometry of the methane molecule, where the atoms reside in three dimensions, is determined by the shape of its electron orbitals. The carbons and the four hydrogen atoms form a shape known as a tetrahedron, with four triangular faces; for this reason, methane is described as having tetrahedral geometry.

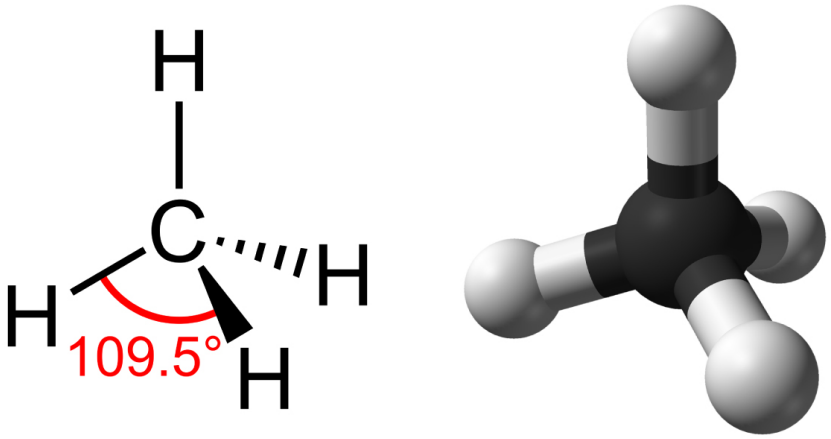


Figure 1.2.4.1: Methane has a tetrahedral geometry, with each of the four hydrogen atoms spaced 109.5° apart.

As the backbone of the large molecules of living things, hydrocarbons may exist as linear carbon chains, carbon rings, or combinations of both. Furthermore, individual carbon-to-carbon bonds may be single, double, or triple covalent bonds, and each type of bond affects the geometry of the molecule in a specific way. This three-dimensional shape or conformation of the large molecules of life (macromolecules) is critical to how they function.

Hydrocarbon Chains

Hydrocarbon chains are formed by successive bonds between carbon atoms and may be branched or unbranched. Furthermore, the overall geometry of the molecule is altered by the different geometries of single, double, and triple covalent bonds, illustrated in Figure 1.2.4.2. The hydrocarbons ethane, ethene, and ethyne serve as examples of how different carbon-to-carbon bonds affect the geometry of the molecule. The names of all three molecules start with the prefix “eth-,” which is the prefix for two carbon hydrocarbons. The suffixes “-ane,” “-ene,” and “-yne” refer to the presence of single, double, or triple carbon-carbon bonds, respectively. Thus, propane, propene, and propyne follow the same pattern with three carbon molecules, butane, butane, and butyne for four carbon molecules, and so on. Double and triple bonds change the geometry of the molecule: single bonds allow rotation along the axis of the bond, whereas double bonds lead to a planar configuration and triple bonds to a linear one. These geometries have a significant impact on the shape a particular molecule can assume.

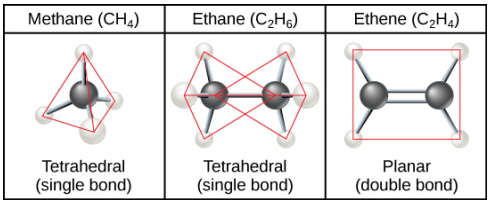


Figure 1.2.4.2: When carbon forms single bonds with other atoms, the shape is tetrahedral. When two carbon atoms form a double bond, the shape is planar, or flat. Single bonds, like those found in ethane, are able to rotate. Double bonds, like those found in ethene cannot rotate, so the atoms on either side are locked in place.

Hydrocarbon Rings

So far, the hydrocarbons we have discussed have been aliphatic hydrocarbons, which consist of linear chains of carbon atoms. Another type of hydrocarbon, aromatic hydrocarbons, consists of closed rings of carbon atoms. Ring structures are found in hydrocarbons, sometimes with the presence of double bonds, which can be seen by comparing the structure of cyclohexane to benzene in Figure 1.2.4.3. Examples of biological molecules that incorporate the benzene ring include some amino acids and cholesterol and its derivatives, including the hormones estrogen and testosterone. The benzene ring is also found in the herbicide 2,4-D. Benzene is a natural component of crude oil and has been classified as a carcinogen. Some hydrocarbons have both aliphatic and aromatic portions; beta-carotene is an example of such a hydrocarbon.

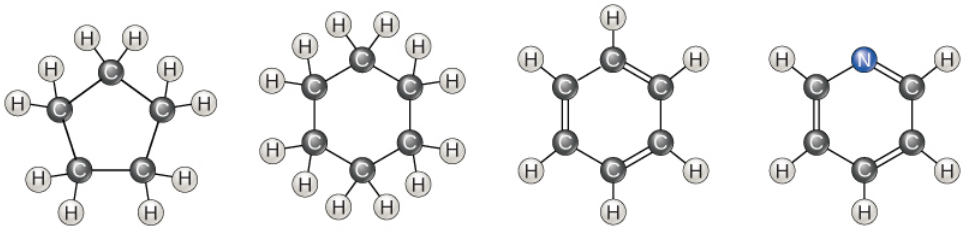


Figure 1.2.4.3: Carbon can form five-and six membered rings. Single or double bonds may connect the carbons in the ring, and nitrogen may be substituted for carbon.

Isomers

The three-dimensional placement of atoms and chemical bonds within organic molecules is central to understanding their chemistry. Molecules that share the same chemical formula but differ in the placement (structure) of their atoms and/or chemical bonds are known as isomers. Structural isomers (like butane and isobutene shown in Figure 1.2.4.4a differ in the placement of their covalent bonds: both molecules have four carbons and ten hydrogens (C_4H_{10}), but the different arrangement of the atoms within the molecules leads to differences in their chemical properties. For example, due to their different chemical properties, butane is suited for use as a fuel for cigarette lighters and torches, whereas isobutene is suited for use as a refrigerant and a propellant in spray cans.

Geometric isomers, on the other hand, have similar placements of their covalent bonds but differ in how these bonds are made to the surrounding atoms, especially in carbon-to-carbon double bonds. In the simple molecule butene (C_4H_8), the two methyl groups (CH_3) can be on either side of the double covalent bond central to the molecule, as illustrated in Figure 1.2.4.4b. When the carbons are bound on the same side of the double bond, this is the *cis* configuration; if they are on opposite sides of the double bond, it is a *trans* configuration. In the *trans* configuration, the carbons form a more or less linear structure, whereas the carbons in the *cis* configuration make a bend (change in direction) of the carbon backbone.

Art Connection

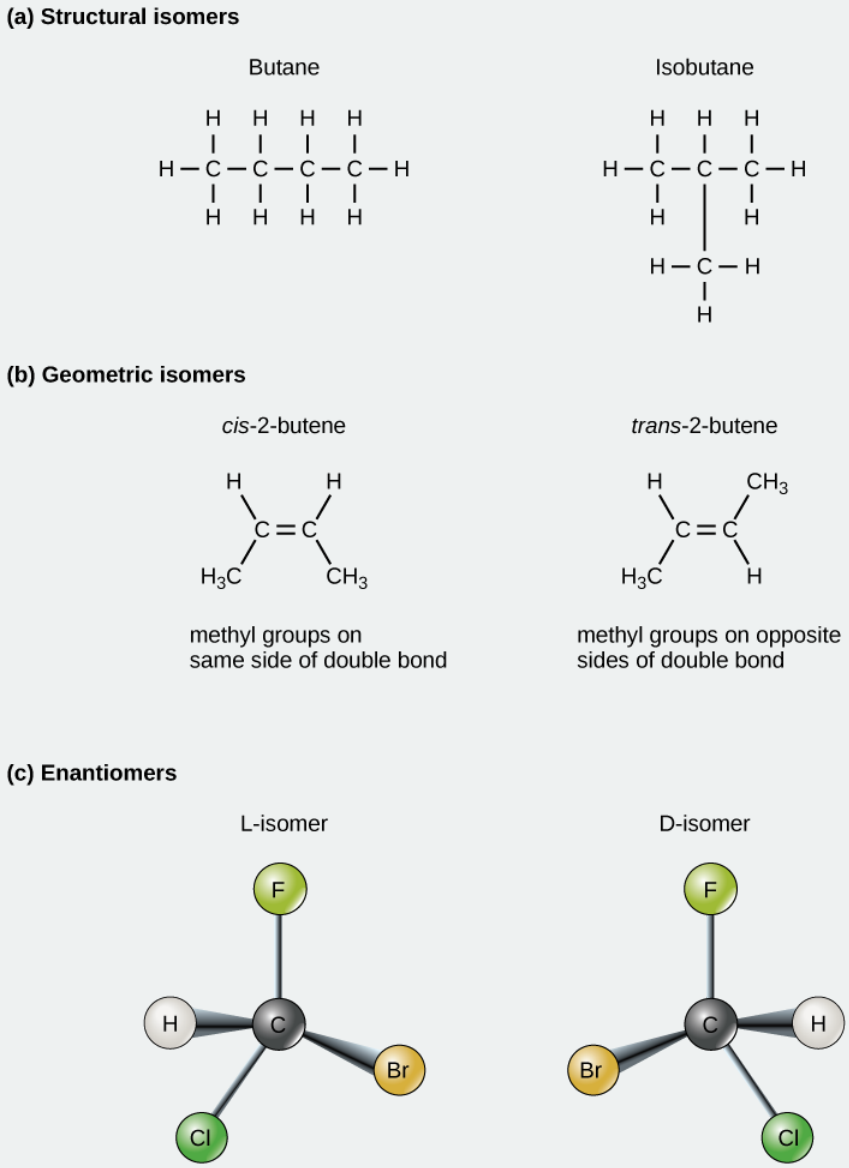


Figure 1.2.4.4: Molecules that have the same number and type of atoms arranged differently are called isomers. (a) Structural isomers have a different covalent arrangement of atoms. (b) Geometric isomers have a different arrangement of atoms around a double bond. (c) Enantiomers are mirror images of each other.

Figure 1.2.4.4: Which of the following statements is false?

A. Molecules with the formulas CH_3CH_2COOH and $C_3H_6O_2$ could be structural isomers.
B. Molecules must have a double bond to be *cis-trans* isomers.
C. To be enantiomers, a molecule must have at least three different atoms or groups connected to a central carbon.
D. To be enantiomers, a molecule must have at least four different atoms or groups connected to a central carbon.

Answer

C

In triglycerides (fats and oils), long carbon chains known as fatty acids may contain double bonds, which can be in either the *cis* or *trans* configuration, illustrated in Figure 1.2.4.5. Fats with at least one double bond between carbon atoms are unsaturated fats. When some of these bonds are in the *cis* configuration, the resulting bend in the carbon backbone of the chain means that triglyceride molecules cannot pack tightly, so they remain liquid (oil) at room temperature. On the other hand, triglycerides with

trans double bonds (popularly called trans fats), have relatively linear fatty acids that are able to pack tightly together at room temperature and form solid fats. In the human diet, trans fats are linked to an increased risk of cardiovascular disease, so many food manufacturers have reduced or eliminated their use in recent years. In contrast to unsaturated fats, triglycerides without double bonds between carbon atoms are called saturated fats, meaning that they contain all the hydrogen atoms available. Saturated fats are a solid at room temperature and usually of animal origin.

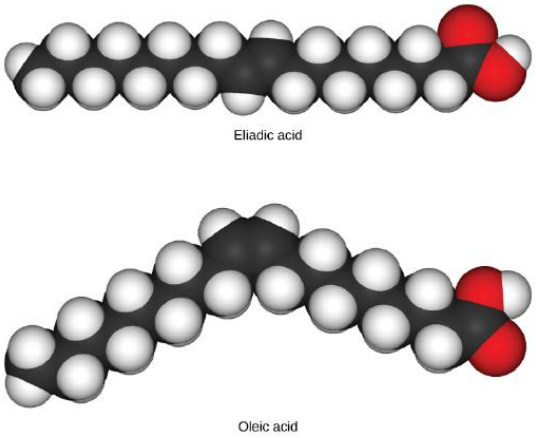


Figure 1.2.4.5: These space-filling models show a *cis* (oleic acid) and a *trans* (eliadic acid) fatty acid. Notice the bend in the molecule cause by the *cis* configuration.

Enantiomers

Enantiomers are molecules that share the same chemical structure and chemical bonds but differ in the three-dimensional placement of atoms so that they are mirror images. As shown in Figure 1.2.4.6, an amino acid alanine example, the two structures are non-superimposable. In nature, only the L-forms of amino acids are used to make proteins. Some D forms of amino acids are seen in the cell walls of bacteria, but never in their proteins. Similarly, the D-form of glucose is the main product of photosynthesis and the L-form of the molecule is rarely seen in nature.

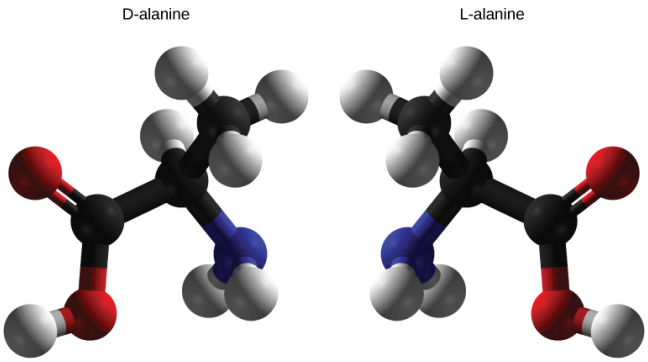


Figure 1.2.4.6: D-alanine and L-alanine are examples of enantiomers or mirror images. Only the L-forms of amino acids are used to make proteins.

Functional Groups

Functional groups are groups of atoms that occur within molecules and confer specific chemical properties to those molecules. They are found along the “carbon backbone” of macromolecules. This carbon backbone is formed by chains and/or rings of carbon atoms with the occasional substitution of an element such as nitrogen or oxygen. Molecules with other elements in their carbon backbone are substituted hydrocarbons.

The functional groups in a macromolecule are usually attached to the carbon backbone at one or several different places along its chain and/or ring structure. Each of the four types of macromolecules—proteins, lipids, carbohydrates, and nucleic acids—has its own characteristic set of functional groups that contributes greatly to its differing chemical properties and its function in living organisms.

A functional group can participate in specific chemical reactions. Some of the important functional groups in biological molecules are shown in Figure 1.2.4.7; they include: hydroxyl, methyl, carbonyl, carboxyl, amino, phosphate, and sulfhydryl. These groups play an important role in the formation of molecules like DNA, proteins, carbohydrates, and lipids. Functional groups are usually classified as hydrophobic or hydrophilic depending on their charge or polarity characteristics. An example of a hydrophobic group is the non-polar methane molecule. Among the hydrophilic functional groups is the carboxyl group found in amino acids, some amino acid side chains, and the fatty acids that form triglycerides and phospholipids. This carboxyl group ionizes to release hydrogen ions (H^+) from the COOH group resulting in the negatively charged COO^- group; this contributes to the hydrophilic nature of whatever molecule it is found on. Other functional groups, such as the carbonyl group, have a partially negatively charged oxygen atom that may form hydrogen bonds with water molecules, again making the molecule more hydrophilic.

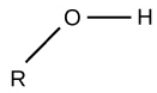
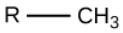
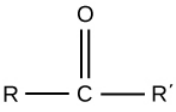
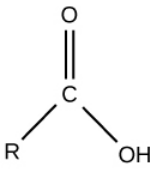
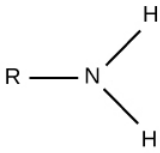
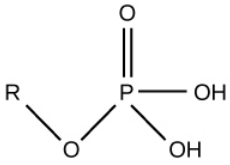
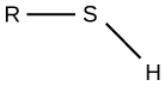
Functional Group	Structure	Properties
Hydroxyl		Polar
Methyl		Nonpolar
Carbonyl		Polar
Carboxyl		Charged, ionizes to release H^+. Since carboxyl groups can release H^+ ions into solution, they are considered acidic.
Amino		Charged, accepts H^+ to form NH_3^+. Since amino groups can remove H^+ from solution, they are considered basic.
Phosphate		Charged, ionizes to release H^+. Since phosphate groups can release H^+ ions into solution, they are considered acidic.
Sulfhydryl		Polar

Figure 1.2.4.7: The functional groups shown here are found in many different biological molecules.

Hydrogen bonds between functional groups (within the same molecule or between different molecules) are important to the function of many macromolecules and help them to fold properly into and maintain the appropriate shape for functioning. Hydrogen bonds are also involved in various recognition processes, such as DNA complementary base pairing and the binding of an enzyme to its substrate, as illustrated in Figure 1.2.4.8.

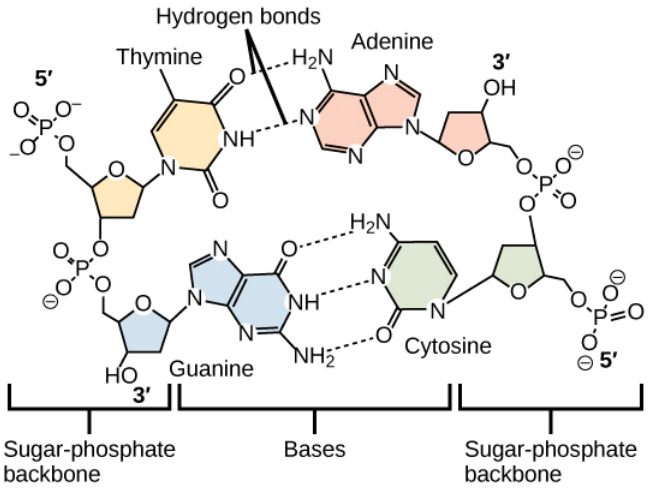


Figure 1.2.4.8: Hydrogen bonds connect two strands of DNA together to create the double-helix structure.

Summary

The unique properties of carbon make it a central part of biological molecules. Carbon binds to oxygen, hydrogen, and nitrogen covalently to form the many molecules important for cellular function. Carbon has four electrons in its outermost shell and can form four bonds. Carbon and hydrogen can form hydrocarbon chains or rings. Functional groups are groups of atoms that confer specific properties to hydrocarbon (or substituted hydrocarbon) chains or rings that define their overall chemical characteristics and function.

Glossary

aliphatic hydrocarbon
: hydrocarbon consisting of a linear chain of carbon atoms

aromatic hydrocarbon
: hydrocarbon consisting of closed rings of carbon atoms

enantiomers
: molecules that share overall structure and bonding patterns, but differ in how the atoms are three dimensionally placed such that they are mirror images of each other

functional group
: group of atoms that provides or imparts a specific function to a carbon skeleton

geometric isomer
: isomer with similar bonding patterns differing in the placement of atoms alongside a double covalent bond

hydrocarbon
: molecule that consists only of carbon and hydrogen

isomers
: molecules that differ from one another even though they share the same chemical formula

organic molecule
: any molecule containing carbon (except carbon dioxide)

structural isomers
: molecules that share a chemical formula but differ in the placement of their chemical bonds

substituted hydrocarbon

hydrocarbon chain or ring containing an atom of another element in place of one of the backbone carbons

---

This page titled 1.2.4: Carbon is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **2.3: Carbon** by OpenStax is licensed CC BY 4.0.

1.2.E: The Chemical Foundation of Life (Exercises)

2.1: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

Review Questions

If xenon has an atomic number of 54 and a mass number of 108, how many neutrons does it have?

A. 54
B. 27
C. 100
D. 108

Answer

A

Atoms that vary in the number of neutrons found in their nuclei are called _____.

A. ions
B. neutrons
C. neutral atoms
D. isotopes

Answer

D

Potassium has an atomic number of 19. What is its electron configuration?

A. shells 1 and 2 are full, and shell 3 has nine electrons
B. shells 1, 2 and 3 are full and shell 4 has three electrons
C. shells 1, 2 and 3 are full and shell 4 has one electron
D. shells 1, 2 and 3 are full and no other electrons are present

Answer

C

Which type of bond represents a weak chemical bond?

A. hydrogen bond
B. atomic bond
C. covalent bond
D. nonpolar covalent bond

Answer

A

Free Response

What makes ionic bonds different from covalent bonds?

Answer

Ionic bonds are created between ions. The electrons are not shared between the atoms, but rather are associated more with one ion than the other. Ionic bonds are strong bonds, but are weaker than covalent bonds, meaning it takes less energy to break an ionic bond compared with a covalent one.

Why are hydrogen bonds and van der Waals interactions necessary for cells?

Answer

Hydrogen bonds and van der Waals interactions form weak associations between different molecules or within different regions of the same molecule. They provide the structure and shape necessary for proteins and DNA within cells so that they function properly.

2.2: Water

Review Questions

Which of the following statements is not true?

A. Water is polar.
B. Water stabilizes temperature.
C. Water is essential for life.
D. Water is the most abundant molecule in the Earth's atmosphere.

Answer

D

When acids are added to a solution, the pH should _____.

A. decrease
B. increase
C. stay the same
D. cannot tell without testing

Answer

A

A molecule that binds up excess hydrogen ions in a solution is called a(n) _____.

A. acid
B. isotope
C. base
D. donator

Answer

C

Which of the following statements is true?

A. Acids and bases cannot mix together.
B. Acids and bases will neutralize each other.
C. Acids, but not bases, can change the pH of a solution.
D. Acids donate hydroxide ions (OH^-); bases donate hydrogen ions (H^+).

Answer

B

Free Response

Discuss how buffers help prevent drastic swings in pH.

Answer

Buffers absorb the free hydrogen ions and hydroxide ions that result from chemical reactions. Because they can bond these ions, they prevent increases or decreases in pH. An example of a buffer system is the bicarbonate system in the human body. This system is able to absorb hydrogen and hydroxide ions to prevent changes in pH and keep cells functioning properly.

Why can some insects walk on water?

Answer

Some insects can walk on water, although they are heavier (denser) than water, because of the surface tension of water. Surface tension results from cohesion, or the attraction between water molecules at the surface of the body of water (the liquid-air/gas interface).

2.3: Carbon

Review Questions

Each carbon molecule can bond with as many as_____ other atom(s) or molecule(s).

A. one
B. two
C. six
D. four

Answer

D

Which of the following is not a functional group that can bond with carbon?

A. sodium
B. hydroxyl
C. phosphate
D. carbonyl

Answer

A

Free Response

What property of carbon makes it essential for organic life?

Answer

Carbon is unique and found in all living things because it can form up to four covalent bonds between atoms or molecules. These can be nonpolar or polar covalent bonds, and they allow for the formation of long chains of carbon molecules that combine to form proteins and DNA.

Compare and contrast saturated and unsaturated triglycerides.

Answer

Saturated triglycerides contain no double bonds between carbon atoms; they are usually solid at room temperature. Unsaturated triglycerides contain at least one double bond between carbon atoms and are usually liquid at room temperature.

This page titled 1.2.E: The Chemical Foundation of Life (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **2.E: The Chemical Foundation of Life (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

1.3: Biological Macromolecules

Food provides the body with the nutrients it needs to survive. Many of these critical nutrients are biological macromolecules, or large molecules, necessary for life. These macromolecules (polymers) are built from different combinations of smaller organic molecules (monomers). What specific types of biological macromolecules do living things require? How are these molecules formed? What functions do they serve? In this chapter, these questions will be explored.

1.3.1: Prelude to Biological Macromolecules
1.3.2: Synthesis of Biological Macromolecules
1.3.3: Carbohydrates
1.3.4: Lipids
1.3.5: Proteins
1.3.6: Nucleic Acids
1.3.E: Biological Macromolecules (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 1.3: Biological Macromolecules is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

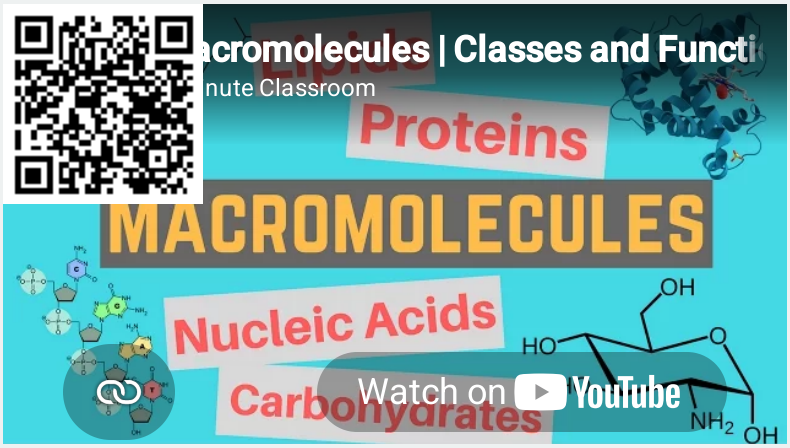
1.3.1: Prelude to Biological Macromolecules



Figure 1.3.1.1: Foods such as bread, fruit, and cheese are rich sources of biological macromolecules. (credit: modification of work by Bengt Nyman)

Food provides the body with the nutrients it needs to survive. Many of these critical nutrients are biological macromolecules, or large molecules, necessary for life. These macromolecules (polymers) are built from different combinations of smaller organic molecules (monomers). What specific types of biological macromolecules do living things require? How are these molecules formed? What functions do they serve? In this chapter, these questions will be explored.

Video



In this 3-minute video, you will learn that macromolecules are large structures that make up all living organisms. All macromolecules have small subunits called monomers which bind together to form larger units called polymers.

This page titled 1.3.1: Prelude to Biological Macromolecules is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.0: Prelude to Biological Macromolecules** by OpenStax is licensed CC BY 4.0.

1.3.2: Synthesis of Biological Macromolecules

Skills to Develop

- Understand the synthesis of macromolecules
- Explain dehydration (or condensation) and hydrolysis reactions

As you've learned, biological macromolecules are large molecules, necessary for life, that are built from smaller organic molecules. There are four major classes of biological macromolecules (carbohydrates, lipids, proteins, and nucleic acids); each is an important cell component and performs a wide array of functions. Combined, these molecules make up the majority of a cell's dry mass (recall that water makes up the majority of its complete mass). Biological macromolecules are organic, meaning they contain carbon. In addition, they may contain hydrogen, oxygen, nitrogen, and additional minor elements.

Dehydration Synthesis

Most macromolecules are made from single subunits, or building blocks, called monomers. The monomers combine with each other using covalent bonds to form larger molecules known as polymers. In doing so, monomers release water molecules as byproducts. This type of reaction is known as dehydration synthesis, which means "to put together while losing water."

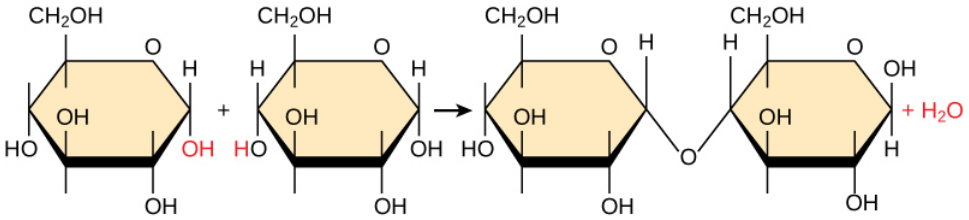


Figure 1.3.2.1: In the dehydration synthesis reaction depicted above, two molecules of glucose are linked together to form the disaccharide maltose. In the process, a water molecule is formed.

In a dehydration synthesis reaction (Figure 1.3.2.1), the hydrogen of one monomer combines with the hydroxyl group of another monomer, releasing a molecule of water. At the same time, the monomers share electrons and form covalent bonds. As additional monomers join, this chain of repeating monomers forms a polymer. Different types of monomers can combine in many configurations, giving rise to a diverse group of macromolecules. Even one kind of monomer can combine in a variety of ways to form several different polymers: for example, glucose monomers are the constituents of starch, glycogen, and cellulose.

Hydrolysis

Polymers are broken down into monomers in a process known as hydrolysis, which means "to split water," a reaction in which a water molecule is used during the breakdown (Figure 1.3.2.2). During these reactions, the polymer is broken into two components: one part gains a hydrogen atom (H+) and the other gains a hydroxyl molecule (OH–) from a split water molecule.

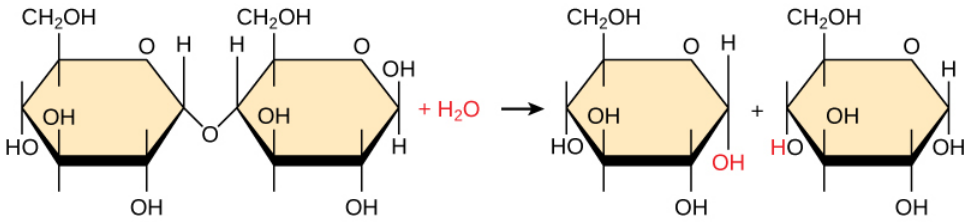
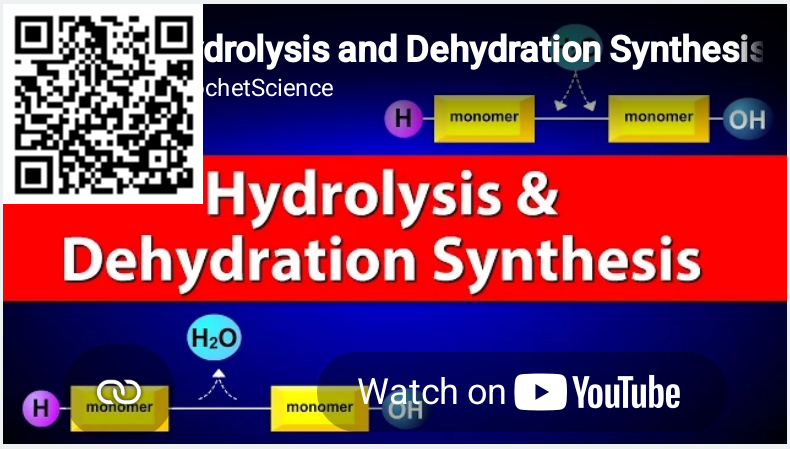


Figure 1.3.2.2: In the hydrolysis reaction shown here, the disaccharide maltose is broken down to form two glucose monomers with the addition of a water molecule. Note that this reaction is the reverse of the synthesis reaction shown in Figure 1.3.2.1.

Dehydration and hydrolysis reactions are catalyzed, or "sped up," by specific enzymes; dehydration reactions involve the formation of new bonds, requiring energy, while hydrolysis reactions break bonds and release energy. These reactions are similar for most macromolecules, but each monomer and polymer reaction is specific for its class. For example, in our bodies, food is hydrolyzed, or broken down, into smaller molecules by catalytic enzymes in the digestive system. This allows for easy absorption of nutrients by cells in the intestine. Each macromolecule is broken down by a specific enzyme. For instance, carbohydrates are broken down

by amylase, sucrase, lactase, or maltase. Proteins are broken down by the enzymes pepsin and peptidase, and by hydrochloric acid. Lipids are broken down by lipases. Breakdown of these macromolecules provides energy for cellular activities.

Link to Learning



Visit this site to see visual representations of dehydration synthesis and hydrolysis.

Summary

Proteins, carbohydrates, nucleic acids, and lipids are the four major classes of biological macromolecules—large molecules necessary for life that are built from smaller organic molecules. Macromolecules are made up of single units known as monomers that are joined by covalent bonds to form larger polymers. The polymer is more than the sum of its parts: it acquires new characteristics, and leads to an osmotic pressure that is much lower than that formed by its ingredients; this is an important advantage in the maintenance of cellular osmotic conditions. A monomer joins with another monomer with the release of a water molecule, leading to the formation of a covalent bond. These types of reactions are known as dehydration or condensation reactions. When polymers are broken down into smaller units (monomers), a molecule of water is used for each bond broken by these reactions; such reactions are known as hydrolysis reactions. Dehydration and hydrolysis reactions are similar for all macromolecules, but each monomer and polymer reaction is specific to its class. Dehydration reactions typically require an investment of energy for new bond formation, while hydrolysis reactions typically release energy by breaking bonds.

Glossary

biological macromolecule
large molecule necessary for life that is built from smaller organic molecules

dehydration synthesis
(also, condensation) reaction that links monomer molecules together, releasing a molecule of water for each bond formed

hydrolysis
reaction causes breakdown of larger molecules into smaller molecules with the utilization of water

monomer
smallest unit of larger molecules called polymers

polymer
chain of monomer residues that is linked by covalent bonds; polymerization is the process of polymer formation from monomers by condensation

This page titled 1.3.2: Synthesis of Biological Macromolecules is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.1: Synthesis of Biological Macromolecules** by OpenStax is licensed CC BY 4.0.

1.3.3: Carbohydrates

Skills to Develop

- Discuss the role of carbohydrates in cells and in the extracellular materials of animals and plants
- Explain the classifications of carbohydrates
- List common monosaccharides, disaccharides, and polysaccharides

Most people are familiar with carbohydrates, one type of macromolecule, especially when it comes to what we eat. To lose weight, some individuals adhere to “low-carb” diets. Athletes, in contrast, often “carb-load” before important competitions to ensure that they have enough energy to compete at a high level. Carbohydrates are, in fact, an essential part of our diet; grains, fruits, and vegetables are all natural sources of carbohydrates. Carbohydrates provide energy to the body, particularly through glucose, a simple sugar that is a component of starch and an ingredient in many staple foods. Carbohydrates also have other important functions in humans, animals, and plants.

Molecular Structures

Carbohydrates can be represented by the stoichiometric formula $(CH_2O)_n$, where n is the number of carbons in the molecule. In other words, the ratio of carbon to hydrogen to oxygen is 1:2:1 in carbohydrate molecules. This formula also explains the origin of the term “carbohydrate”: the components are carbon (“carbo”) and the components of water (hence, “hydrate”). Carbohydrates are classified into three subtypes: monosaccharides, disaccharides, and polysaccharides.

Monosaccharides

Monosaccharides (mono- = “one”; sacchar- = “sweet”) are simple sugars, the most common of which is glucose. In monosaccharides, the number of carbons usually ranges from three to seven. Most monosaccharide names end with the suffix -ose. If the sugar has an aldehyde group (the functional group with the structure R-CHO), it is known as an aldose, and if it has a ketone group (the functional group with the structure RC(=O)R'), it is known as a ketose. Depending on the number of carbons in the sugar, they also may be known as trioses (three carbons), pentoses (five carbons), and or hexoses (six carbons). See Figure 1.3.3.1 for an illustration of the monosaccharides.

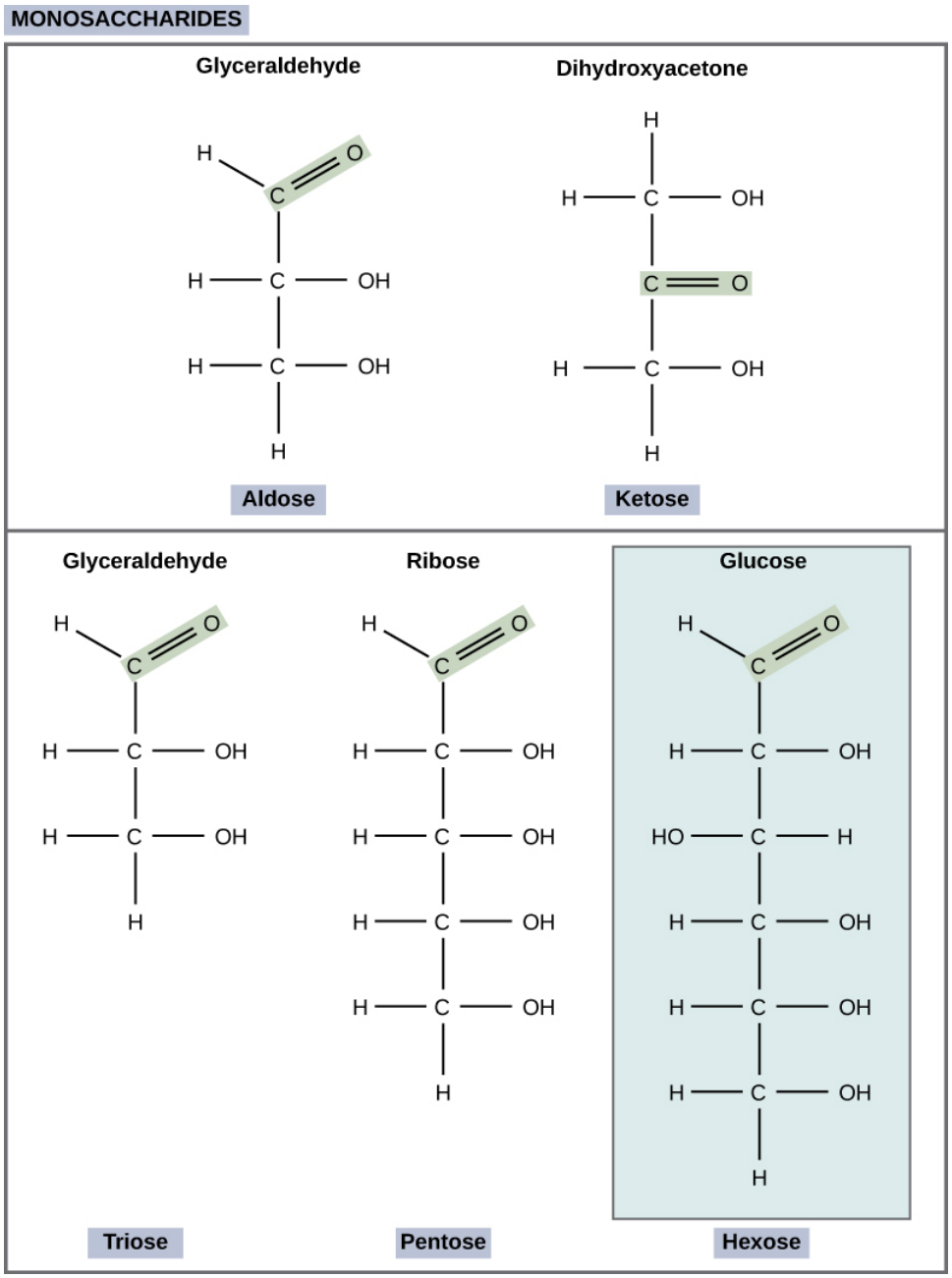


Figure 1.3.3.1: Monosaccharides are classified based on the position of their carbonyl group and the number of carbons in the backbone. Aldoses have a carbonyl group (indicated in green) at the end of the carbon chain, and ketoses have a carbonyl group in the middle of the carbon chain. Trioses, pentoses, and hexoses have three, five, and six carbon backbones, respectively.

The chemical formula for glucose is $C_6H_{12}O_6$. In humans, glucose is an important source of energy. During cellular respiration, energy is released from glucose, and that energy is used to help make adenosine triphosphate (ATP). Plants synthesize glucose using carbon dioxide and water, and glucose in turn is used for energy requirements for the plant. Excess glucose is often stored as starch that is catabolized (the breakdown of larger molecules by cells) by humans and other animals that feed on plants.

Galactose (part of lactose, or milk sugar) and fructose (found in sucrose, in fruit) are other common monosaccharides. Although glucose, galactose, and fructose all have the same chemical formula ($C_6H_{12}O_6$), they differ structurally and chemically (and are known as isomers) because of the different arrangement of functional groups around the asymmetric carbon; all of these monosaccharides have more than one asymmetric carbon (Figure1.3.3.2).

Art Connection

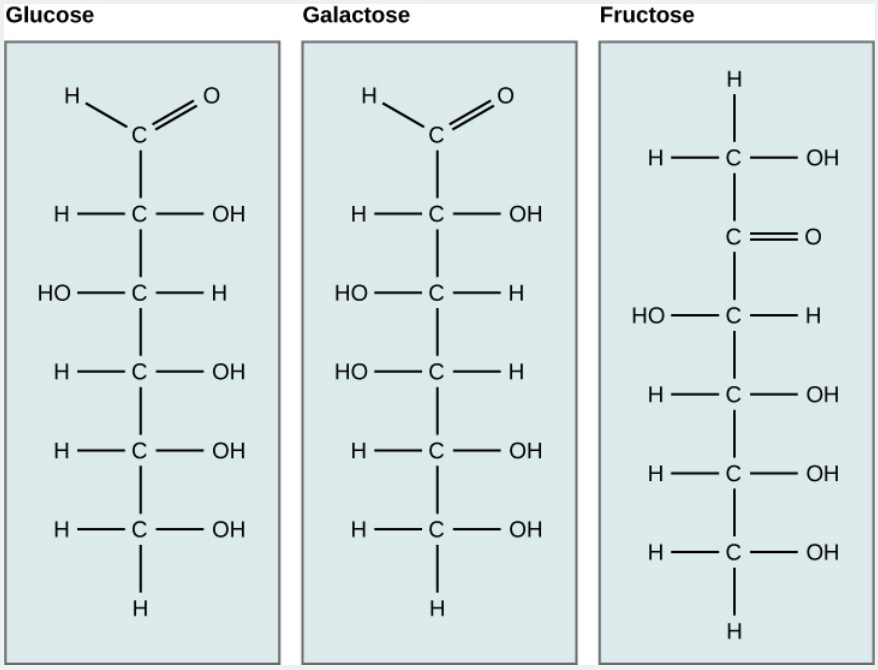


Figure 1.3.3.2: Glucose, galactose, and fructose are all hexoses. They are structural isomers, meaning they have the same chemical formula ($C_6H_{12}O_6$) but a different arrangement of atoms.

What kind of sugars are these, aldose or ketose?

Glucose, galactose, and fructose are isomeric monosaccharides (hexoses), meaning they have the same chemical formula but have slightly different structures. Glucose and galactose are aldoses, and fructose is a ketose.

Monosaccharides can exist as a linear chain or as ring-shaped molecules; in aqueous solutions they are usually found in ring forms (Figure 1.3.3.3). Glucose in a ring form can have two different arrangements of the hydroxyl group (OH) around the anomeric carbon (carbon 1 that becomes asymmetric in the process of ring formation). If the hydroxyl group is below carbon number 1 in the sugar, it is said to be in the alpha (α) position, and if it is above the plane, it is said to be in the beta (β) position.

https://bio.libretexts.org/@go/page/82848

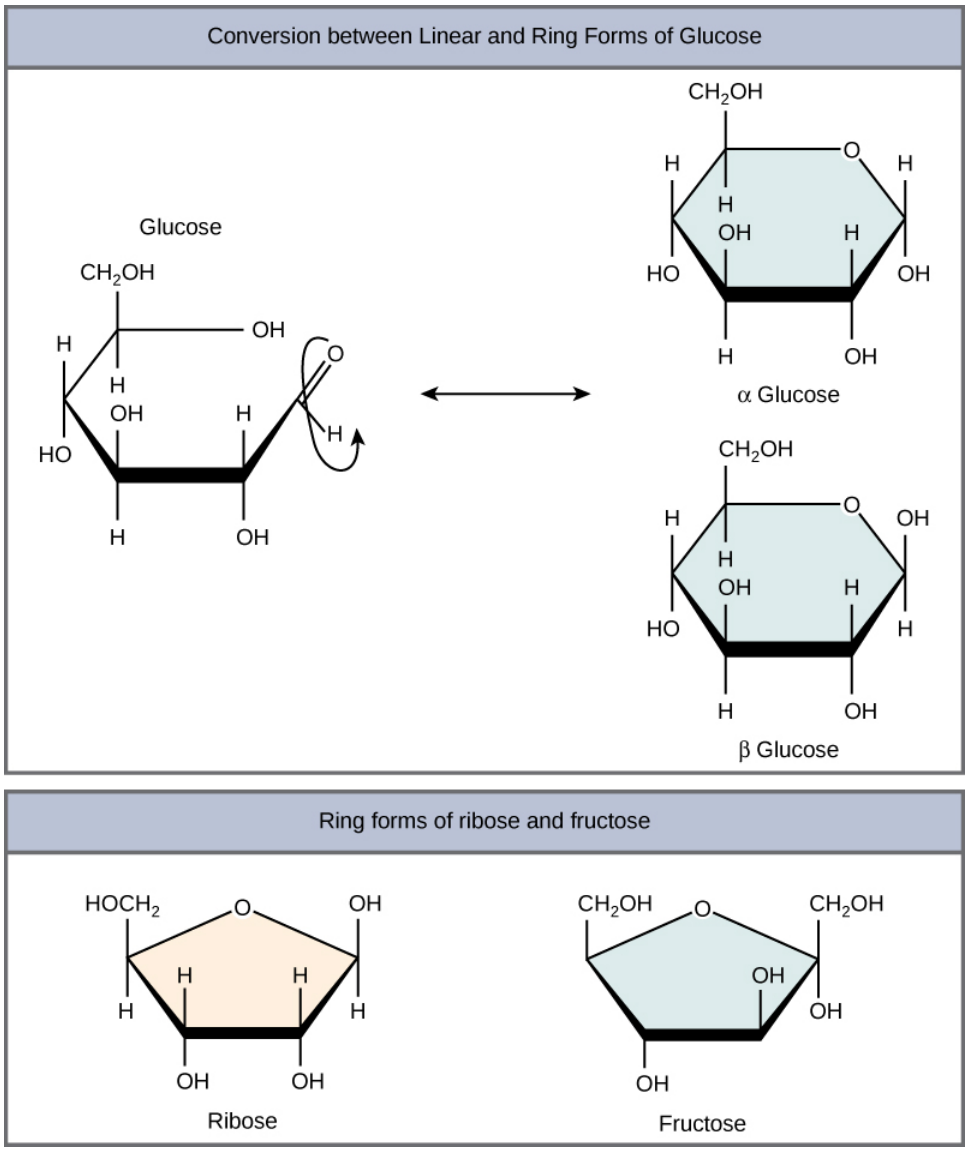


Figure 1.3.3.3: Five and six carbon monosaccharides exist in equilibrium between linear and ring forms. When the ring forms, the side chain it closes on is locked into an α or β position. Fructose and ribose also form rings, although they form five-membered rings as opposed to the six-membered ring of glucose.

Disaccharides

Disaccharides (di- = “two”) form when two monosaccharides undergo a dehydration reaction (also known as a condensation reaction or dehydration synthesis). During this process, the hydroxyl group of one monosaccharide combines with the hydrogen of another monosaccharide, releasing a molecule of water and forming a covalent bond. A covalent bond formed between a carbohydrate molecule and another molecule (in this case, between two monosaccharides) is known as a glycosidic bond (Figure 1.3.3.4). Glycosidic bonds (also called glycosidic linkages) can be of the alpha or the beta type.

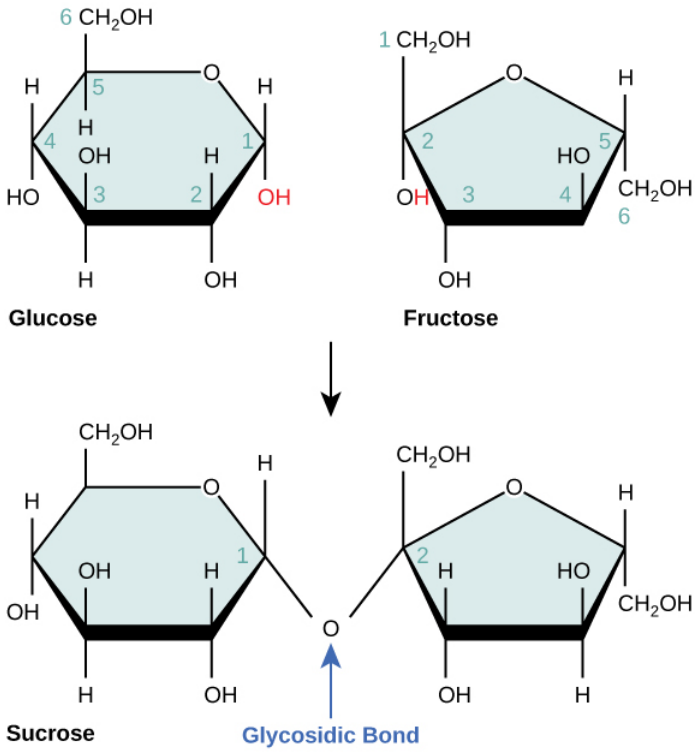


Figure 1.3.3.4: Sucrose is formed when a monomer of glucose and a monomer of fructose are joined in a dehydration reaction to form a glycosidic bond. In the process, a water molecule is lost. By convention, the carbon atoms in a monosaccharide are numbered from the terminal carbon closest to the carbonyl group. In sucrose, a glycosidic linkage is formed between carbon 1 in glucose and carbon 2 in fructose.

Common disaccharides include lactose, maltose, and sucrose (Figure 1.3.3.5). Lactose is a disaccharide consisting of the monomers glucose and galactose. It is found naturally in milk. Maltose, or malt sugar, is a disaccharide formed by a dehydration reaction between two glucose molecules. The most common disaccharide is sucrose, or table sugar, which is composed of the monomers glucose and fructose.

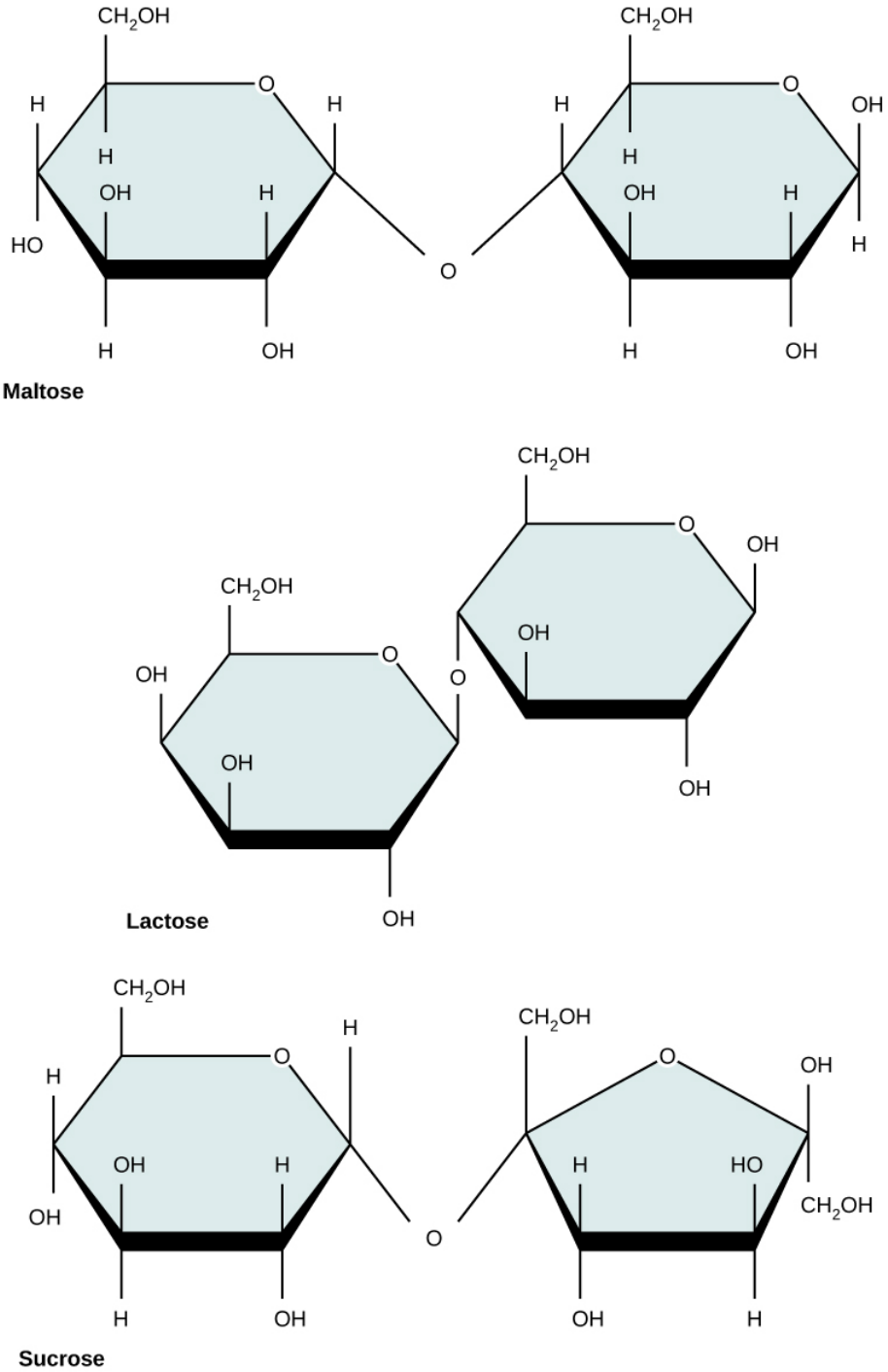


Figure 1.3.3.5: Common disaccharides include maltose (grain sugar), lactose (milk sugar), and sucrose (table sugar).

Polysaccharides

A long chain of monosaccharides linked by glycosidic bonds is known as a polysaccharide (poly- = “many”). The chain may be branched or unbranched, and it may contain different types of monosaccharides. The molecular weight may be 100,000 daltons or more depending on the number of monomers joined. Starch, glycogen, cellulose, and chitin are primary examples of polysaccharides.

Starch is the stored form of sugars in plants and is made up of a mixture of amylose and amylopectin (both polymers of glucose). Plants are able to synthesize glucose, and the excess glucose, beyond the plant’s immediate energy needs, is stored as starch in different plant parts, including roots and seeds. The starch in the seeds provides food for the embryo as it germinates and can also

act as a source of food for humans and animals. The starch that is consumed by humans is broken down by enzymes, such as salivary amylases, into smaller molecules, such as maltose and glucose. The cells can then absorb the glucose.

Starch is made up of glucose monomers that are joined by α 1-4 or α 1-6 glycosidic bonds. The numbers 1-4 and 1-6 refer to the carbon number of the two residues that have joined to form the bond. As illustrated in Figure 1.3.3.6, amylose is starch formed by unbranched chains of glucose monomers (only α 1-4 linkages), whereas amylopectin is a branched polysaccharide (α 1-6 linkages at the branch points).

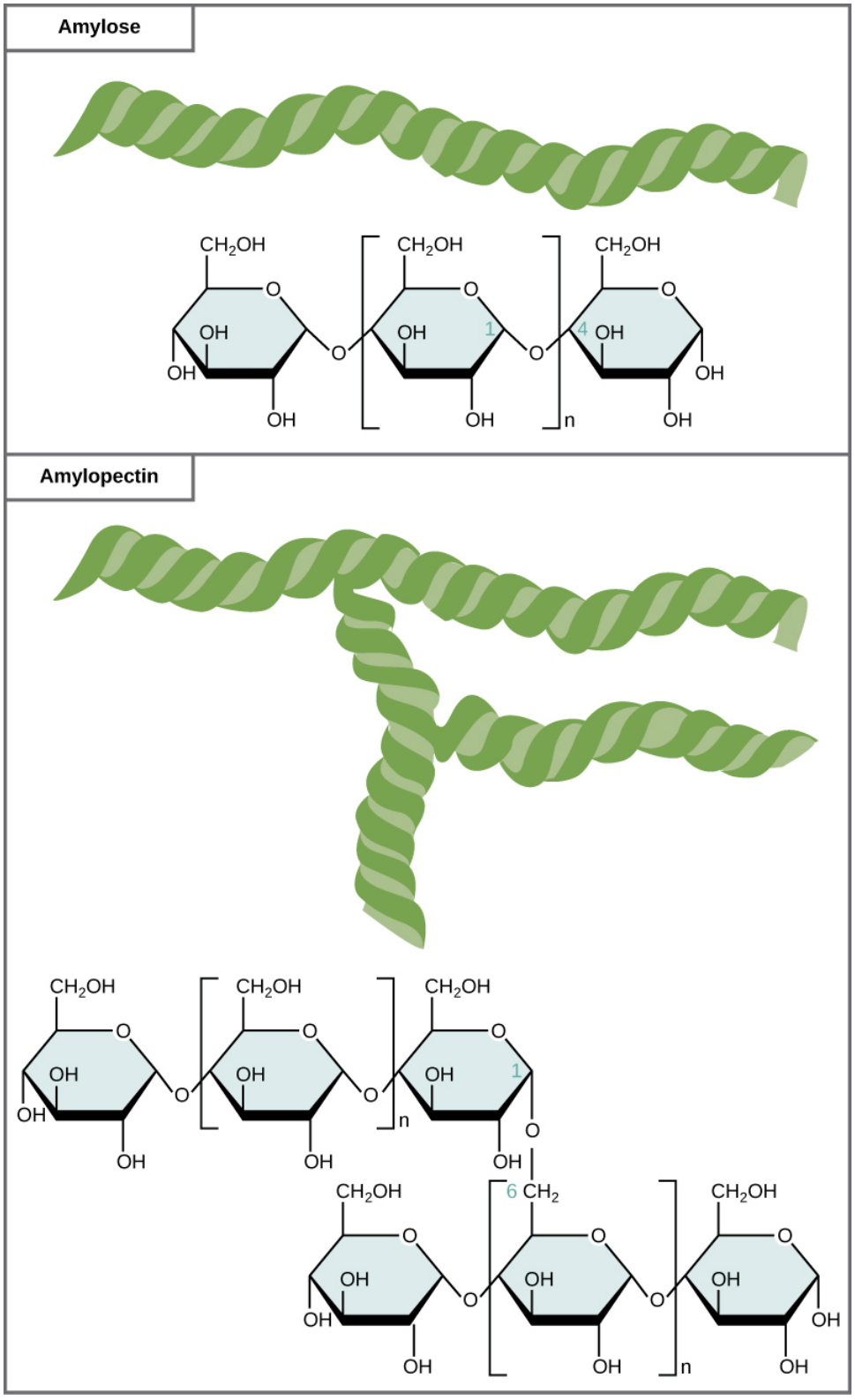


Figure 1.3.3.6: Amylose and amylopectin are two different forms of starch. Amylose is composed of unbranched chains of glucose monomers connected by α 1,4 glycosidic linkages. Amylopectin is composed of branched chains of glucose monomers connected by α 1,4 and α 1,6 glycosidic linkages. Because of the way the subunits are joined, the glucose chains have a helical structure. Glycogen (not shown) is similar in structure to amylopectin but more highly branched.

Glycogen is the storage form of glucose in humans and other vertebrates and is made up of monomers of glucose. Glycogen is the animal equivalent of starch and is a highly branched molecule usually stored in liver and muscle cells. Whenever blood glucose

levels decrease, glycogen is broken down to release glucose in a process known as glycogenolysis.

Cellulose is the most abundant natural biopolymer. The cell wall of plants is mostly made of cellulose; this provides structural support to the cell. Wood and paper are mostly cellulosic in nature. Cellulose is made up of glucose monomers that are linked by β 1-4 glycosidic bonds (Figure 1.3.3.7).

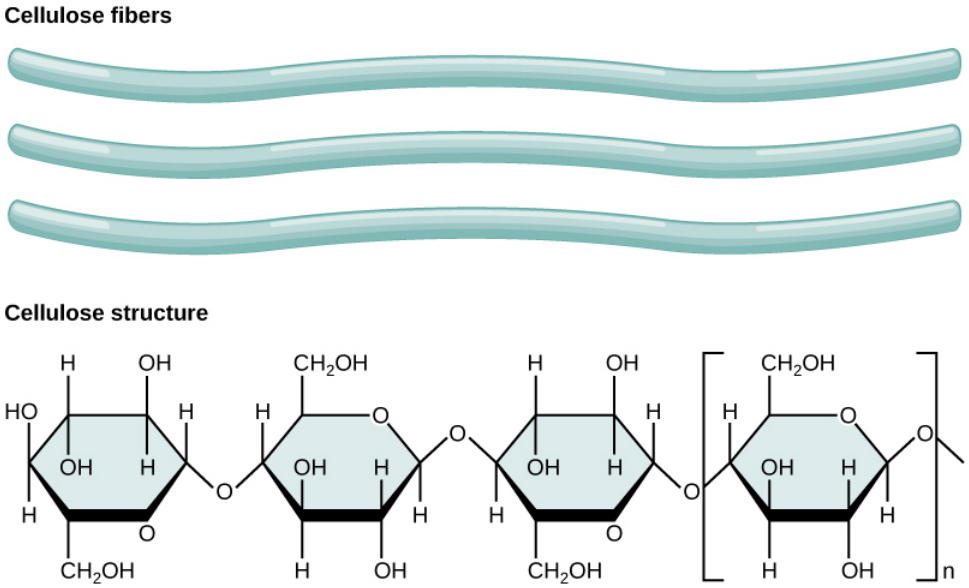


Figure 1.3.3.7: In cellulose, glucose monomers are linked in unbranched chains by β 1-4 glycosidic linkages. Because of the way the glucose subunits are joined, every glucose monomer is flipped relative to the next one resulting in a linear, fibrous structure.

As shown in Figure 1.3.3.7, every other glucose monomer in cellulose is flipped over, and the monomers are packed tightly as extended long chains. This gives cellulose its rigidity and high tensile strength—which is so important to plant cells. While the β 1-4 linkage cannot be broken down by human digestive enzymes, herbivores such as cows, koalas, buffalos, and horses are able, with the help of the specialized flora in their stomach, to digest plant material that is rich in cellulose and use it as a food source. In these animals, certain species of bacteria and protists reside in the rumen (part of the digestive system of herbivores) and secrete the enzyme cellulase. The appendix of grazing animals also contains bacteria that digest cellulose, giving it an important role in the digestive systems of ruminants. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal. Termites are also able to break down cellulose because of the presence of other organisms in their bodies that secrete cellulases.

Carbohydrates serve various functions in different animals. Arthropods (insects, crustaceans, and others) have an outer skeleton, called the exoskeleton, which protects their internal body parts (as seen in the bee in Figure 1.3.3.8). This exoskeleton is made of the biological macromolecule chitin, which is a polysaccharide-containing nitrogen. It is made of repeating units of N-acetyl-β-d-glucosamine, a modified sugar. Chitin is also a major component of fungal cell walls; fungi are neither animals nor plants and form a kingdom of their own in the domain Eukarya.



Figure 1.3.3.8: Insects have a hard outer exoskeleton made of chitin, a type of polysaccharide. (credit: Louise Docker)

Career Connections: Registered Dietitian

Obesity is a worldwide health concern, and many diseases such as diabetes and heart disease are becoming more prevalent because of obesity. This is one of the reasons why registered dietitians are increasingly sought after for advice. Registered dietitians help plan nutrition programs for individuals in various settings. They often work with patients in health care facilities, designing nutrition plans to treat and prevent diseases. For example, dietitians may teach a patient with diabetes how to manage blood sugar levels by eating the correct types and amounts of carbohydrates. Dietitians may also work in nursing homes, schools, and private practices.

To become a registered dietitian, one needs to earn at least a bachelor's degree in dietetics, nutrition, food technology, or a related field. In addition, registered dietitians must complete a supervised internship program and pass a national exam. Those who pursue careers in dietetics take courses in nutrition, chemistry, biochemistry, biology, microbiology, and human physiology. Dietitians must become experts in the chemistry and physiology (biological functions) of food (proteins, carbohydrates, and fats).

Benefits of Carbohydrates

Are carbohydrates good for you? People who wish to lose weight are often told that carbohydrates are bad for them and should be avoided. Some diets completely forbid carbohydrate consumption, claiming that a low-carbohydrate diet helps people to lose weight faster. However, carbohydrates have been an important part of the human diet for thousands of years; artifacts from ancient civilizations show the presence of wheat, rice, and corn in our ancestors' storage areas.

Carbohydrates should be supplemented with proteins, vitamins, and fats to be parts of a well-balanced diet. Calorie-wise, a gram of carbohydrate provides 4.3 Kcal. For comparison, fats provide 9 Kcal/g, a less desirable ratio. Carbohydrates contain soluble and insoluble elements; the insoluble part is known as fiber, which is mostly cellulose. Fiber has many uses; it promotes regular bowel movement by adding bulk, and it regulates the rate of consumption of blood glucose. Fiber also helps to remove excess cholesterol from the body: fiber binds to the cholesterol in the small intestine, then attaches to the cholesterol and prevents the cholesterol particles from entering the bloodstream, and then cholesterol exits the body via the feces. Fiber-rich diets also have a protective role in reducing the occurrence of colon cancer. In addition, a meal containing whole grains and vegetables gives a feeling of fullness. As an immediate source of energy, glucose is broken down during the process of cellular respiration, which produces ATP, the energy currency of the cell. Without the consumption of carbohydrates, the availability of "instant energy" would be reduced. Eliminating carbohydrates from the diet is not the best way to lose weight. A low-calorie diet that is rich in whole grains, fruits, vegetables, and lean meat, together with plenty of exercise and plenty of water, is the more sensible way to lose weight.

Link to Learning

For an additional perspective on carbohydrates, explore “Biomolecules: the Carbohydrates” through this interactive animation.

Summary

Carbohydrates are a group of macromolecules that are a vital energy source for the cell and provide structural support to plant cells, fungi, and all of the arthropods that include lobsters, crabs, shrimp, insects, and spiders. Carbohydrates are classified as monosaccharides, disaccharides, and polysaccharides depending on the number of monomers in the molecule. Monosaccharides are linked by glycosidic bonds that are formed as a result of dehydration reactions, forming disaccharides and polysaccharides with the elimination of a water molecule for each bond formed. Glucose, galactose, and fructose are common monosaccharides, whereas common disaccharides include lactose, maltose, and sucrose. Starch and glycogen, examples of polysaccharides, are the storage forms of glucose in plants and animals, respectively. The long polysaccharide chains may be branched or unbranched. Cellulose is an example of an unbranched polysaccharide, whereas amylopectin, a constituent of starch, is a highly branched molecule. Storage of glucose, in the form of polymers like starch of glycogen, makes it slightly less accessible for metabolism; however, this prevents it from leaking out of the cell or creating a high osmotic pressure that could cause excessive water uptake by the cell.

Art Connections

Figure 1.3.3.2: What kind of sugars are these, aldose or ketose?

Answer

Glucose and galactose are aldoses. Fructose is a ketose.

Glossary

carbohydrate
biological macromolecule in which the ratio of carbon to hydrogen and to oxygen is 1:2:1; carbohydrates serve as energy sources and structural support in cells and form the a cellular exoskeleton of arthropods

cellulose
polysaccharide that makes up the cell wall of plants; provides structural support to the cell

chitin
type of carbohydrate that forms the outer skeleton of all arthropods that include crustaceans and insects; it also forms the cell walls of fungi

disaccharide
two sugar monomers that are linked together by a glycosidic bond

glycogen
storage carbohydrate in animals

glycosidic bond
bond formed by a dehydration reaction between two monosaccharides with the elimination of a water molecule

monosaccharide

single unit or monomer of carbohydrates

polysaccharide

long chain of monosaccharides; may be branched or unbranched

starch

storage carbohydrate in plants

This page titled 1.3.3: Carbohydrates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.2: Carbohydrates** by OpenStax is licensed CC BY 4.0.

1.3.4: Lipids

Skills to Develop

- Describe the four major types of lipids
- Explain the role of fats in storing energy
- Differentiate between saturated and unsaturated fatty acids
- Describe phospholipids and their role in cells
- Define the basic structure of a steroid and some functions of steroids
- Explain the how cholesterol helps to maintain the fluid nature of the plasma membrane

Lipids include a diverse group of compounds that are largely nonpolar in nature. This is because they are hydrocarbons that include mostly nonpolar carbon–carbon or carbon–hydrogen bonds. Non-polar molecules are hydrophobic ("water fearing"), or insoluble in water. Lipids perform many different functions in a cell. Cells store energy for long-term use in the form of fats. Lipids also provide insulation from the environment for plants and animals (Figure 1.3.4.1). For example, they help keep aquatic birds and mammals dry when forming a protective layer over fur or feathers because of their water-repellant hydrophobic nature. Lipids are also the building blocks of many hormones and are an important constituent of all cellular membranes. Lipids include fats, oils, waxes, phospholipids, and steroids.



Figure 1.3.4.1: Hydrophobic lipids in the fur of aquatic mammals, such as this river otter, protect them from the elements. (credit: Ken Bosma)

Fats and Oils

A fat molecule consists of two main components—glycerol and fatty acids. Glycerol is an organic compound (alcohol) with three carbons, five hydrogens, and three hydroxyl (OH) groups. Fatty acids have a long chain of hydrocarbons to which a carboxyl group is attached, hence the name "fatty acid." The number of carbons in the fatty acid may range from 4 to 36; most common are those containing 12–18 carbons. In a fat molecule, the fatty acids are attached to each of the three carbons of the glycerol molecule with an ester bond through an oxygen atom (Figure 1.3.4.2).

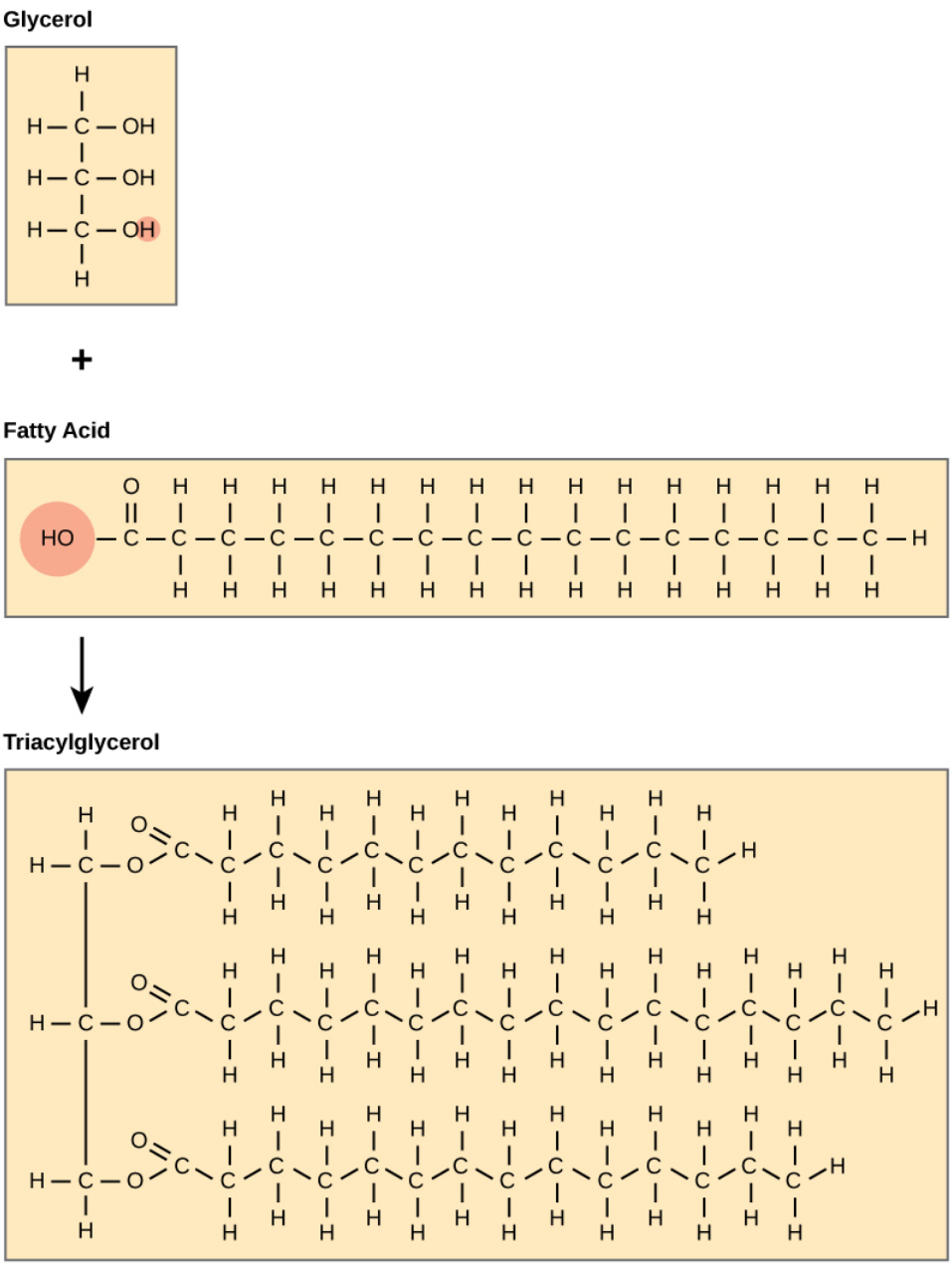


Figure 1.3.4.2: Triacylglycerol is formed by the joining of three fatty acids to a glycerol backbone in a dehydration reaction. Three molecules of water are released in the process.

During this ester bond formation, three water molecules are released. The three fatty acids in the triacylglycerol may be similar or dissimilar. Fats are also called triacylglycerols or triglycerides because of their chemical structure. Some fatty acids have common names that specify their origin. For example, palmitic acid, a saturated fatty acid, is derived from the palm tree. Arachidic acid is derived from *Arachis hypogea*, the scientific name for groundnuts or peanuts.

Fatty acids may be saturated or unsaturated. In a fatty acid chain, if there are only single bonds between neighboring carbons in the hydrocarbon chain, the fatty acid is said to be saturated. Saturated fatty acids are saturated with hydrogen; in other words, the number of hydrogen atoms attached to the carbon skeleton is maximized. Stearic acid is an example of a saturated fatty acid (Figure 1.3.4.3)

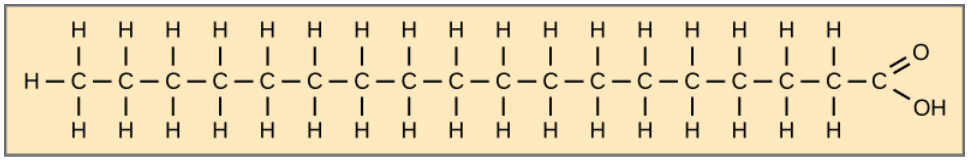


Figure 1.3.4.3: Stearic acid is a common saturated fatty acid.

When the hydrocarbon chain contains a double bond, the fatty acid is said to be unsaturated. Oleic acid is an example of an unsaturated fatty acid (Figure 1.3.4.4).

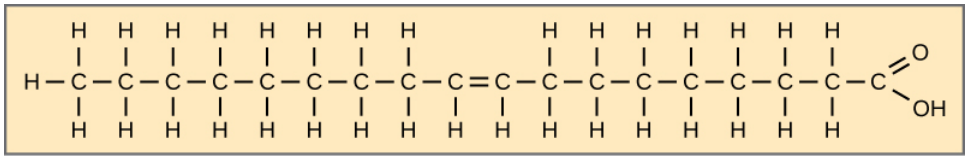


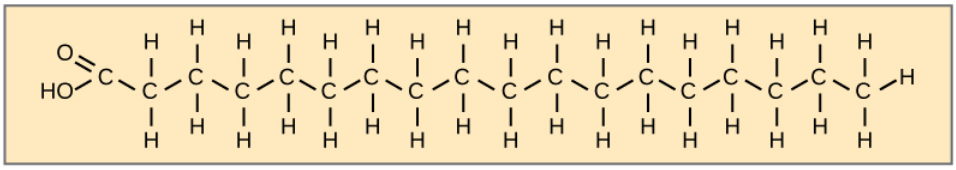
Figure 1.3.4.4: Oleic acid is a common unsaturated fatty acid.

Most unsaturated fats are liquid at room temperature and are called oils. If there is one double bond in the molecule, then it is known as a monounsaturated fat (e.g., olive oil), and if there is more than one double bond, then it is known as a polyunsaturated fat (e.g., canola oil).

When a fatty acid has no double bonds, it is known as a saturated fatty acid because no more hydrogen may be added to the carbon atoms of the chain. A fat may contain similar or different fatty acids attached to glycerol. Long straight fatty acids with single bonds tend to get packed tightly and are solid at room temperature. Animal fats with stearic acid and palmitic acid (common in meat) and the fat with butyric acid (common in butter) are examples of saturated fats. Mammals store fats in specialized cells called adipocytes, where globules of fat occupy most of the cell's volume. In plants, fat or oil is stored in many seeds and is used as a source of energy during seedling development. Unsaturated fats or oils are usually of plant origin and contain *cis* unsaturated fatty acids. *Cis* and *trans* indicate the configuration of the molecule around the double bond. If hydrogens are present in the same plane, it is referred to as a cis fat; if the hydrogen atoms are on two different planes, it is referred to as a trans fat. The *cis* double bond causes a bend or a "kink" that prevents the fatty acids from packing tightly, keeping them liquid at room temperature (Figure 1.3.4.5). Olive oil, corn oil, canola oil, and cod liver oil are examples of unsaturated fats. Unsaturated fats help to lower blood cholesterol levels whereas saturated fats contribute to plaque formation in the arteries.

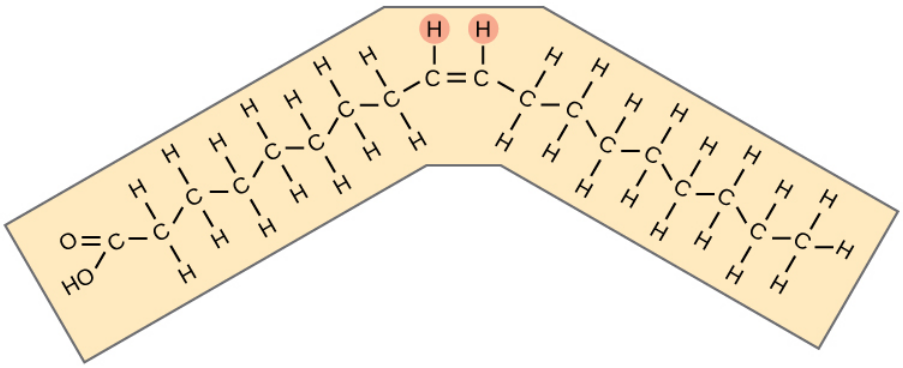
Saturated fatty acid

Stearic acid



Unsaturated fatty acids

Cis oleic acid



Trans oleic acid

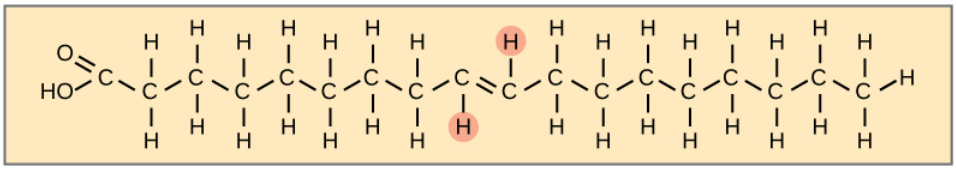


Figure 1.3.4.5: Saturated fatty acids have hydrocarbon chains connected by single bonds only. Unsaturated fatty acids have one or more double bonds. Each double bond may be in a *cis* or *trans* configuration. In the *cis* configuration, both hydrogens are on the same side of the hydrocarbon chain. In the *trans* configuration, the hydrogens are on opposite sides. A *cis* double bond causes a kink in the chain.

Trans Fats

In the food industry, oils are artificially hydrogenated to make them semi-solid and of a consistency desirable for many processed food products. Simply speaking, hydrogen gas is bubbled through oils to solidify them. During this hydrogenation process, double bonds of the *cis*- conformation in the hydrocarbon chain may be converted to double bonds in the trans- conformation.

Margarine, some types of peanut butter, and shortening are examples of artificially hydrogenated trans fats. Recent studies have shown that an increase in trans fats in the human diet may lead to an increase in levels of low-density lipoproteins (LDL), or “bad” cholesterol, which in turn may lead to plaque deposition in the arteries, resulting in heart disease. Many fast food restaurants have recently banned the use of trans fats, and food labels are required to display the trans fat content.

Omega Fatty Acids

Essential fatty acids are fatty acids required but not synthesized by the human body. Consequently, they have to be supplemented through ingestion via the diet. Omega-3 fatty acids (like that shown in Figure 1.3.4.6) fall into this category and are one of only two known for humans (the other being omega-6 fatty acid). These are polyunsaturated fatty acids and are called omega-3 because the third carbon from the end of the hydrocarbon chain is connected to its neighboring carbon by a double bond.

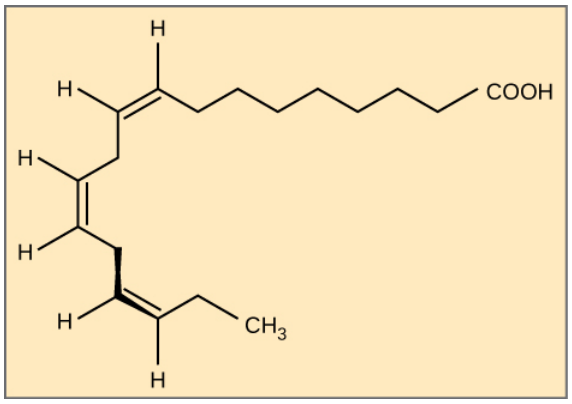


Figure 1.3.4.6: Alpha-linolenic acid is an example of an omega-3 fatty acid. It has three *cis* double bonds and, as a result, a curved shape. For clarity, the carbons are not shown. Each singly bonded carbon has two hydrogens associated with it, also not shown.

The farthest carbon away from the carboxyl group is numbered as the omega (ω) carbon, and if the double bond is between the third and fourth carbon from that end, it is known as an omega-3 fatty acid. Nutritionally important because the body does not make them, omega-3 fatty acids include alpha-linoleic acid (ALA), eicosapentaenoic acid (EPA), and docosahexaenoic acid (DHA), all of which are polyunsaturated. Salmon, trout, and tuna are good sources of omega-3 fatty acids. Research indicates that omega-3 fatty acids reduce the risk of sudden death from heart attacks, reduce triglycerides in the blood, lower blood pressure, and prevent thrombosis by inhibiting blood clotting. They also reduce inflammation, and may help reduce the risk of some cancers in animals.

Like carbohydrates, fats have received a lot of bad publicity. It is true that eating an excess of fried foods and other “fatty” foods leads to weight gain. However, fats do have important functions. Many vitamins are fat soluble, and fats serve as a long-term storage form of fatty acids: a source of energy. They also provide insulation for the body. Therefore, “healthy” fats in moderate amounts should be consumed on a regular basis.

Waxes

Wax covers the feathers of some aquatic birds and the leaf surfaces of some plants. Because of the hydrophobic nature of waxes, they prevent water from sticking on the surface (Figure 1.3.4.7). Waxes are made up of long fatty acid chains esterified to long-chain alcohols.



Figure 1.3.4.7: Waxy coverings on some leaves are made of lipids. (credit: Roger Griffith)

Phospholipids

Phospholipids are major constituents of the plasma membrane, the outermost layer of animal cells. Like fats, they are composed of fatty acid chains attached to a glycerol or sphingosine backbone. Instead of three fatty acids attached as in triglycerides, however, there are two fatty acids forming diacylglycerol, and the third carbon of the glycerol backbone is occupied by a modified phosphate group (Figure 1.3.4.8). A phosphate group alone attached to a diaglycerol does not qualify as a phospholipid; it is phosphatidate

(diacylglycerol 3-phosphate), the precursor of phospholipids. The phosphate group is modified by an alcohol. Phosphatidylcholine and phosphatidylserine are two important phospholipids that are found in plasma membranes.

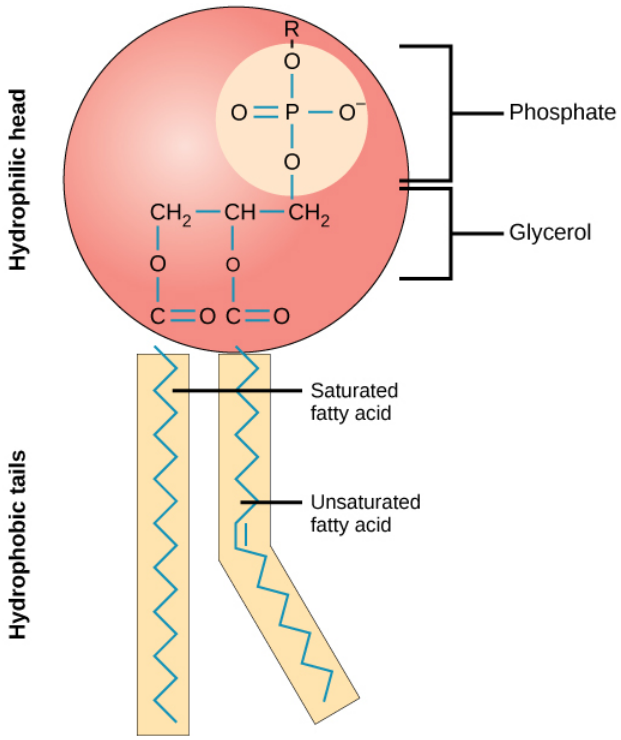


Figure 1.3.4.8: A phospholipid is a molecule with two fatty acids and a modified phosphate group attached to a glycerol backbone. The phosphate may be modified by the addition of charged or polar chemical groups. Two chemical groups that may modify the phosphate, choline and serine, are shown here. Both choline and serine attach to the phosphate group at the position labeled R via the hydroxyl group indicated in green.

A phospholipid is an amphipathic molecule, meaning it has a hydrophobic and a hydrophilic part. The fatty acid chains are hydrophobic and cannot interact with water, whereas the phosphate-containing group is hydrophilic and interacts with water (Figure 1.3.4.9).

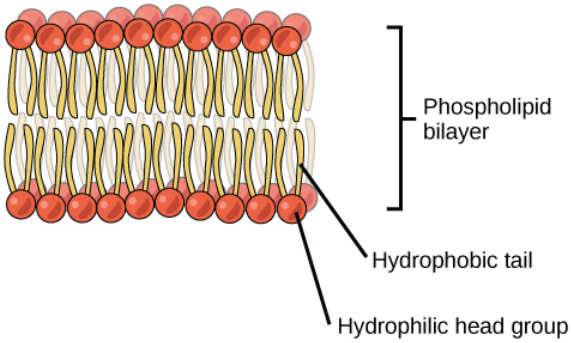


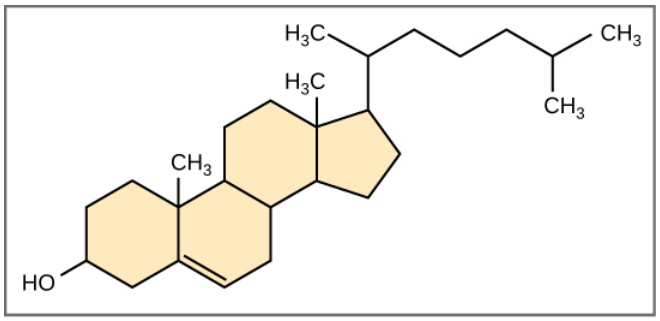
Figure 1.3.4.9: The phospholipid bilayer is the major component of all cellular membranes. The hydrophilic head groups of the phospholipids face the aqueous solution. The hydrophobic tails are sequestered in the middle of the bilayer.

The head is the hydrophilic part, and the tail contains the hydrophobic fatty acids. In a membrane, a bilayer of phospholipids forms the matrix of the structure, the fatty acid tails of phospholipids face inside, away from water, whereas the phosphate group faces the outside, aqueous side (Figure 1.3.4.9).

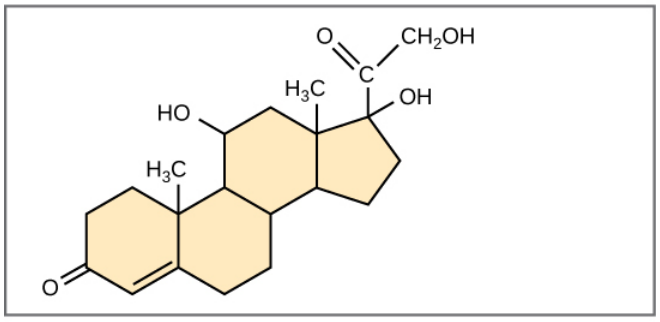
Phospholipids are responsible for the dynamic nature of the plasma membrane. If a drop of phospholipids is placed in water, it spontaneously forms a structure known as a micelle, where the hydrophilic phosphate heads face the outside and the fatty acids face the interior of this structure.

Steroids

Unlike the phospholipids and fats discussed earlier, steroids have a fused ring structure. Although they do not resemble the other lipids, they are grouped with them because they are also hydrophobicand insoluble in water. All steroids have four linked carbon rings and several of them, like cholesterol, have a short tail (Figure 1.3.4.10). Many steroids also have the –OH functional group, which puts them in the alcohol classification (sterols).



Cholesterol



Cortisol

Figure 1.3.4.10: Steroids such as cholesterol and cortisol are composed of four fused hydrocarbon rings.

Cholesterol is the most common steroid. Cholesterol is mainly synthesized in the liver and is the precursor to many steroid hormones such as testosterone and estradiol, which are secreted by the gonads and endocrine glands. It is also the precursor to Vitamin D. Cholesterol is also the precursor of bile salts, which help in the emulsification of fats and their subsequent absorption by cells. Although cholesterol is often spoken of in negative terms by lay people, it is necessary for proper functioning of the body. It is a component of the plasma membrane of animal cells and is found within the phospholipid bilayer. Being the outermost structure in animal cells, the plasma membrane is responsible for the transport of materials and cellular recognition and it is involved in cell-to-cell communication.

Link to Learning

For an additional perspective on lipids, explore the interactive animation "Biomolecules: The Lipids".

Summary

Lipids are a class of macromolecules that are nonpolar and hydrophobic in nature. Major types include fats and oils, waxes, phospholipids, and steroids. Fats are a stored form of energy and are also known as triacylglycerols or triglycerides. Fats are made up of fatty acids and either glycerol or sphingosine. Fatty acids may be unsaturated or saturated, depending on the presence or absence of double bonds in the hydrocarbon chain. If only single bonds are present, they are known as saturated fatty acids. Unsaturated fatty acids may have one or more double bonds in the hydrocarbon chain. Phospholipids make up the matrix of membranes. They have a glycerol or sphingosine backbone to which two fatty acid chains and a phosphate-containing group are attached. Steroids are another class of lipids. Their basic structure has four fused carbon rings. Cholesterol is a type of steroid and is an important constituent of the plasma membrane, where it helps to maintain the fluid nature of the membrane. It is also the precursor of steroid hormones such as testosterone.

Glossary

lipid
: macromolecule that is nonpolar and insoluble in water

omega fat
: type of polyunsaturated fat that is required by the body; the numbering of the carbon omega starts from the methyl end or the end that is farthest from the carboxylic end

phospholipid
: major constituent of the membranes; composed of two fatty acids and a phosphate-containing group attached to a glycerol backbone

saturated fatty acid
: long-chain of hydrocarbon with single covalent bonds in the carbon chain; the number of hydrogen atoms attached to the carbon skeleton is maximized

steroid
: type of lipid composed of four fused hydrocarbon rings forming a planar structure

trans fat
: fat formed artificially by hydrogenating oils, leading to a different arrangement of double bond(s) than those found in naturally occurring lipids

triacylglycerol (also, triglyceride)
: fat molecule; consists of three fatty acids linked to a glycerol molecule

unsaturated fatty acid
: long-chain hydrocarbon that has one or more double bonds in the hydrocarbon chain

wax
: lipid made of a long-chain fatty acid that is esterified to a long-chain alcohol; serves as a protective coating on some feathers, aquatic mammal fur, and leaves

---

This page titled 1.3.4: Lipids is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.3: Lipids** by OpenStax is licensed CC BY 4.0.

1.3.5: Proteins

Skills to Develop

- Describe the functions proteins perform in the cell and in tissues
- Discuss the relationship between amino acids and proteins
- Explain the four levels of protein organization
- Describe the ways in which protein shape and function are linked

Proteins are one of the most abundant organic molecules in living systems and have the most diverse range of functions of all macromolecules. Proteins may be structural, regulatory, contractile, or protective; they may serve in transport, storage, or membranes; or they may be toxins or enzymes. Each cell in a living system may contain thousands of proteins, each with a unique function. Their structures, like their functions, vary greatly. They are all, however, polymers of amino acids, arranged in a linear sequence.

Types and Functions of Proteins

Enzymes, which are produced by living cells, are catalysts in biochemical reactions (like digestion) and are usually complex or conjugated proteins. Each enzyme is specific for the substrate (a reactant that binds to an enzyme) it acts on. The enzyme may help in breakdown, rearrangement, or synthesis reactions. Enzymes that break down their substrates are called catabolic enzymes, enzymes that build more complex molecules from their substrates are called anabolic enzymes, and enzymes that affect the rate of reaction are called catalytic enzymes. It should be noted that all enzymes increase the rate of reaction and, therefore, are considered to be organic catalysts. An example of an enzyme is salivary amylase, which hydrolyzes its substrate amylose, a component of starch.

Hormones are chemical-signaling molecules, usually small proteins or steroids, secreted by endocrine cells that act to control or regulate specific physiological processes, including growth, development, metabolism, and reproduction. For example, insulin is a protein hormone that helps to regulate the blood glucose level. The primary types and functions of proteins are listed in Table 1.3.5.1.

Table 1.3.5.1: Protein Types and Functions

Type	Examples	Functions
Digestive Enzymes	Amylase, lipase, pepsin, trypsin	Help in digestion of food by catabolizing nutrients into monomeric units
Transport	Hemoglobin, albumin	Carry substances in the blood or lymph throughout the body
Structural	Actin, tubulin, keratin	Construct different structures, like the cytoskeleton
Hormones	Insulin, thyroxine	Coordinate the activity of different body systems
Defense	Immunoglobulins	Protect the body from foreign pathogens
Contractile	Actin, myosin	Effect muscle contraction
Storage	Legume storage proteins, egg white (albumin)	Provide nourishment in early development of the embryo and the seedling

Proteins have different shapes and molecular weights; some proteins are globular in shape whereas others are fibrous in nature. For example, hemoglobin is a globular protein, but collagen, found in our skin, is a fibrous protein. Protein shape is critical to its function, and this shape is maintained by many different types of chemical bonds. Changes in temperature, pH, and exposure to

chemicals may lead to permanent changes in the shape of the protein, leading to loss of function, known as denaturation. All proteins are made up of different arrangements of the same 20 types of amino acids.

Amino Acids

Amino acids are the monomers that make up proteins. Each amino acid has the same fundamental structure, which consists of a central carbon atom, also known as the alpha (α) carbon, bonded to an amino group (NH_2), a carboxyl group (COOH), and to a hydrogen atom. Every amino acid also has another atom or group of atoms bonded to the central atom known as the R group (Figure 1.3.5.1).

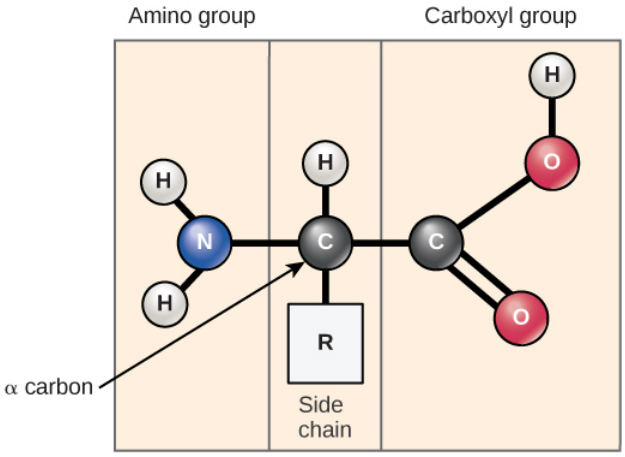


Figure 1.3.5.1: Amino acids have a central asymmetric carbon to which an amino group, a carboxyl group, a hydrogen atom, and a side chain (R group) are attached.

The name "amino acid" is derived from the fact that they contain both amino group and carboxyl-acid-group in their basic structure. As mentioned, there are 20 amino acids present in proteins. Ten of these are considered essential amino acids in humans because the human body cannot produce them and they are obtained from the diet. For each amino acid, the R group (or side chain) is different (Figure 1.3.5.2).

Art Connection

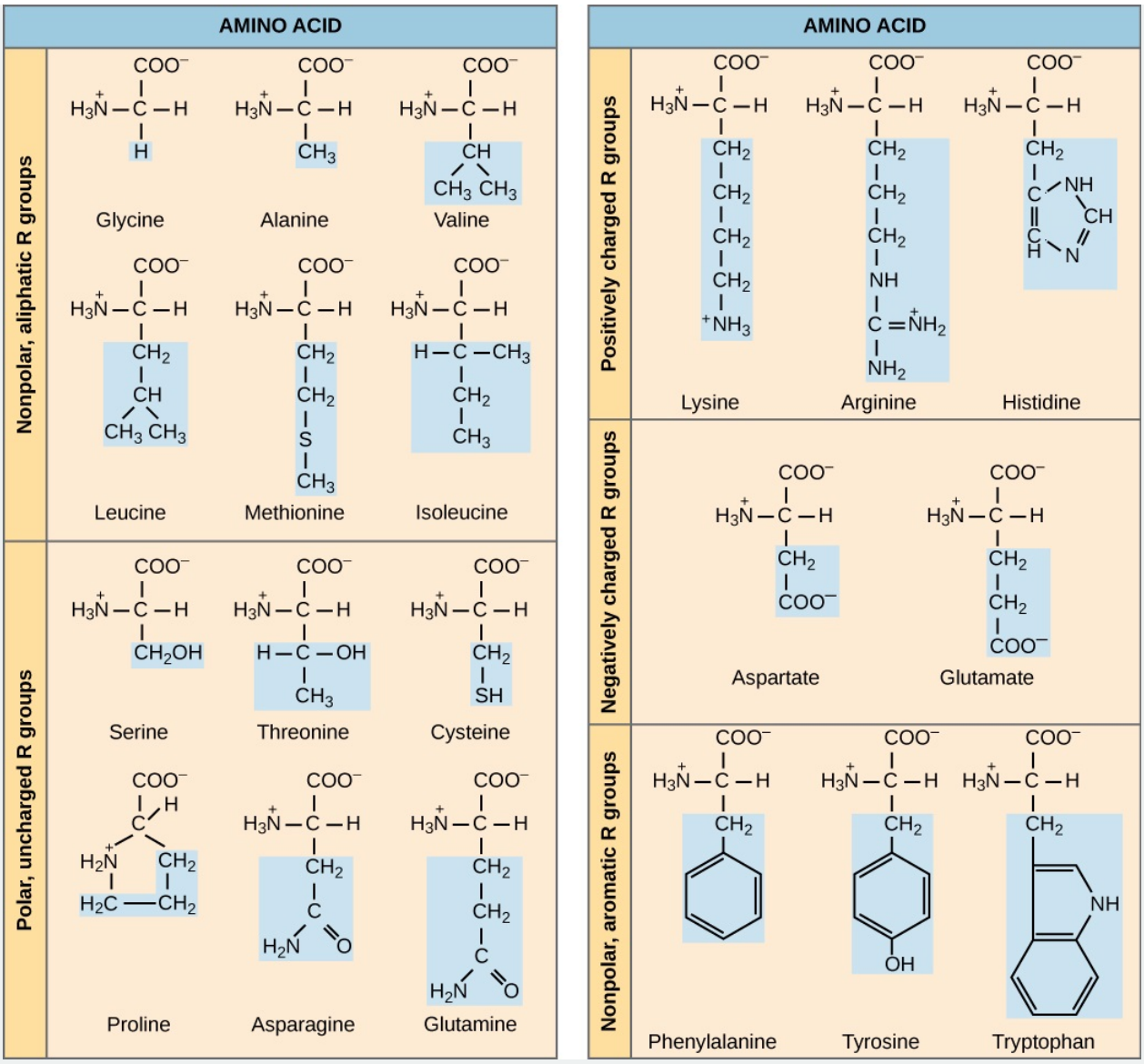


Figure 1.3.5.2: There are 20 common amino acids commonly found in proteins, each with a different R group (variant group) that determines its chemical nature.

Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

The chemical nature of the side chain determines the nature of the amino acid (that is, whether it is acidic, basic, polar, or nonpolar). For example, the amino acid glycine has a hydrogen atom as the R group. Amino acids such as valine, methionine, and alanine are nonpolar or hydrophobic in nature, while amino acids such as serine, threonine, and cysteine are polar and have hydrophilic side chains. The side chains of lysine and arginine are positively charged, and therefore these amino acids are also known as basic amino acids. Proline has an R group that is linked to the amino group, forming a ring-like structure. Proline is an exception to the standard structure of an animo acid since its amino group is not separate from the side chain (Figure 1.3.5.2).

Amino acids are represented by a single upper case letter or a three-letter abbreviation. For example, valine is known by the letter V or the three-letter symbol val. Just as some fatty acids are essential to a diet, some amino acids are necessary as well. They are known as essential amino acids, and in humans they include isoleucine, leucine, and cysteine. Essential amino acids refer to those necessary for construction of proteins in the body, although not produced by the body; which amino acids are essential varies from organism to organism.

The sequence and the number of amino acids ultimately determine the protein's shape, size, and function. Each amino acid is attached to another amino acid by a covalent bond, known as a peptide bond, which is formed by a dehydration reaction. The carboxyl group of one amino acid and the amino group of the incoming amino acid combine, releasing a molecule of water. The resulting bond is the peptide bond (Figure 1.3.5.3).

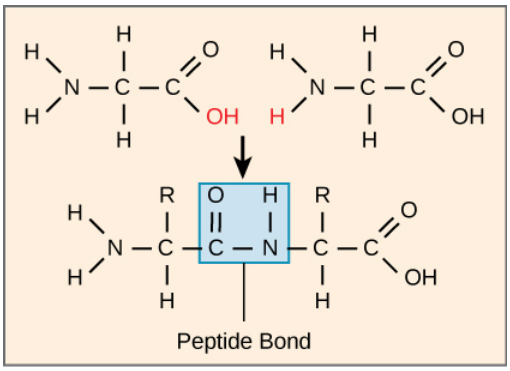


Figure 1.3.5.3: Peptide bond formation is a dehydration synthesis reaction. The carboxyl group of one amino acid is linked to the amino group of the incoming amino acid. In the process, a molecule of water is released.

The products formed by such linkages are called peptides. As more amino acids join to this growing chain, the resulting chain is known as a polypeptide. Each polypeptide has a free amino group at one end. This end is called the N terminal, or the amino terminal, and the other end has a free carboxyl group, also known as the C or carboxyl terminal. While the terms polypeptide and protein are sometimes used interchangeably, a polypeptide is technically a polymer of amino acids, whereas the term protein is used for a polypeptide or polypeptides that have combined together, often have bound non-peptide prosthetic groups, have a distinct shape, and have a unique function. After protein synthesis (translation), most proteins are modified. These are known as post-translational modifications. They may undergo cleavage, phosphorylation, or may require the addition of other chemical groups. Only after these modifications is the protein completely functional.

Evolution Connection

The Evolutionary Significance of Cytochrome cCytochrome c is an important component of the electron transport chain, a part of cellular respiration, and it is normally found in the cellular organelle, the mitochondrion. This protein has a heme prosthetic group, and the central ion of the heme gets alternately reduced and oxidized during electron transfer. Because this essential protein's role in producing cellular energy is crucial, it has changed very little over millions of years. Protein sequencing has shown that there is a considerable amount of cytochrome c amino acid sequence homology among different species; in other words, evolutionary kinship can be assessed by measuring the similarities or differences among various species' DNA or protein sequences.

Scientists have determined that human cytochrome c contains 104 amino acids. For each cytochrome c molecule from different organisms that has been sequenced to date, 37 of these amino acids appear in the same position in all samples of cytochrome c. This indicates that there may have been a common ancestor. On comparing the human and chimpanzee protein sequences, no sequence difference was found. When human and rhesus monkey sequences were compared, the single difference found was in one amino acid. In another comparison, human to yeast sequencing shows a difference in the 44th position.

Protein Structure

As discussed earlier, the shape of a protein is critical to its function. For example, an enzyme can bind to a specific substrate at a site known as the active site. If this active site is altered because of local changes or changes in overall protein structure, the enzyme may be unable to bind to the substrate. To understand how the protein gets its final shape or conformation, we need to understand the four levels of protein structure: primary, secondary, tertiary, and quaternary.

Primary Structure

The unique sequence of amino acids in a polypeptide chain is its primary structure. For example, the pancreatic hormone insulin has two polypeptide chains, A and B, and they are linked together by disulfide bonds. The N terminal amino acid of the A chain is

glycine, whereas the C terminal amino acid is asparagine (Figure 1.3.5.4). The sequences of amino acids in the A and B chains are unique to insulin.

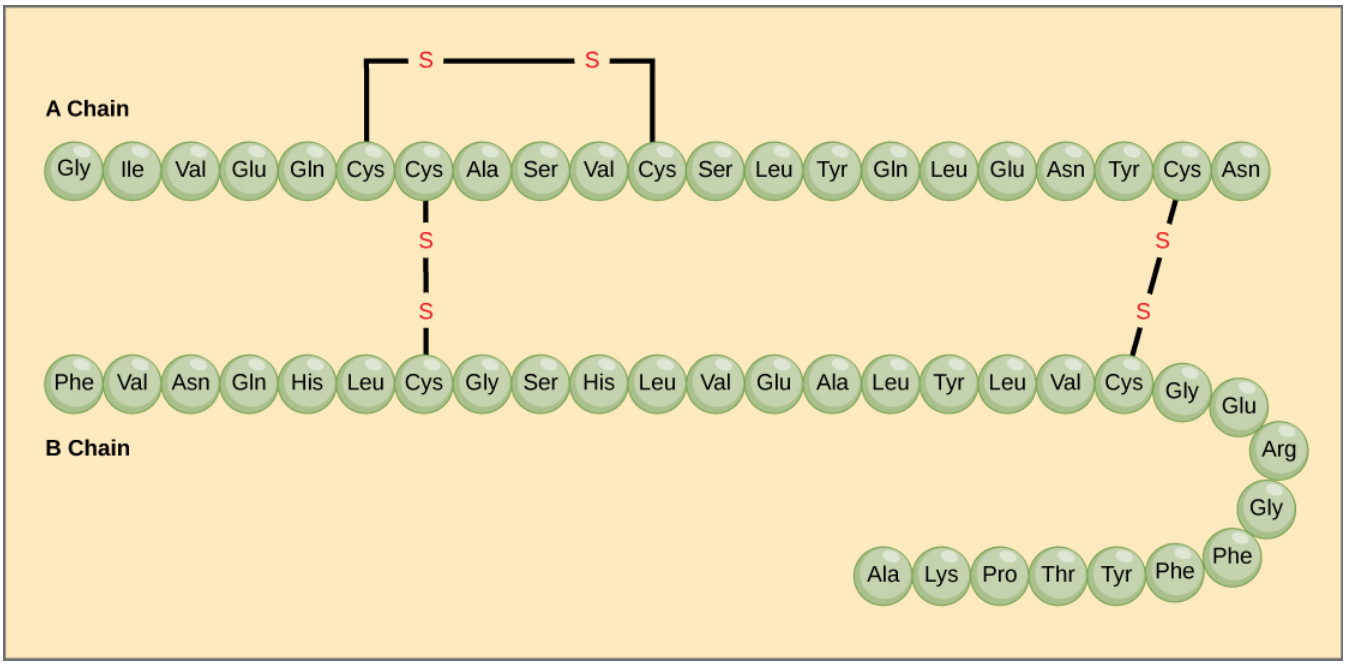


Figure 1.3.5.4: Bovine serum insulin is a protein hormone made of two peptide chains, A (21 amino acids long) and B (30 amino acids long). In each chain, primary structure is indicated by three-letter abbreviations that represent the names of the amino acids in the order they are present. The amino acid cysteine (cys) has a sulfhydryl (SH) group as a side chain. Two sulfhydryl groups can react in the presence of oxygen to form a disulfide (S-S) bond. Two disulfide bonds connect the A and B chains together, and a third helps the A chain fold into the correct shape. Note that all disulfide bonds are the same length, but are drawn different sizes for clarity.

The unique sequence for every protein is ultimately determined by the gene encoding the protein. A change in nucleotide sequence of the gene's coding region may lead to a different amino acid being added to the growing polypeptide chain, causing a change in protein structure and function. In sickle cell anemia, the hemoglobin β chain (a small portion of which is shown in Figure 1.3.5.5) has a single amino acid substitution, causing a change in protein structure and function. Specifically, the amino acid glutamic acid is substituted by valine in the β chain. What is most remarkable to consider is that a hemoglobin molecule is made up of two alpha chains and two beta chains that each consist of about 150 amino acids. The molecule, therefore, has about 600 amino acids. The structural difference between a normal hemoglobin molecule and a sickle cell molecule—which dramatically decreases life expectancy—is a single amino acid of the 600. What is even more remarkable is that those 600 amino acids are encoded by three nucleotides each, and the mutation is caused by a single base change (point mutation), 1 in 1800 bases.

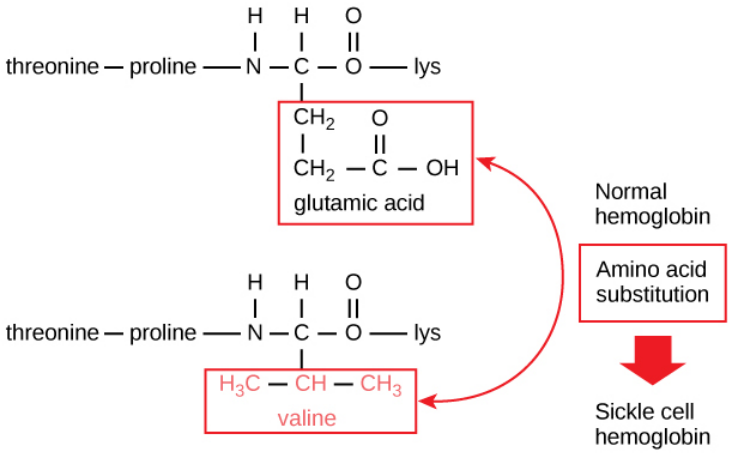


Figure 1.3.5.5: The beta chain of hemoglobin is 147 residues in length, yet a single amino acid substitution leads to sickle cell anemia. In normal hemoglobin, the amino acid at position seven is glutamate. In sickle cell hemoglobin, this glutamate is replaced by a valine.

Because of this change of one amino acid in the chain, hemoglobin molecules form long fibers that distort the biconcave, or disc-shaped, red blood cells and assume a crescent or "sickle" shape, which clogs arteries (Figure 1.3.5.6). This can lead to myriad serious health problems such as breathlessness, dizziness, headaches, and abdominal pain for those affected by this disease.

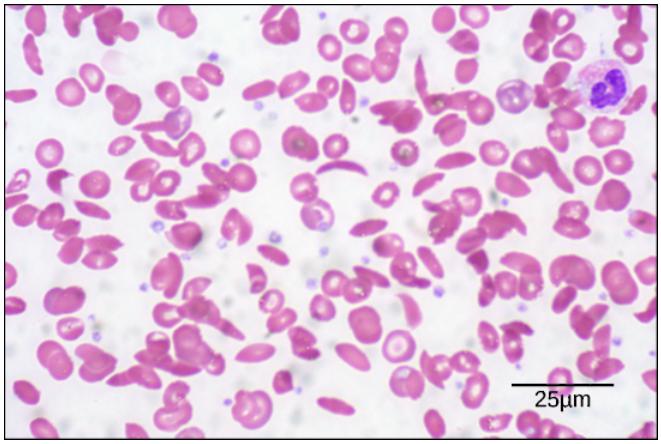


Figure 1.3.5.6: In this blood smear, visualized at 535x magnification using bright field microscopy, sickle cells are crescent shaped, while normal cells are disc-shaped. (credit: modification of work by Ed Uthman; scale-bar data from Matt Russell)

Secondary Structure

The local folding of the polypeptide in some regions gives rise to the secondary structure of the protein. The most common are the α-helix and β-pleated sheet structures (Figure 1.3.5.7). Both structures are the α-helix structure—the helix held in shape by hydrogen bonds. The hydrogen bonds form between the oxygen atom in the carbonyl group in one amino acid and another amino acid that is four amino acids farther along the chain.

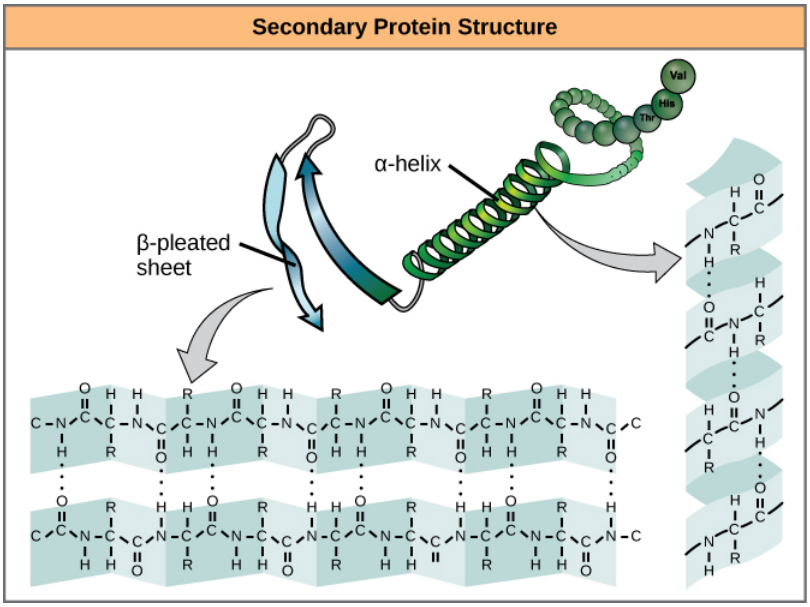


Figure 1.3.5.7: The α-helix and β-pleated sheet are secondary structures of proteins that form because of hydrogen bonding between carbonyl and amino groups in the peptide backbone. Certain amino acids have a propensity to form an α-helix, while others have a propensity to form a β-pleated sheet.

Every helical turn in an alpha helix has 3.6 amino acid residues. The R groups (the variant groups) of the polypeptide protrude out from the α-helix chain. In the β-pleated sheet, the "pleats" are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain. The R groups are attached to the carbons and extend above and below the folds of the pleat. The pleated segments align parallel or antiparallel to each other, and hydrogen bonds form between the partially positive nitrogen atom in the amino group and the partially negative oxygen atom in the carbonyl group of the peptide backbone. The α-helix and β-pleated sheet structures are found in most globular and fibrous proteins and they play an important structural role.

Tertiary Structure

The unique three-dimensional structure of a polypeptide is its tertiary structure (Figure 1.3.5.8). This structure is in part due to chemical interactions at work on the polypeptide chain. Primarily, the interactions among R groups creates the complex three-dimensional tertiary structure of a protein. The nature of the R groups found in the amino acids involved can counteract the formation of the hydrogen bonds described for standard secondary structures. For example, R groups with like charges are repelled by each other and those with unlike charges are attracted to each other (ionic bonds). When protein folding takes place, the hydrophobic R groups of nonpolar amino acids lay in the interior of the protein, whereas the hydrophilic R groups lay on the outside. The former types of interactions are also known as hydrophobic interactions. Interaction between cysteine side chains forms disulfide linkages in the presence of oxygen, the only covalent bond forming during protein folding.

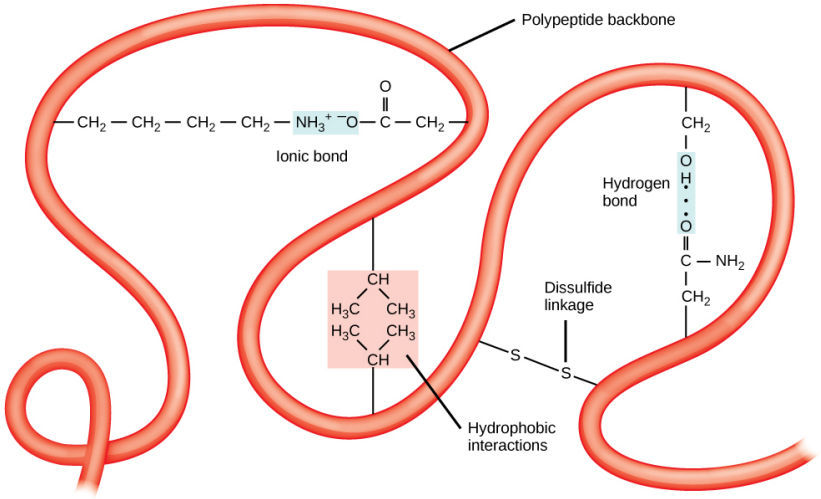


Figure 1.3.5.8: The tertiary structure of proteins is determined by a variety of chemical interactions. These include hydrophobic interactions, ionic bonding, hydrogen bonding and disulfide linkages.

All of these interactions, weak and strong, determine the final three-dimensional shape of the protein. When a protein loses its three-dimensional shape, it may no longer be functional.

Quaternary Structure

In nature, some proteins are formed from several polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure. Weak interactions between the subunits help to stabilize the overall structure. For example, insulin (a globular protein) has a combination of hydrogen bonds and disulfide bonds that cause it to be mostly clumped into a ball shape. Insulin starts out as a single polypeptide and loses some internal sequences in the presence of post-translational modification after the formation of the disulfide linkages that hold the remaining chains together. Silk (a fibrous protein), however, has a β-pleated sheet structure that is the result of hydrogen bonding between different chains.

The four levels of protein structure (primary, secondary, tertiary, and quaternary) are illustrated in Figure 1.3.5.9.

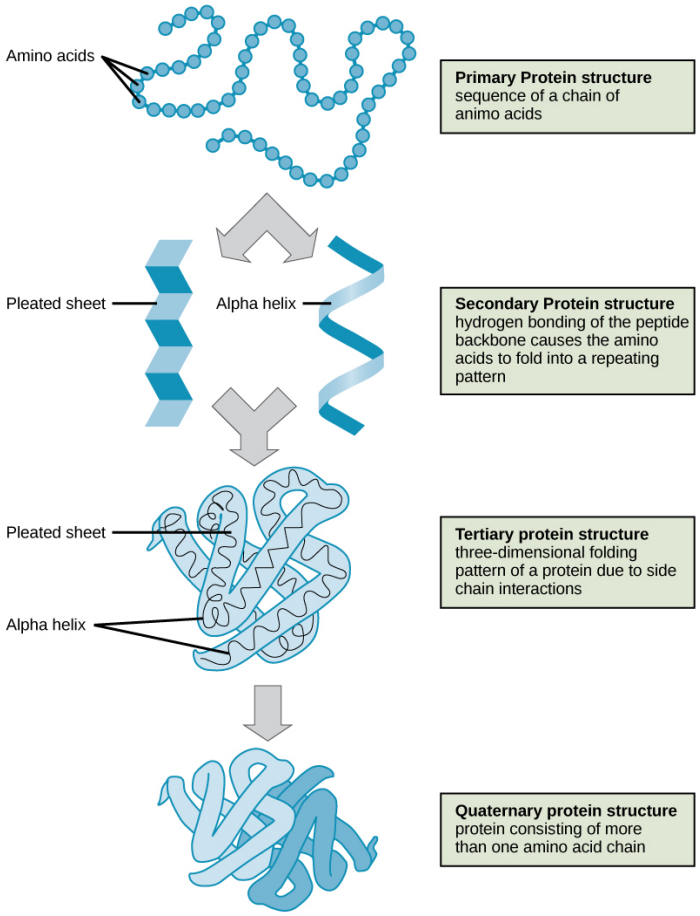


Figure 1.3.5.9: The four levels of protein structure can be observed in these illustrations. (credit: modification of work by National Human Genome Research Institute)

Denaturation and Protein Folding

Each protein has its own unique sequence and shape that are held together by chemical interactions. If the protein is subject to changes in temperature, pH, or exposure to chemicals, the protein structure may change, losing its shape without losing its primary sequence in what is known as denaturation. Denaturation is often reversible because the primary structure of the polypeptide is conserved in the process if the denaturing agent is removed, allowing the protein to resume its function. Sometimes denaturation is irreversible, leading to loss of function. One example of irreversible protein denaturation is when an egg is fried. The albumin protein in the liquid egg white is denatured when placed in a hot pan. Not all proteins are denatured at high temperatures; for instance, bacteria that survive in hot springs have proteins that function at temperatures close to boiling. The stomach is also very acidic, has a low pH, and denatures proteins as part of the digestion process; however, the digestive enzymes of the stomach retain their activity under these conditions.

Protein folding is critical to its function. It was originally thought that the proteins themselves were responsible for the folding process. Only recently was it found that often they receive assistance in the folding process from protein helpers known as chaperones (or chaperonins) that associate with the target protein during the folding process. They act by preventing aggregation of polypeptides that make up the complete protein structure, and they disassociate from the protein once the target protein is folded.

Summary

Proteins are a class of macromolecules that perform a diverse range of functions for the cell. They help in metabolism by providing structural support and by acting as enzymes, carriers, or hormones. The building blocks of proteins (monomers) are amino acids. Each amino acid has a central carbon that is linked to an amino group, a carboxyl group, a hydrogen atom, and an R group or side chain. There are 20 commonly occurring amino acids, each of which differs in the R group. Each amino acid is linked to its neighbors by a peptide bond. A long chain of amino acids is known as a polypeptide.

Proteins are organized at four levels: primary, secondary, tertiary, and (optional) quaternary. The primary structure is the unique sequence of amino acids. The local folding of the polypeptide to form structures such as the α helix and β-pleated sheet constitutes the secondary structure. The overall three-dimensional structure is the tertiary structure. When two or more polypeptides combine to form the complete protein structure, the configuration is known as the quaternary structure of a protein. Protein shape and function are intricately linked; any change in shape caused by changes in temperature or pH may lead to protein denaturation and a loss in function.

Art Connections

Figure 1.3.5.2: Which categories of amino acid would you expect to find on the surface of a soluble protein, and which would you expect to find in the interior? What distribution of amino acids would you expect to find in a protein embedded in a lipid bilayer?

Answer

Polar and charged amino acid residues (the remainder after peptide bond formation) are more likely to be found on the surface of soluble proteins where they can interact with water, and nonpolar (e.g., amino acid side chains) are more likely to be found in the interior where they are sequestered from water. In membrane proteins, nonpolar and hydrophobic amino acid side chains associate with the hydrophobic tails of phospholipids, while polar and charged amino acid side chains interact with the polar head groups or with the aqueous solution. However, there are exceptions. Sometimes, positively and negatively charged amino acid side chains interact with one another in the interior of a protein, and polar or charged amino acid side chains that interact with a ligand can be found in the ligand binding pocket.

Glossary

alpha-helix structure (α-helix)
type of secondary structure of proteins formed by folding of the polypeptide into a helix shape with hydrogen bonds stabilizing the structure

amino acid
monomer of a protein; has a central carbon or alpha carbon to which an amino group, a carboxyl group, a hydrogen, and an R group or side chain is attached; the R group is different for all 20 amino acids

beta-pleated sheet (β-pleated)
secondary structure found in proteins in which “pleats” are formed by hydrogen bonding between atoms on the backbone of the polypeptide chain

chaperone
(also, chaperonin) protein that helps nascent protein in the folding process

denaturation
loss of shape in a protein as a result of changes in temperature, pH, or exposure to chemicals

enzyme
catalyst in a biochemical reaction that is usually a complex or conjugated protein

hormone
chemical signaling molecule, usually protein or steroid, secreted by endocrine cells that act to control or regulate specific physiological processes

peptide bond
bond formed between two amino acids by a dehydration reaction

polypeptide

long chain of amino acids linked by peptide bonds

primary structure

linear sequence of amino acids in a protein

protein

biological macromolecule composed of one or more chains of amino acids

quaternary structure

association of discrete polypeptide subunits in a protein

secondary structure

regular structure formed by proteins by intramolecular hydrogen bonding between the oxygen atom of one amino acid residue and the hydrogen attached to the nitrogen atom of another amino acid residue

tertiary structure

three-dimensional conformation of a protein, including interactions between secondary structural elements; formed from interactions between amino acid side chains

---

This page titled 1.3.5: Proteins is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.4: Proteins** by OpenStax is licensed CC BY 4.0.

1.3.6: Nucleic Acids

Skills to Develop

- Describe the structure of nucleic acids and define the two types of nucleic acids
- Explain the structure and role of DNA
- Explain the structure and roles of RNA

Nucleic acids are the most important macromolecules for the continuity of life. They carry the genetic blueprint of a cell and carry instructions for the functioning of the cell.

DNA and RNA

The two main types of nucleic acids are deoxyribonucleic acid (DNA) and ribonucleic acid (RNA). DNA is the genetic material found in all living organisms, ranging from single-celled bacteria to multicellular mammals. It is found in the nucleus of eukaryotes and in the organelles, chloroplasts, and mitochondria. In prokaryotes, the DNA is not enclosed in a membranous envelope.

The entire genetic content of a cell is known as its genome, and the study of genomes is genomics. In eukaryotic cells but not in prokaryotes, DNA forms a complex with histone proteins to form chromatin, the substance of eukaryotic chromosomes. A chromosome may contain tens of thousands of genes. Many genes contain the information to make protein products; other genes code for RNA products. DNA controls all of the cellular activities by turning the genes “on” or “off.”

The other type of nucleic acid, RNA, is mostly involved in protein synthesis. The DNA molecules never leave the nucleus but instead use an intermediary to communicate with the rest of the cell. This intermediary is the messenger RNA (mRNA). Other types of RNA—like rRNA, tRNA, and microRNA—are involved in protein synthesis and its regulation.

DNA and RNA are made up of monomers known as nucleotides. The nucleotides combine with each other to form a polynucleotide, DNA or RNA. Each nucleotide is made up of three components: a nitrogenous base, a pentose (five-carbon) sugar, and a phosphate group (Figure 1.3.6.1). Each nitrogenous base in a nucleotide is attached to a sugar molecule, which is attached to one or more phosphate groups.

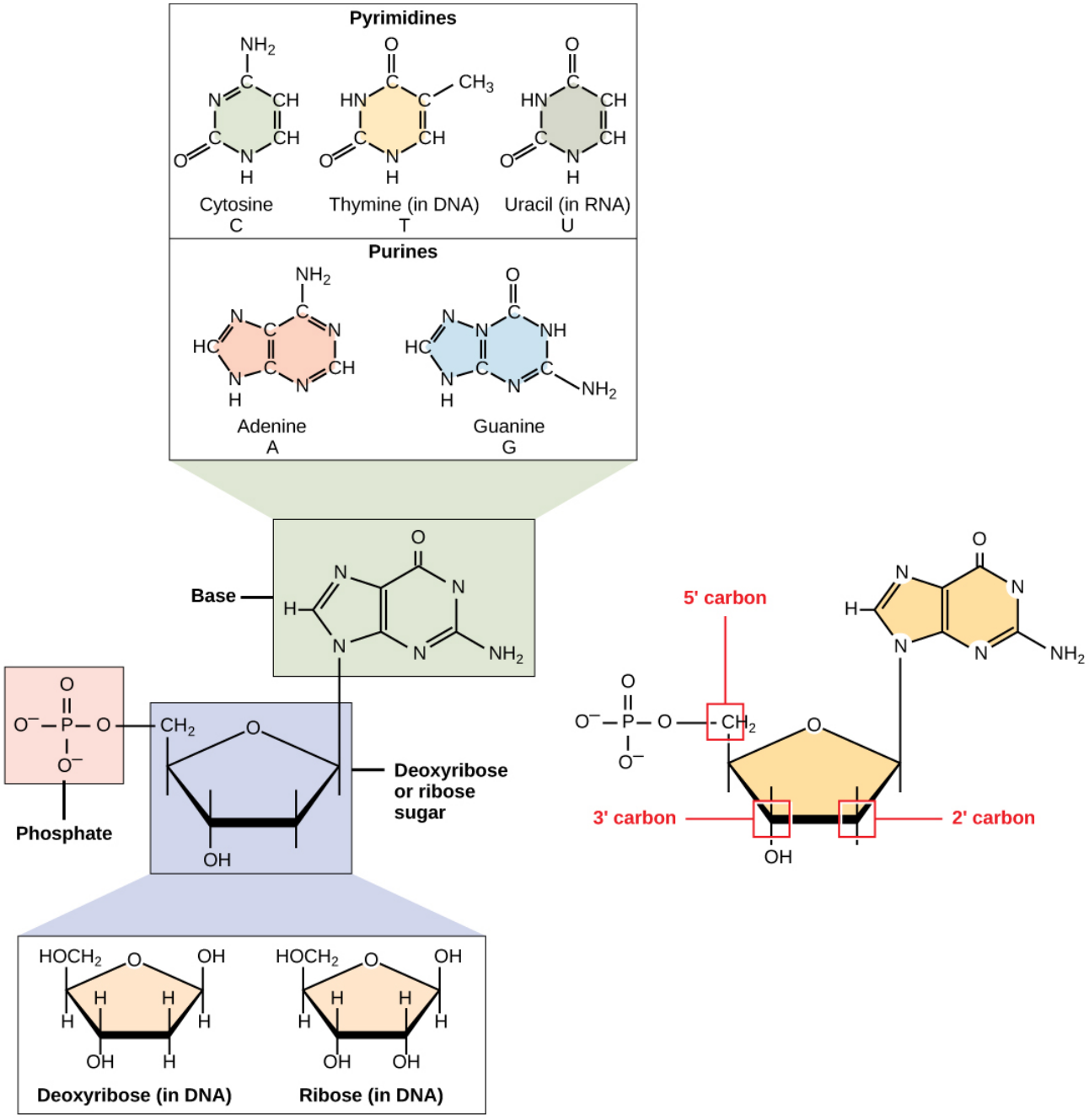


Figure 1.3.6.1: A nucleotide is made up of three components: a nitrogenous base, a pentose sugar, and one or more phosphate groups. Carbon residues in the pentose are numbered 1′ through 5′ (the prime distinguishes these residues from those in the base, which are numbered without using a prime notation). The base is attached to the 1′ position of the ribose, and the phosphate is attached to the 5′ position. When a polynucleotide is formed, the 5′ phosphate of the incoming nucleotide attaches to the 3′ hydroxyl group at the end of the growing chain. Two types of pentose are found in nucleotides, deoxyribose (found in DNA) and ribose (found in RNA). Deoxyribose is similar in structure to ribose, but it has an H instead of an OH at the 2′ position. Bases can be divided into two categories: purines and pyrimidines. Purines have a double ring structure, and pyrimidines have a single ring.

The nitrogenous bases, important components of nucleotides, are organic molecules and are so named because they contain carbon and nitrogen. They are bases because they contain an amino group that has the potential of binding an extra hydrogen, and thus, decreases the hydrogen ion concentration in its environment, making it more basic. Each nucleotide in DNA contains one of four possible nitrogenous bases: adenine (A), guanine (G) cytosine (C), and thymine (T).

Adenine and guanine are classified as purines. The primary structure of a purine is two carbon-nitrogen rings. Cytosine, thymine, and uracil are classified as pyrimidines which have a single carbon-nitrogen ring as their primary structure (Figure 1.3.6.1). Each of

these basic carbon-nitrogen rings has different functional groups attached to it. In molecular biology shorthand, the nitrogenous bases are simply known by their symbols A, T, G, C, and U. DNA contains A, T, G, and C whereas RNA contains A, U, G, and C.

The pentose sugar in DNA is deoxyribose, and in RNA, the sugar is ribose (Figure 1.3.6.1). The difference between the sugars is the presence of the hydroxyl group on the second carbon of the ribose and hydrogen on the second carbon of the deoxyribose. The carbon atoms of the sugar molecule are numbered as 1′, 2′, 3′, 4′, and 5′ (1′ is read as “one prime”). The phosphate residue is attached to the hydroxyl group of the 5′ carbon of one sugar and the hydroxyl group of the 3′ carbon of the sugar of the next nucleotide, which forms a 5′–3′ phosphodiester linkage. The phosphodiester linkage is not formed by simple dehydration reaction like the other linkages connecting monomers in macromolecules: its formation involves the removal of two phosphate groups. A polynucleotide may have thousands of such phosphodiester linkages.

DNA Double-Helix Structure

DNA has a double-helix structure (Figure 1.3.6.2). The sugar and phosphate lie on the outside of the helix, forming the backbone of the DNA. The nitrogenous bases are stacked in the interior, like the steps of a staircase, in pairs; the pairs are bound to each other by hydrogen bonds. Every base pair in the double helivx is separated from the next base pair by 0.34 nm. The two strands of the helix run in opposite directions, meaning that the 5′ carbon end of one strand will face the 3′ carbon end of its matching strand. (This is referred to as antiparallel orientation and is important to DNA replication and in many nucleic acid interactions.)

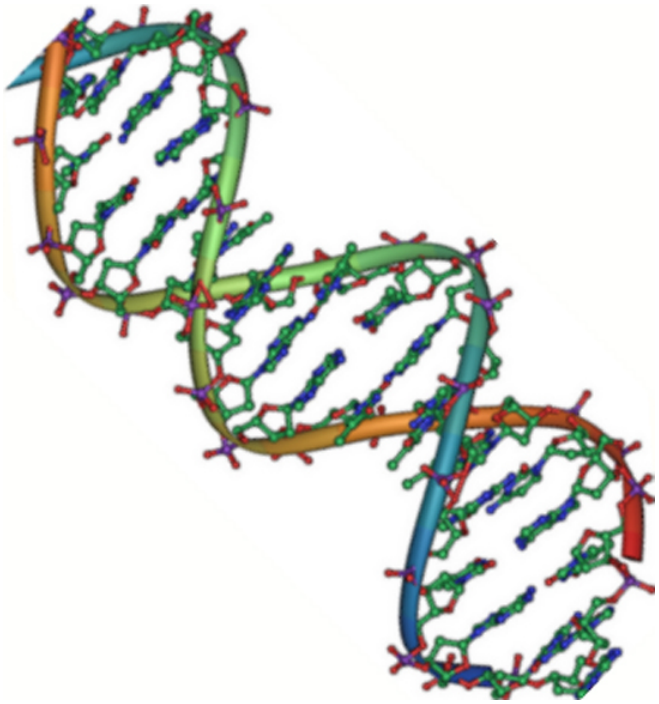


Figure 1.3.6.2: Native DNA is an antiparallel double helix. The phosphate backbone (indicated by the curvy lines) is on the outside, and the bases are on the inside. Each base from one strand interacts via hydrogen bonding with a base from the opposing strand. (credit: Jerome Walker/Dennis Myts)

Only certain types of base pairing are allowed. For example, a certain purine can only pair with a certain pyrimidine. This means A can pair with T, and G can pair with C, as shown in Figure 1.3.6.3. This is known as the base complementary rule. In other words, the DNA strands are complementary to each other. If the sequence of one strand is AATTGGCC, the complementary strand would have the sequence TTAACCGG. During DNA replication, each strand is copied, resulting in a daughter DNA double helix containing one parental DNA strand and a newly synthesized strand.

Art Connection

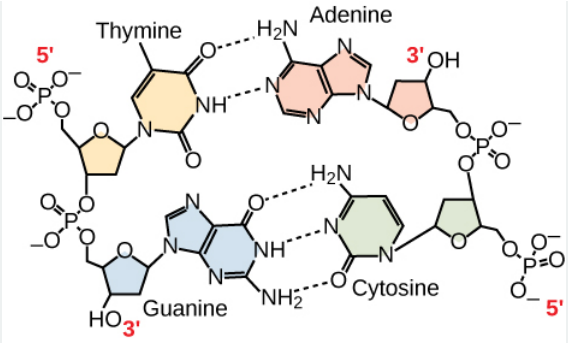


Figure 1.3.6.3: In a double stranded DNA molecule, the two strands run antiparallel to one another so that one strand runs 5′ to 3′ and the other 3′ to 5′. The phosphate backbone is located on the outside, and the bases are in the middle. Adenine forms hydrogen bonds (or base pairs) with thymine, and guanine base pairs with cytosine.

A mutation occurs, and cytosine is replaced with adenine. What impact do you think this will have on the DNA structure?

RNA

Ribonucleic acid, or RNA, is mainly involved in the process of protein synthesis under the direction of DNA. RNA is usually single-stranded and is made of ribonucleotides that are linked by phosphodiester bonds. A ribonucleotide in the RNA chain contains ribose (the pentose sugar), one of the four nitrogenous bases (A, U, G, and C), and the phosphate group.

There are four major types of RNA: messenger RNA (mRNA), ribosomal RNA (rRNA), transfer RNA (tRNA), and microRNA (miRNA). The first, mRNA, carries the message from DNA, which controls all of the cellular activities in a cell. If a cell requires a certain protein to be synthesized, the gene for this product is turned “on” and the messenger RNA is synthesized in the nucleus. The RNA base sequence is complementary to the coding sequence of the DNA from which it has been copied. However, in RNA, the base T is absent and U is present instead. If the DNA strand has a sequence AATTGCGC, the sequence of the complementary RNA is UUAACGCG. In the cytoplasm, the mRNA interacts with ribosomes and other cellular machinery (Figure 1.3.6.4).

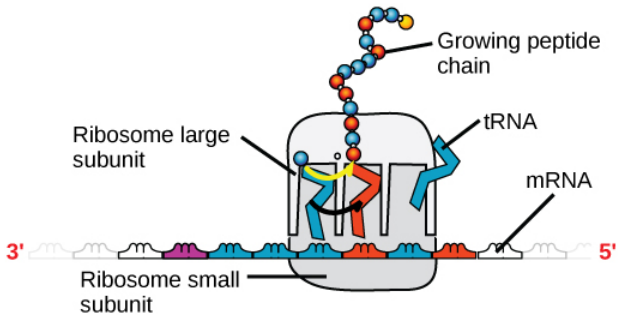


Figure 1.3.6.4: A ribosome has two parts: a large subunit and a small subunit. The mRNA sits in between the two subunits. A tRNA molecule recognizes a codon on the mRNA, binds to it by complementary base pairing, and adds the correct amino acid to the growing peptide chain.

The mRNA is read in sets of three bases known as codons. Each codon codes for a single amino acid. In this way, the mRNA is read and the protein product is made. Ribosomal RNA (rRNA) is a major constituent of ribosomes on which the mRNA binds. The rRNA ensures the proper alignment of the mRNA and the ribosomes; the rRNA of the ribosome also has an enzymatic activity (peptidyl transferase) and catalyzes the formation of the peptide bonds between two aligned amino acids. Transfer RNA (tRNA) is one of the smallest of the four types of RNA, usually 70–90 nucleotides long. It carries the correct amino acid to the site of protein synthesis. It is the base pairing between the tRNA and mRNA that allows for the correct amino acid to be inserted in the polypeptide chain. microRNAs are the smallest RNA molecules and their role involves the regulation of gene expression by interfering with the expression of certain mRNA messages. Table 1.3.6.1 below summarizes features of DNA and RNA.

Table 1.3.6.1: Features of DNA and RNA.

	DNA	RNA
Function	Carries genetic information	Involved in protein synthesis
Location	Remains in the nucleus	Leaves the nucleus
Structure	Double helix	Usually single-stranded
Sugar	Deoxyribose	Ribose
Pyrimidines	Cytosine, thymine	Cytosine, uracil
Purines	Adenine, guanine	Adenine, guanine

Even though the RNA is single stranded, most RNA types show extensive intramolecular base pairing between complementary sequences, creating a predictable three-dimensional structure essential for their function.

As you have learned, information flow in an organism takes place from DNA to RNA to protein. DNA dictates the structure of mRNA in a process known as transcription, and RNA dictates the structure of protein in a process known as translation. This is known as the Central Dogma of Life, which holds true for all organisms; however, exceptions to the rule occur in connection with viral infections.

Link to Learning

To learn more about DNA, explore the Howard Hughes Medical Institute BioInteractive animations on the topic of DNA.

Summary

Nucleic acids are molecules made up of nucleotides that direct cellular activities such as cell division and protein synthesis. Each nucleotide is made up of a pentose sugar, a nitrogenous base, and a phosphate group. There are two types of nucleic acids: DNA and RNA. DNA carries the genetic blueprint of the cell and is passed on from parents to offspring (in the form of chromosomes). It has a double-helical structure with the two strands running in opposite directions, connected by hydrogen bonds, and complementary to each other. RNA is single-stranded and is made of a pentose sugar (ribose), a nitrogenous base, and a phosphate group. RNA is involved in protein synthesis and its regulation. Messenger RNA (mRNA) is copied from the DNA, is exported from the nucleus to the cytoplasm, and contains information for the construction of proteins. Ribosomal RNA (rRNA) is a part of the ribosomes at the site of protein synthesis, whereas transfer RNA (tRNA) carries the amino acid to the site of protein synthesis. microRNA regulates the use of mRNA for protein synthesis.

Art Connections

Figure 1.3.6.3: A mutation occurs, and cytosine is replaced with adenine. What impact do you think this will have on the DNA structure?

Answer

Adenine is larger than cytosine and will not be able to base pair properly with the guanine on the opposing strand. This will cause the DNA to bulge. DNA repair enzymes may recognize the bulge and replace the incorrect nucleotide.

Glossary

deoxyribonucleic acid (DNA)
double-helical molecule that carries the hereditary information of the cell

messenger RNA (mRNA)
RNA that carries information from DNA to ribosomes during protein synthesis

nucleic acid
biological macromolecule that carries the genetic blueprint of a cell and carries instructions for the functioning of the cell

nucleotide
monomer of nucleic acids; contains a pentose sugar, one or more phosphate groups, and a nitrogenous base

phosphodiester
linkage covalent chemical bond that holds together the polynucleotide chains with a phosphate group linking two pentose sugars of neighboring nucleotides

polynucleotide
long chain of nucleotides

purine
type of nitrogenous base in DNA and RNA; adenine and guanine are purines

pyrimidine
type of nitrogenous base in DNA and RNA; cytosine, thymine, and uracil are pyrimidines

ribonucleic acid (RNA)
single-stranded, often internally base paired, molecule that is involved in protein synthesis

ribosomal RNA (rRNA)
RNA that ensures the proper alignment of the mRNA and the ribosomes during protein synthesis and catalyzes the formation of the peptide linkage

transcription
process through which messenger RNA forms on a template of DNA

transfer RNA (tRNA)
RNA that carries activated amino acids to the site of protein synthesis on the ribosome

translation
process through which RNA directs the formation of protein

This page titled 1.3.6: Nucleic Acids is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.5: Nucleic Acids** by OpenStax is licensed CC BY 4.0.

1.3.E: Biological Macromolecules (Exercises)

3.1: Synthesis of Biological Macromolecules

Review Questions

Dehydration synthesis leads to formation of

A. monomers
B. polymers
C. water and polymers
D. none of the above

Answer

C

During the breakdown of polymers, which of the following reactions takes place?

A. hydrolysis
B. dehydration
C. condensation
D. covalent bond

Answer

A

Free Response

Why are biological macromolecules considered organic?

Answer

Biological macromolecules are organic because they contain carbon.

What role do electrons play in dehydration synthesis and hydrolysis?

Answer

In a dehydration synthesis reaction, the hydrogen of one monomer combines with the hydroxyl group of another monomer, releasing a molecule of water. This creates an opening in the outer shells of atoms in the monomers, which can share electrons and form covalent bonds.

3.2: Carbohydrates

Review Questions

An example of a monosaccharide is _____.

A. fructose
B. glucose
C. galactose
D. all of the above

Answer

D

Cellulose and starch are examples of:

A. monosaccharides
B. disaccharides
C. lipids
D. polysaccharides

Answer

D

Plant cell walls contain which of the following in abundance?

A. starch
B. cellulose
C. glycogen
D. lactose

Answer

B

Lactose is a disaccharide formed by the formation of a _____ bond between glucose and _____.

A. glycosidic; lactose
B. glycosidic; galactose
C. hydrogen; sucrose
D. hydrogen; fructose

Answer

B

Free Response

Describe the similarities and differences between glycogen and starch.

Answer

Glycogen and starch are polysaccharides. They are the storage form of glucose. Glycogen is stored in animals in the liver and in muscle cells, whereas starch is stored in the roots, seeds, and leaves of plants. Starch has two different forms, one unbranched (amylose) and one branched (amylopectin), whereas glycogen is a single type of a highly branched molecule.

Why is it impossible for humans to digest food that contains cellulose?

Answer

The β 1-4 glycosidic linkage in cellulose cannot be broken down by human digestive enzymes. Herbivores such as cows, buffalos, and horses are able to digest grass that is rich in cellulose and use it as a food source because bacteria and protists in their digestive systems, especially in the rumen, secrete the enzyme cellulase. Cellulases can break down cellulose into glucose monomers that can be used as an energy source by the animal.

3.3: Lipids

Review Questions

Saturated fats have all of the following characteristics except:

A. they are solid at room temperature
B. they have single bonds within the carbon chain
C. they are usually obtained from animal sources
D. they tend to dissolve in water easily

Answer

D

Phospholipids are important components of _____.

A. the plasma membrane of animal cells
B. the ring structure of steroids
C. the waxy covering on leaves
D. the double bond in hydrocarbon chains

Answer

A

Free Response

Explain at least three functions that lipids serve in plants and/or animals.

Answer

Fat serves as a valuable way for animals to store energy. It can also provide insulation. Waxes can protect plant leaves and mammalian fur from getting wet. Phospholipids and steroids are important components of animal cell membranes, as well as plant, fungal, and bacterial membranes.

Why have trans fats been banned from some restaurants? How are they created?

Answer

Trans fats are created artificially when hydrogen gas is bubbled through oils to solidify them. The double bonds of the *cis* conformation in the hydrocarbon chain may be converted to double bonds in the *trans* configuration. Some restaurants are banning trans fats because they cause higher levels of LDL, or “bad” cholesterol.

3.4: Proteins

Review Questions

The monomers that make up proteins are called _____.

A. nucleotides
B. disaccharides
C. amino acids
D. chaperones

Answer

C

The α helix and the β-pleated sheet are part of which protein structure?

A. primary
B. secondary
C. tertiary
D. quaternary

Answer

B

Free Response

Explain what happens if even one amino acid is substituted for another in a polypeptide chain. Provide a specific example.

Answer

A change in gene sequence can lead to a different amino acid being added to a polypeptide chain instead of the normal one. This causes a change in protein structure and function. For example, in sickle cell anemia, the hemoglobin β chain has a single amino acid substitution—the amino acid glutamic acid in position six is substituted by valine. Because of this change, hemoglobin molecules form aggregates, and the disc-shaped red blood cells assume a crescent shape, which results in serious health problems.

Describe the differences in the four protein structures.

Answer

The sequence and number of amino acids in a polypeptide chain is its primary structure. The local folding of the polypeptide in some regions is the secondary structure of the protein. The three-dimensional structure of a polypeptide is known as its tertiary structure, created in part by chemical interactions such as hydrogen bonds between polar side chains, van der Waals interactions, disulfide linkages, and hydrophobic interactions. Some proteins are formed from multiple polypeptides, also known as subunits, and the interaction of these subunits forms the quaternary structure.

3.5: Nucleic Acids

Review Questions

A nucleotide of DNA may contain _____.

A. ribose, uracil, and a phosphate group
B. deoxyribose, uracil, and a phosphate group
C. deoxyribose, thymine, and a phosphate group
D. ribose, thymine, and a phosphate group

Answer

C

The building blocks of nucleic acids are _____.

A. sugars
B. nitrogenous bases
C. peptides
D. nucleotides

Answer

D

Free Response

What are the structural differences between RNA and DNA?

Answer

DNA has a double-helix structure. The sugar and the phosphate are on the outside of the helix and the nitrogenous bases are in the interior. The monomers of DNA are nucleotides containing deoxyribose, one of the four nitrogenous bases (A, T, G and C), and a phosphate group. RNA is usually single-stranded and is made of ribonucleotides that are linked by phosphodiester linkages. A ribonucleotide contains ribose (the pentose sugar), one of the four nitrogenous bases (A,U, G, and C), and the phosphate group.

What are the four types of RNA and how do they function?

Answer

The four types of RNA are messenger RNA, ribosomal RNA, transfer RNA, and microRNA. Messenger RNA carries the information from the DNA that controls all cellular activities. The mRNA binds to the ribosomes that are constructed of proteins and rRNA, and tRNA transfers the correct amino acid to the site of protein synthesis. microRNA regulates the availability of mRNA for translation.

This page titled 1.3.E: Biological Macromolecules (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **3.E: Biological Macromolecules (Exercises)** by OpenStax is licensed CC BY 4.0.

SECTION OVERVIEW

2: Unit II- The Cell

Unit 2: Students will gain solid understanding of the structures, functions, and processes of the most basic unit of life: the cell.

2.1: Cell Structure

2.1.1: Prelude to Cell Structure
2.1.2: Studying Cells
2.1.3: Prokaryotic Cells
2.1.4: Eukaryotic Cells
2.1.5: The Endomembrane System and Proteins
2.1.6: The Cytoskeleton
2.1.7: Connections between Cells and Cellular Activities
2.1.E: Cell Structure (Exercises)

2.2: Structure and Function of Plasma Membranes

2.2.1: Prelude to Structure and Function of Plasma Membranes
2.2.2: Components and Structure
2.2.3: Passive Transport
2.2.4: Active Transport
2.2.5: Bulk Transport
2.2.E: Structure and Function of Plasma Membranes (Exercises)

2.3: Metabolism

2.3.1: Prelude to Metabolism
2.3.2: Energy and Metabolism
2.3.3: Potential, Kinetic, Free, and Activation Energy
2.3.4: The Laws of Thermodynamics
2.3.5: ATP- Adenosine Triphosphate
2.3.6: Enzymes
2.3.E: Metabolism (Exercises)

2.4: Cellular Respiration

2.4.1: Prelude to Cellular Respiration
2.4.2: Energy in Living Systems
2.4.3: Glycolysis
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
2.4.5: Oxidative Phosphorylation
2.4.6: Metabolism without Oxygen
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
2.4.E: Cellular Respiration (Exercises)

2.5: Photosynthesis

2.5.1: Prelude to Photosynthesis
2.5.2: Overview of Photosynthesis
2.5.3: The Light-Dependent Reactions of Photosynthesis
2.5.4: Using Light Energy to Make Organic Molecules
2.5.E: Photosynthesis (Exercises)

2.6: Cell Communication

2.6.1: Prelude to Cell Communication
2.6.2: Signaling Molecules and Cellular Receptors
2.6.3: Propagation of the Signal
2.6.4: Response to the Signal
2.6.5: Signaling in Single-Celled Organisms
2.6.E: Cell Communication (Exercises)

2.7: Cell Reproduction

2.7.1: Preface
2.7.2: Cell Division
2.7.3: The Cell Cycle
2.7.4: Control of the Cell Cycle
2.7.5: Cancer and the Cell Cycle
2.7.6: Prokaryotic Cell Division
2.7.E: Cell Reproduction (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2: Unit II- The Cell is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

2.1: Cell Structure

Your body has many kinds of cells, each specialized for a specific purpose. Just as a home is made from a variety of building materials, the human body is constructed from many cell types. For example, epithelial cells protect the surface of the body and cover the organs and body cavities within. Bone cells help to support and protect the body. Cells of the immune system 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 growth, development, and day-to-day maintenance of the body. In spite of their enormous variety, however, cells from all organisms—even ones as diverse as bacteria, onion, and human—share certain fundamental characteristics.

2.1.1: Prelude to Cell Structure
2.1.2: Studying Cells
2.1.3: Prokaryotic Cells
2.1.4: Eukaryotic Cells
2.1.5: The Endomembrane System and Proteins
2.1.6: The Cytoskeleton
2.1.7: Connections between Cells and Cellular Activities
2.1.E: Cell Structure (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.1: Cell Structure is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

2.1.1: Prelude to Cell Structure

Close your eyes and picture a brick wall. What is the basic building block of that wall? A single brick, of course. Like a brick wall, your body is composed of basic building blocks, and the building blocks of your body are cells.

Video



This 3-minute video introduces the wonder of cells.

Your body has many kinds of cells, each specialized for a specific purpose. Just as a home is made from a variety of building materials, the human body is constructed from many cell types. For example, epithelial cells protect the surface of the body and cover the organs and body cavities within. Bone cells help to support and protect the body. Cells of the immune system 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 growth, development, and day-to-day maintenance of the body. In spite of their enormous variety, however, cells from all organisms—even ones as diverse as bacteria, onion, and human—share certain fundamental characteristics.

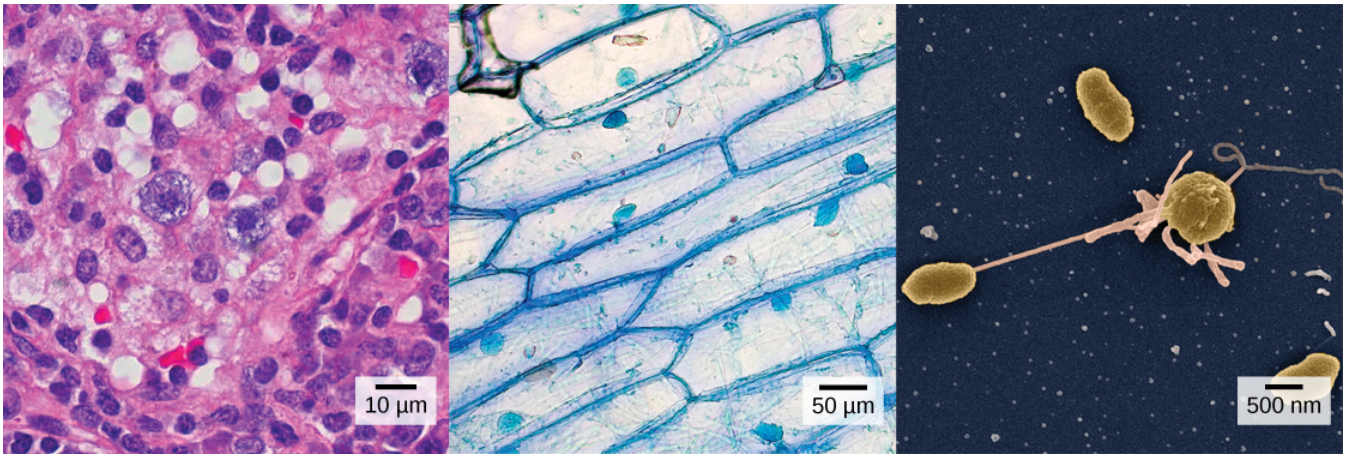


Figure \(\PageIndex{1}\): (a) Nasal sinus cells (viewed with a light microscope), (b) onion cells (viewed with a light microscope), and (c) *Vibrio tasmaniensis* bacterial cells (seen through a scanning electron microscope) are from very different organisms, yet all share certain characteristics of basic cell structure. (credit a: modification of work by Ed Uthman, MD; credit b: modification of work by Umberto Salvagnin; credit c: modification of work by Anthony D'Onofrio, William H. Fowle, Eric J. Stewart, and Kim Lewis of the Lewis Lab at Northeastern University; scale-bar data from Matt Russell)

This page titled 2.1.1: Prelude to Cell Structure is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.0: Prelude to Cell Structure** by OpenStax is licensed CC BY 4.0.

2.1.2: Studying Cells

Skills to Develop

- Describe the role of cells in organisms
- Compare and contrast light microscopy and electron microscopy
- Summarize cell theory

A cell is the smallest unit of a living thing. A living thing, whether made of one cell (like bacteria) or many cells (like a human), is called an organism. Thus, cells are the basic building blocks of all organisms.

Several cells of one kind that interconnect with each other and perform a shared function form tissues, several tissues combine to form an organ (your stomach, heart, or brain), and several organs make up 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, all grouped into one of two broad categories: prokaryotic and eukaryotic. For example, both animal and plant cells are classified as eukaryotic cells, whereas bacterial cells are classified as prokaryotic. Before discussing the criteria for determining whether a cell is prokaryotic or eukaryotic, let's first examine how biologists study cells.

Microscopy

Cells vary in size. With few exceptions, individual cells cannot be seen with the naked eye, so scientists use microscopes (micro- = "small"; -scope = "to look at") to study them. A microscope is an instrument that magnifies an object. Most photographs of cells are taken with a microscope, and these images can also be called micrographs.

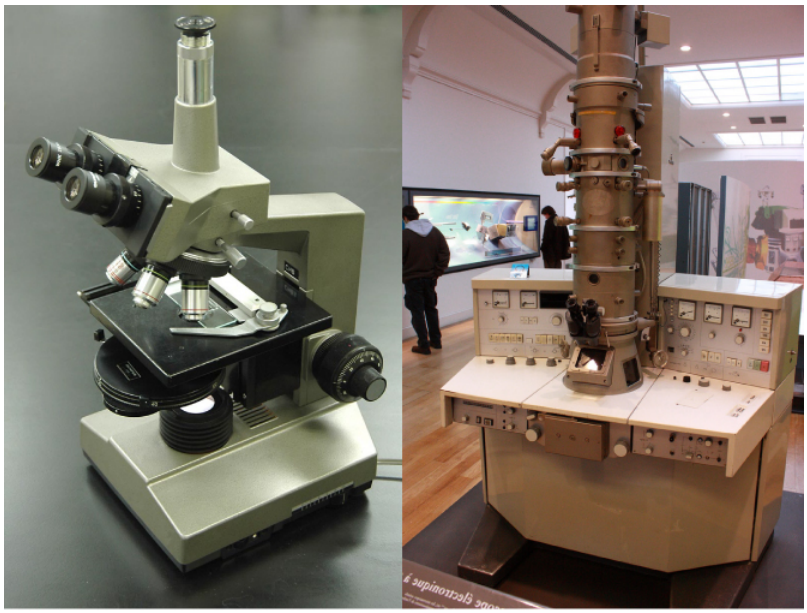
The optics of a microscope's lenses change the orientation of the image that the user sees. A specimen that is right-side up and facing right on the microscope slide will appear upside-down and facing left when viewed through a microscope, and vice versa. Similarly, if the slide is moved left while looking through the microscope, it will appear to move right, and if moved down, it will seem to move up. This occurs because microscopes use two sets of lenses to magnify the image. Because of the manner by which light travels through the lenses, this system of two lenses produces an inverted image (binocular, or dissecting microscopes, work in a similar manner, but include an additional magnification system that makes the final image appear to be upright).

Light Microscopes

To give you a sense of cell size, a typical human red blood cell is about eight millionths of a meter or eight micrometers (abbreviated as eight µm) in diameter; the head of a pin of is about two thousandths of a meter (two mm) in diameter. That means about 250 red blood cells could fit on the head of a pin.

Most student microscopes are classified as light microscopes (Figure 2.1.2.1a). Visible light passes and is bent through the lens system to enable the user to see the specimen. Light microscopes are advantageous for viewing living organisms, but since individual cells are generally transparent, their components are not distinguishable unless they are colored with special stains. Staining, however, usually kills the cells.

Light microscopes commonly used in the undergraduate college laboratory magnify up to approximately 400 times. Two parameters that are important in microscopy are magnification and resolving power. Magnification is the process of enlarging an object in appearance. Resolving power is the ability of a microscope to distinguish two adjacent structures as separate: the higher the resolution, the better the clarity and detail of the image. When oil immersion lenses are used for the study of small objects, magnification is usually increased to 1,000 times. In order to gain a better understanding of cellular structure and function, scientists typically use electron microscopes.



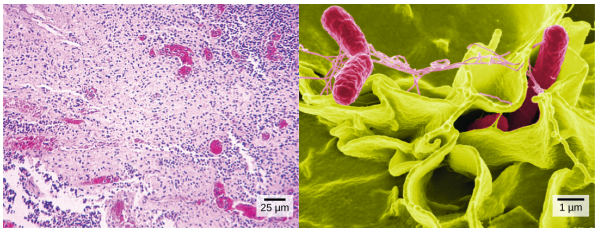
(a) (b)

Figure 2.1.2.1: (a) Most light microscopes used in a college biology lab can magnify cells up to approximately 400 times and have a resolution of about 200 nanometers. (b) Electron microscopes provide a much higher magnification, 100,000x, and a have a resolution of 50 picometers. (credit a: modification of work by "GcG"/Wikimedia Commons; credit b: modification of work by Evan Bench)

Electron Microscopes

In contrast to light microscopes, electron microscopes (Figure 2.1.2.1b) use a beam of electrons instead of a beam of light. Not only does this allow for higher magnification and, thus, more detail (Figure 2.1.2.2), it also provides higher resolving power. The method used to prepare the specimen for viewing with an electron microscope kills the specimen. Electrons have short wavelengths (shorter than photons) that move best in a vacuum, so living cells cannot be viewed with an electron microscope.

In a scanning electron microscope, a beam of electrons moves back and forth across a cell's surface, creating details of cell surface characteristics. In a transmission electron microscope, the electron beam penetrates the cell and provides details of a cell's internal structures. As you might imagine, electron microscopes are significantly more bulky and expensive than light microscopes.



(a) (b)

Figure 2.1.2.2: (a) These *Salmonella* bacteria appear as tiny purple dots when viewed with a light microscope. (b) This scanning electron microscope micrograph shows *Salmonella* bacteria (in red) invading human cells (yellow). Even though subfigure (b) shows a different *Salmonella* specimen than subfigure (a), you can still observe the comparative increase in magnification and detail. (credit a: modification of work by CDC/Armed Forces Institute of Pathology, Charles N. Farmer, Rocky Mountain Laboratories; credit b: modification of work by NIAID, NIH; scale-bar data from Matt Russell)

Link to Learning

For another perspective on cell size, try the HowBig interactive at this site.

Cell Theory

The microscopes we use today are far more complex than those used in the 1600s by Antony van Leeuwenhoek, a Dutch shopkeeper who had great skill in crafting lenses. Despite the limitations of his now-ancient lenses, van Leeuwenhoek observed the movements of protista (a type of single-celled organism) and sperm, which he collectively termed “animalcules.”

In a 1665 publication called *Micrographia*, experimental scientist Robert Hooke coined the term “cell” for the box-like structures he observed when viewing cork tissue through a lens. In the 1670s, van Leeuwenhoek discovered bacteria and protozoa. Later advances in lenses, microscope construction, and staining techniques enabled other scientists to see some components inside cells.

By the late 1830s, botanist Matthias Schleiden and zoologist Theodor Schwann were studying tissues and proposed the unified cell theory, which states that all living things are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells. Rudolf Virchow later made important contributions to this theory.

Career Connection: Cytotechnologist

Have you ever heard of a medical test called a Pap smear (Figure 2.1.2.3)? In this test, a doctor takes a small sample of cells from the uterine cervix of a patient and sends it to a medical lab where a cytotechnologist stains the cells and examines them for any changes that could indicate cervical cancer or a microbial infection.

Cytotechnologists (cyto- = “cell”) are professionals who study cells via microscopic examinations and other laboratory tests. They are trained to determine which cellular changes are within normal limits and which are abnormal. Their focus is not limited to cervical cells; they study cellular specimens that come from all organs. When they notice abnormalities, they consult a pathologist, who is a medical doctor who can make a clinical diagnosis.

Cytotechnologists play a vital role in saving people’s lives. When abnormalities are discovered early, a patient’s treatment can begin sooner, which usually increases the chances of a successful outcome.

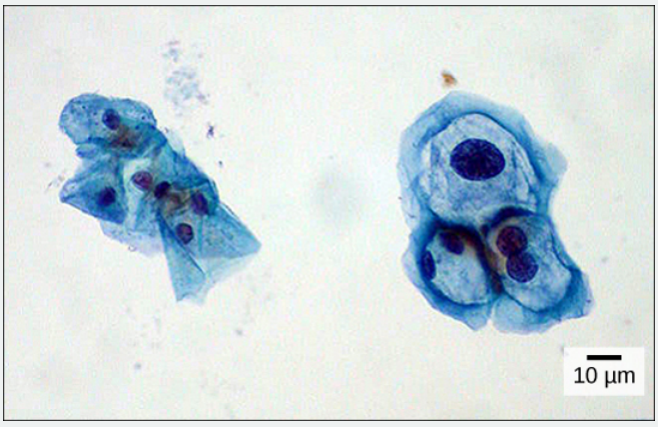


Figure 2.1.2.3: These uterine cervix cells, viewed through a light microscope, were obtained from a Pap smear. Normal cells are on the left. The cells on the right are infected with human papillomavirus (HPV). Notice that the infected cells are larger; also, two of these cells each have two nuclei instead of one, the normal number. (credit: modification of work by Ed Uthman, MD; scale-bar data from Matt Russell)

Summary

A cell is the smallest unit of life. Most cells are so tiny that they cannot be seen with the naked eye. Therefore, scientists use microscopes to study cells. Electron microscopes provide higher magnification, higher resolution, and more detail than light microscopes. The unified cell theory states that all organisms are composed of one or more cells, the cell is the basic unit of life, and new cells arise from existing cells.

Glossary

cell theory
see unified cell theory

electron microscope
an instrument that magnifies an object using a beam of electrons passed and bent through a lens system to visualize a specimen

light microscope
an instrument that magnifies an object using a beam visible light passed and bent through a lens system to visualize a specimen

microscope
an instrument that magnifies an object

unified cell theory
a biological concept that states that all organisms are composed of one or more cells; the cell is the basic unit of life; and new cells arise from existing cells

---

This page titled 2.1.2: Studying Cells is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.1: Studying Cells** by OpenStax is licensed CC BY 4.0.

2.1.3: Prokaryotic Cells

Learning Objectives

- Name examples of prokaryotic and eukaryotic organisms
- Compare and contrast prokaryotic cells and eukaryotic cells
- Describe the relative sizes of different kinds of cells
- Explain why cells must be small

Cells fall into one of two broad categories: prokaryotic and eukaryotic. Only the predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (pro- = “before”; -kary- = “nucleus”). Cells of animals, plants, fungi, and protists are all eukaryotes (eu- = “true”) and are made up of eukaryotic cells.

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 cytosol within the cell in which other cellular components are found; 3) DNA, the genetic material of the cell; and 4) ribosomes, which synthesize proteins. However, prokaryotes differ from eukaryotic cells in several ways.

A prokaryote is a simple, mostly 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 a central part of the cell: the nucleoid (Figure 2.1.3.1).

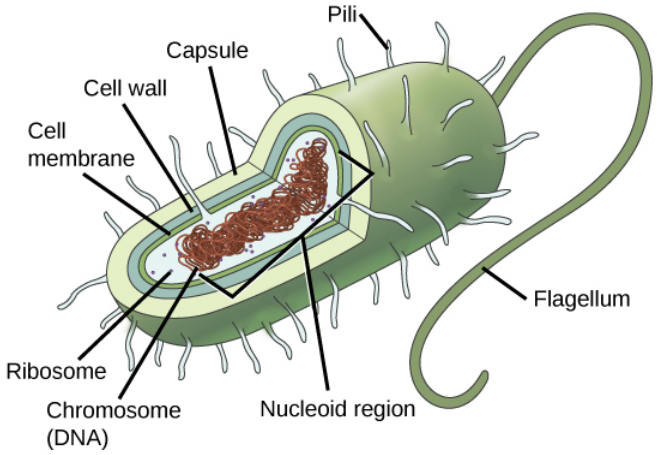


Figure 2.1.3.1: This figure shows the generalized structure of a prokaryotic cell. All prokaryotes have chromosomal DNA localized in a nucleoid, ribosomes, a cell membrane, and a cell wall. The other structures shown are present in some, but not all, bacteria.

Most prokaryotes have a peptidoglycan cell wall and many have a polysaccharide capsule (Figure 2.1.3.1). 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. Pili are used to exchange genetic material during a type of reproduction called conjugation. Fimbriae are used by bacteria to attach to a host cell.

Career Connection: Microbiologist

The most effective action anyone can take to prevent the spread of contagious illnesses is to wash his or her hands. Why? Because microbes (organisms so tiny that they can only be seen with microscopes) are ubiquitous. They live on doorknobs, money, your hands, and many other surfaces. If someone sneezes into his hand and touches a doorknob, and afterwards you touch that same doorknob, the microbes from the sneezer’s mucus are now on your hands. If you touch your hands to your mouth, nose, or eyes, those microbes can enter your body and could make you sick.

However, not all microbes (also called microorganisms) cause disease; most are actually beneficial. You have microbes in your gut that make vitamin K. Other microorganisms are used to ferment beer and wine.

Microbiologists are scientists who study microbes. Microbiologists can pursue a number of careers. Not only do they work in the food industry, they are also employed in the veterinary and medical fields. They can work in the pharmaceutical sector, serving key roles in research and development by identifying new sources of antibiotics that could be used to treat bacterial infections.

Environmental microbiologists may look for new ways to use specially selected or genetically engineered microbes for the removal of pollutants from soil or groundwater, as well as hazardous elements from contaminated sites. These uses of microbes are called bioremediation technologies. Microbiologists can also work in the field of bioinformatics, providing specialized knowledge and insight for the design, development, and specificity of computer models of, for example, bacterial epidemics.

Cell Size

At 0.1 to 5.0 μm in diameter, prokaryotic cells are significantly smaller than eukaryotic cells, which have diameters ranging from 10 to 100 μm (Figure 2.1.3.2). The small size of prokaryotes allows ions and organic molecules that enter them to quickly diffuse to other parts of the cell. Similarly, any wastes produced within a prokaryotic cell can quickly diffuse out. This is not the case in eukaryotic cells, which have developed different structural adaptations to enhance intracellular transport.

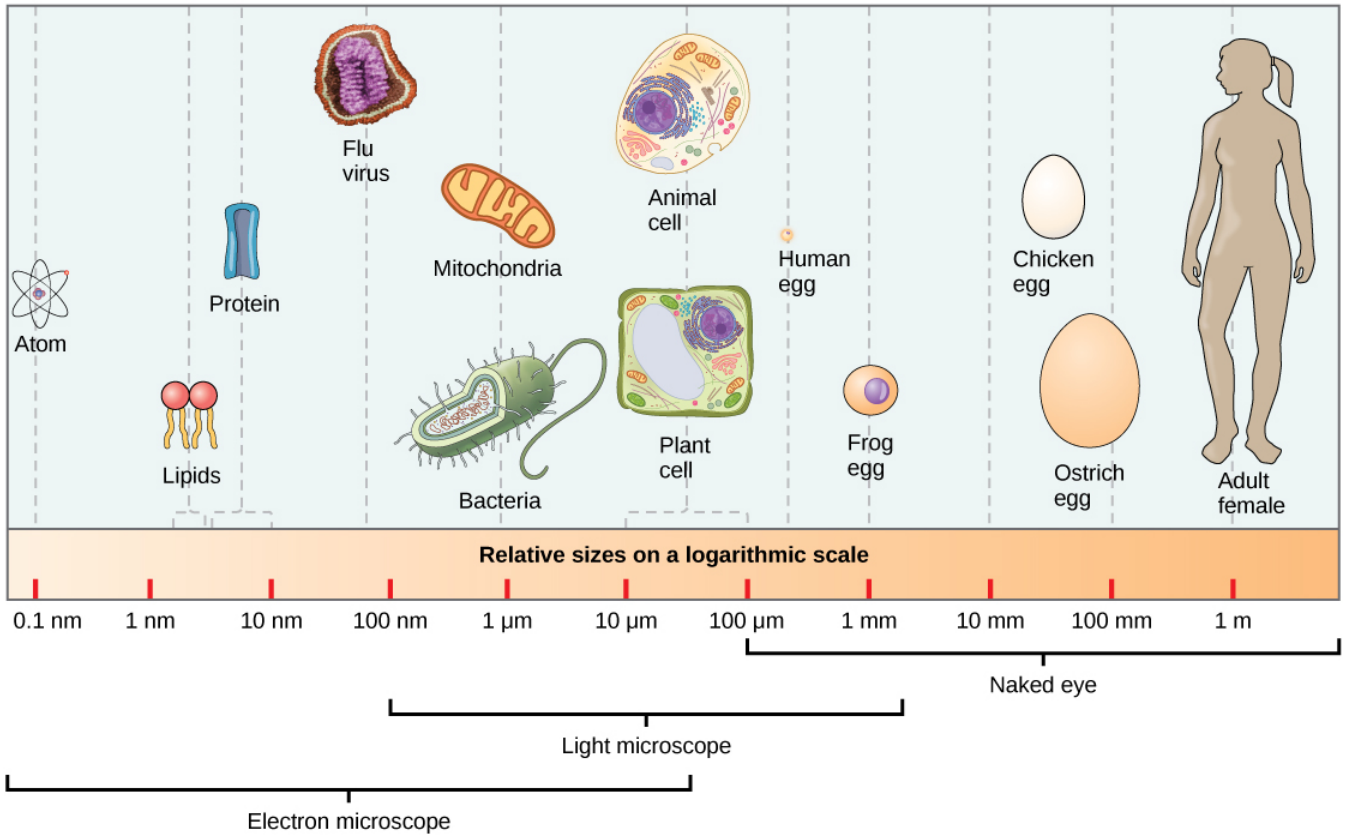


Figure 2.1.3.2: This figure shows relative sizes of microbes on a logarithmic scale (recall that each unit of increase in a logarithmic scale represents a 10-fold increase in the quantity being measured).

Small size, in general, is necessary for all cells, whether prokaryotic or eukaryotic. Let's examine why that is so. First, we'll consider the area and volume of a typical cell. Not all cells are spherical in shape, but most tend to approximate a sphere. You may remember from your high school geometry course that the formula for the surface area of a sphere is $4\pi r^2$, while the formula for its volume is $4\pi r^2/3$. Thus, as the radius of a cell increases, its surface area increases as the square of its radius, but its volume increases as the cube of its radius (much more rapidly). Therefore, as a cell increases in size, its surface area-to-volume ratio decreases. This same principle would apply if the cell had the shape of a cube (Figure 2.1.3.3). If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume. In other

words, as a cell grows, it becomes less efficient. One way to become more efficient is to divide; another way is to develop organelles that perform specific tasks. These adaptations lead to the development of more sophisticated cells called eukaryotic cells.

Art Connection

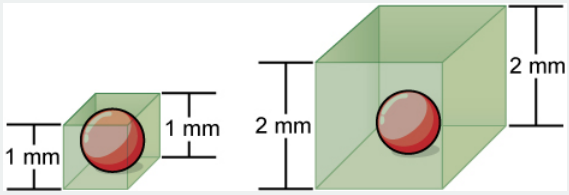


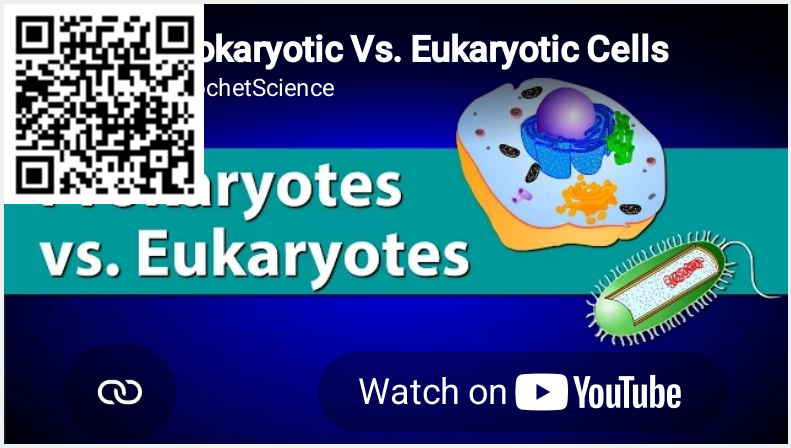
Figure 2.1.3.3: Notice that as a cell increases in size, its surface area-to-volume ratio decreases. When there is insufficient surface area to support a cell's increasing volume, a cell will either divide or die. The cell on the left has a volume of $1\ \text{mm}^3$ and a surface area of $6\ \text{mm}^2$, with a surface area-to-volume ratio of 6 to 1, whereas the cell on the right has a volume of $8\ \text{mm}^3$ and a surface area of $24\ \text{mm}^2$, with a surface area-to-volume ratio of 3 to 1.

Prokaryotic cells are much smaller than eukaryotic cells. What advantages might small cell size confer on a cell? What advantages might large cell size have?

Answer

Substances can diffuse more quickly through small cells. Small cells have no need for organelles and therefore do not need to expend energy getting substances across organelle membranes. Large cells have organelles that can separate cellular processes, enabling them to build molecules that are more complex.

Video



This 4-minute video highlights the similarities and differences between prokaryotic and eukaryotic cells.

Summary

Prokaryotes are predominantly single-celled organisms of the domains Bacteria and Archaea. All prokaryotes have plasma membranes, cytoplasm, ribosomes, and DNA that is not membrane-bound. Most have peptidoglycan cell walls and many have polysaccharide capsules. Prokaryotic cells range in diameter from 0.1 to 5.0 µm.

As a cell increases in size, its surface area-to-volume ratio decreases. If the cell grows too large, the plasma membrane will not have sufficient surface area to support the rate of diffusion required for the increased volume.

Glossary

nucleoid

central part of a prokaryotic cell in which the chromosome is found

prokaryote

unicellular organism that lacks a nucleus or any other membrane-bound organelle

---

This page titled 2.1.3: Prokaryotic Cells is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.2: Prokaryotic Cells** by OpenStax is licensed CC BY 4.0.

2.1.4: Eukaryotic Cells

Learning Objectives

- Describe the structure of eukaryotic cells
- Compare animal cells with plant cells
- State the role of the plasma membrane
- Summarize the functions of the major cell organelles

Have you ever heard the phrase “form follows function?” It’s a philosophy practiced in many industries. In architecture, this means that buildings should be constructed to support the activities that will be carried out inside them. For example, a skyscraper should be built with several elevator banks; a hospital should be built so that its emergency room is easily accessible.

Our natural world also utilizes the principle of form following function, especially in cell biology, and this will become clear as we explore eukaryotic cells (Figure 2.1.4.1). Unlike prokaryotic cells, eukaryotic cells have: 1) a membrane-bound nucleus; 2) numerous membrane-bound organelles such as the endoplasmic reticulum, Golgi apparatus, chloroplasts, mitochondria, and others; and 3) several, rod-shaped chromosomes. Because a eukaryotic cell’s nucleus is surrounded by a membrane, it is often said to have a “true nucleus.” The word “organelle” means “little organ,” and, as already mentioned, organelles have specialized cellular functions, just as the organs of your body have specialized functions.

At this point, it should be clear to you that eukaryotic cells have a more complex structure than prokaryotic cells. Organelles allow different functions to be compartmentalized in different areas of the cell. Before turning to organelles, let’s first examine two important components of the cell: the plasma membrane and the cytoplasm.

Video



This 8-minute animation by Nucleus shows you the function of plant and animal cells

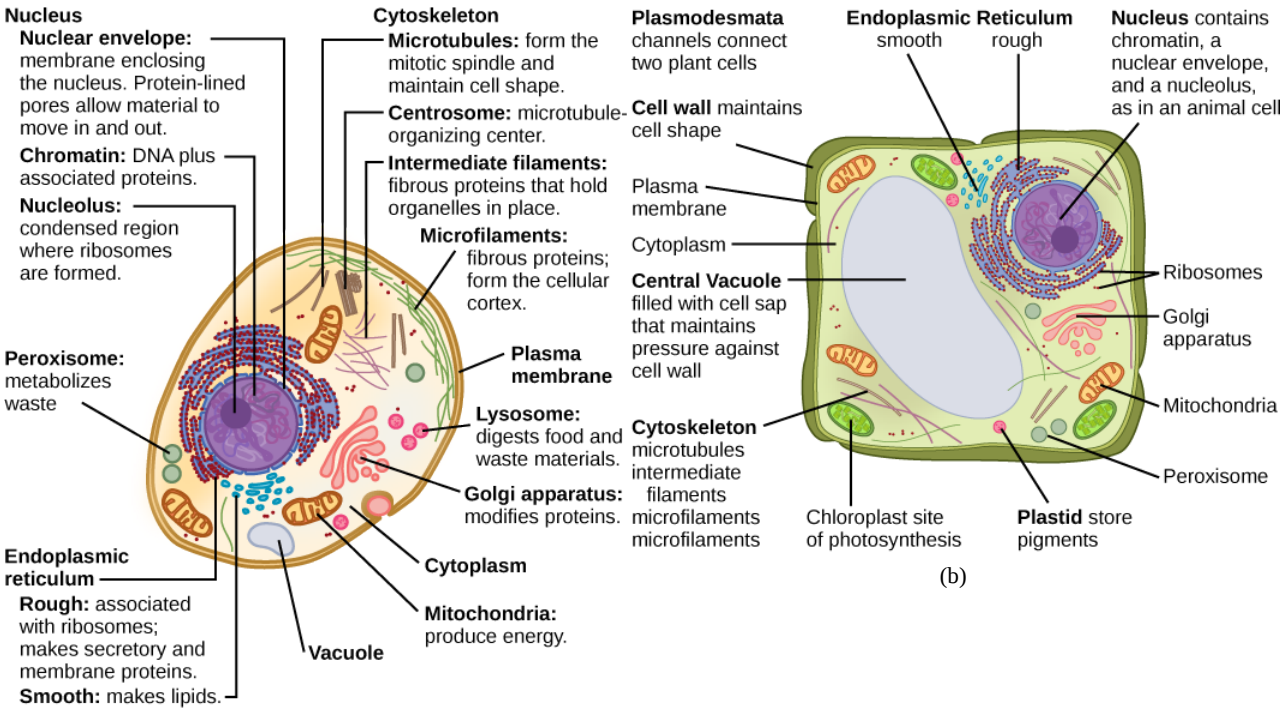


Figure 2.1.4.1: These figures show the major organelles and other cell components of (a) a typical animal cell and (b) a typical eukaryotic plant cell. The plant cell has a cell wall, chloroplasts, plastids, and a central vacuole—structures not found in animal cells. Plant cells do not have lysosomes or centrosomes.

Question: Figure 2.1.4.1: If the nucleolus were not able to carry out its function, what other cellular organelles would be affected?

Answer

Free ribosomes and rough endoplasmic reticulum (which contains ribosomes) would not be able to form.

The Plasma Membrane

Like prokaryotes, eukaryotic cells have a plasma membrane (Figure 2.1.4.2), a phospholipid bilayer with embedded proteins that separates the internal contents of the cell from its surrounding environment. A phospholipid is a lipid molecule with two fatty acid chains and a phosphate-containing group. The plasma membrane controls the passage of organic molecules, ions, water, and oxygen into and out of the cell. Wastes (such as carbon dioxide and ammonia) also leave the cell by passing through the plasma membrane.

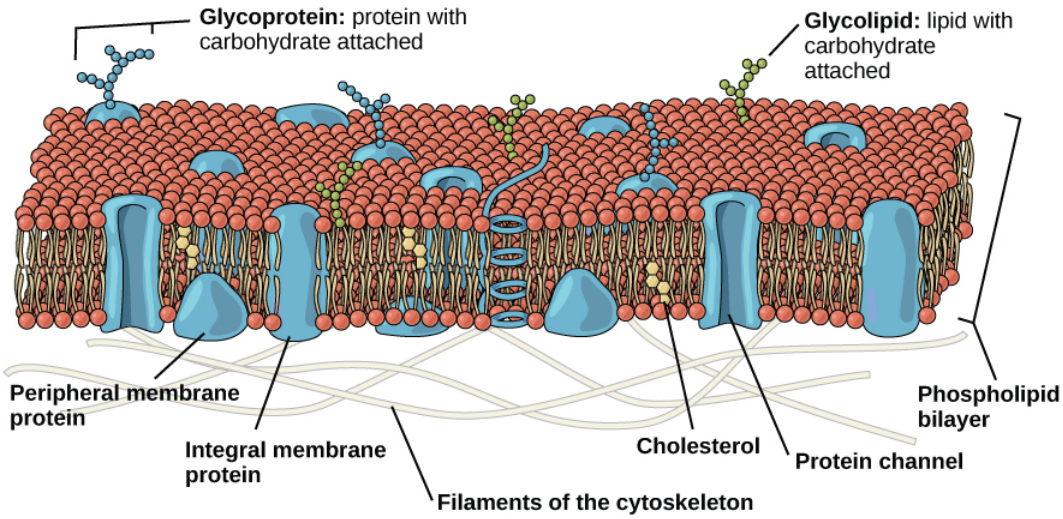


Figure 2.1.4.2: The eukaryotic plasma membrane is a phospholipid bilayer with proteins and cholesterol embedded in it.

The plasma membranes of cells that specialize in absorption are folded into fingerlike projections called microvilli (singular = microvillus); (Figure 2.1.4.3). Such cells are typically found lining the small intestine, the organ that absorbs nutrients from digested food. This is an excellent example of form following function. People with celiac disease have an immune response to gluten, which is a protein found in wheat, barley, and rye. The immune response damages microvilli, and thus, afflicted individuals cannot absorb nutrients. This leads to malnutrition, cramping, and diarrhea. Patients suffering from celiac disease must follow a gluten-free diet. More on the plasma membrane will be covered in the next Chapter.

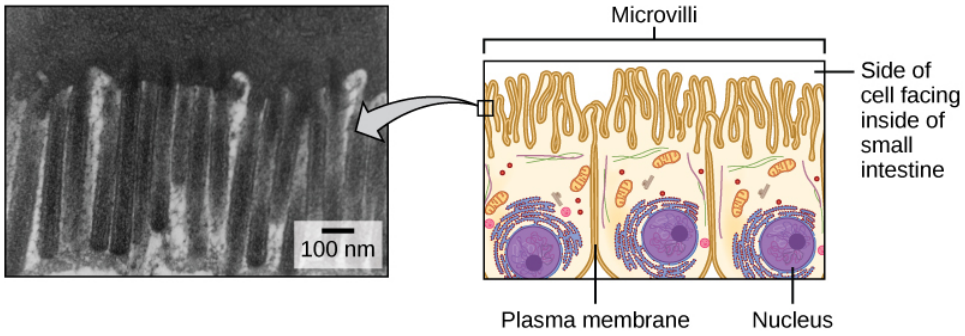
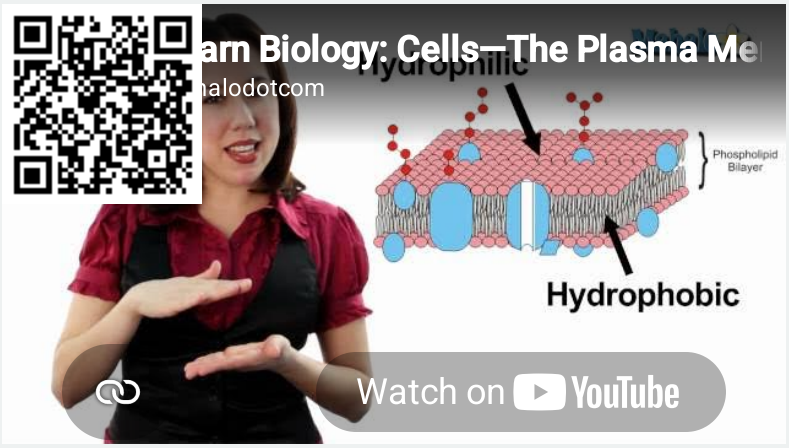


Figure 2.1.4.3: Microvilli, shown here as they appear on cells lining the small intestine, increase the surface area available for absorption. These microvilli are only found on the area of the plasma membrane that faces the cavity from which substances will be absorbed. (credit "micrograph": modification of work by Louisa Howard)

Video



In this 2-minute video, the structure and function of the plasma membrane are reviewed.

The Cytoplasm

The cytoplasm is the entire region of a cell between the plasma membrane and the nuclear envelope (a structure to be discussed shortly). It is made up of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals (Figure 2.1.4.1). Even though the cytoplasm consists of 70 to 80 percent water, it has a semi-solid consistency, which comes from the proteins within it. However, proteins are not the only organic molecules found in the cytoplasm. Glucose and other simple sugars, polysaccharides, amino acids, nucleic acids, fatty acids, and derivatives of glycerol are found there, too. Ions of sodium, potassium, calcium, and many other elements are also dissolved in the cytoplasm. Many metabolic reactions, including protein synthesis, take place in the cytoplasm.

The Nucleus

Typically, the nucleus is the most prominent organelle in a cell (Figure 2.1.4.1). The nucleus (plural = nuclei) houses the cell's DNA and directs the synthesis of ribosomes and proteins. Let's look at it in more detail (Figure 2.1.4.4).

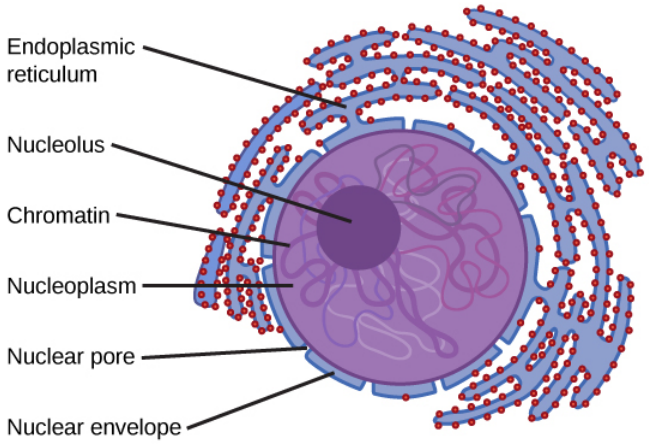


Figure 2.1.4.4: The nucleus stores chromatin (DNA plus proteins) in a gel-like substance called the nucleoplasm. The nucleolus is a condensed region of chromatin where ribosome synthesis occurs. The boundary of the nucleus is called the nuclear envelope. It consists of two phospholipid bilayers: an outer membrane and an inner membrane. The nuclear membrane is continuous with the endoplasmic reticulum. Nuclear pores allow substances to enter and exit the nucleus.

Video



In this 1-minute video, the structure and function of the nucleus are reviewed.

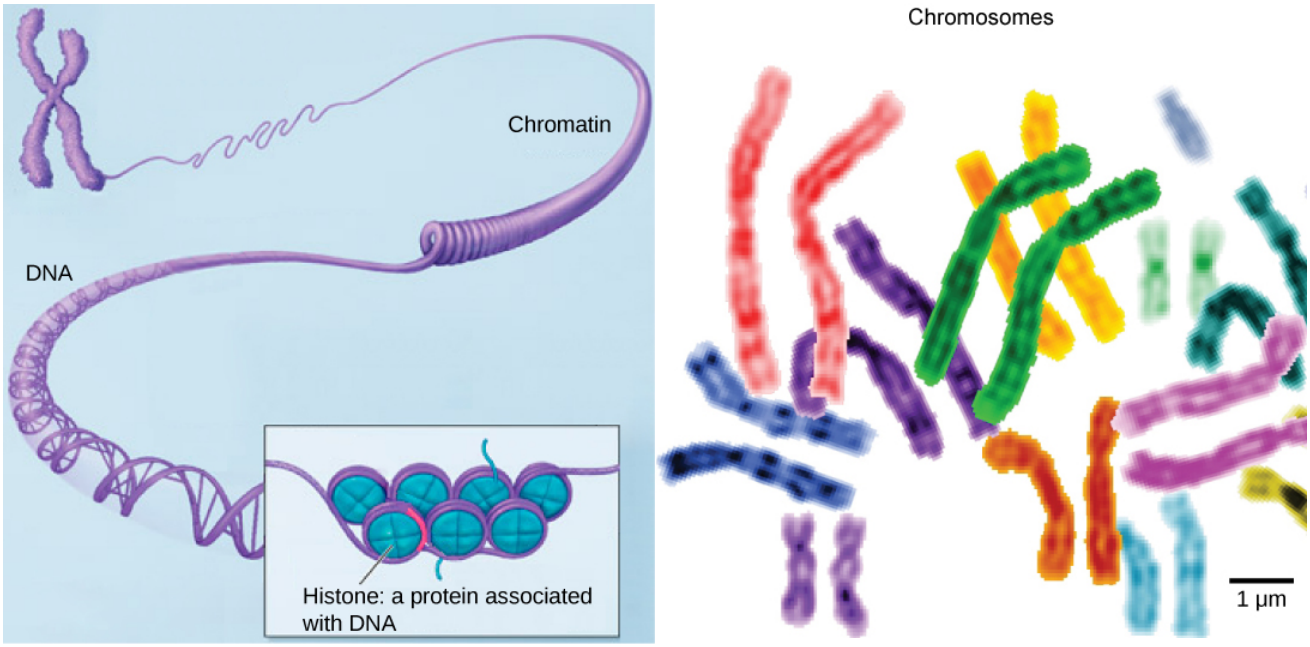
The Nuclear Envelope

The nuclear envelope is a double-membrane structure that constitutes the outermost portion of the nucleus (Figure 2.1.4.4). Both the inner and outer membranes of the nuclear envelope are phospholipid bilayers.

The nuclear envelope is punctuated with pores that control the passage of ions, molecules, and RNA between the nucleoplasm and cytoplasm. The nucleoplasm is the semi-solid fluid inside the nucleus, where we find the chromatin and the nucleolus.

Chromatin and Chromosomes

To understand chromatin, it is helpful to first consider chromosomes. Chromosomes are structures within the nucleus that are made up of DNA, the hereditary material. You may remember that in prokaryotes, DNA is organized into a single circular chromosome. In eukaryotes, chromosomes are linear structures. Every eukaryotic species has a specific number of chromosomes in the nuclei of its body's cells. For example, in humans, the chromosome number is 46, while in fruit flies, it is eight. Chromosomes are only visible and distinguishable from one another when the cell is getting ready to divide. When the cell is in the growth and maintenance phases of its life cycle, proteins are attached to chromosomes, and they resemble an unwound, jumbled bunch of threads. These unwound protein-chromosome complexes are called chromatin (Figure 2.1.4.5); chromatin describes the material that makes up the chromosomes both when condensed and decondensed.



(a) (b)

Figure 2.1.4.5: (a) This image shows various levels of the organization of chromatin (DNA and protein). (b) This image shows paired chromosomes. (credit b: modification of work by NIH; scale-bar data from Matt Russell)

The Nucleolus

We already know that the nucleus directs the synthesis of ribosomes, but how does it do this? Some chromosomes have sections of DNA that encode ribosomal RNA. A darkly staining area within the nucleus called the nucleolus (plural = nucleoli) aggregates the ribosomal RNA with associated proteins to assemble the ribosomal subunits that are then transported out through the pores in the nuclear envelope to the cytoplasm.

Ribosomes

Ribosomes are the cellular structures responsible for protein synthesis. When viewed through an electron microscope, ribosomes appear either as clusters (polyribosomes) or single, tiny dots that float freely in the cytoplasm. They may be attached to the cytoplasmic side of the plasma membrane or the cytoplasmic side of the endoplasmic reticulum and the outer membrane of the nuclear envelope (Figure 2.1.4.1). Electron microscopy has shown us that ribosomes, which are large complexes of protein and RNA, consist of two subunits, aptly called large and small (Figure 2.1.4.6). Ribosomes receive their "orders" for protein synthesis from the nucleus where the DNA is transcribed into messenger RNA (mRNA). The mRNA travels to the ribosomes, which translate the code provided by the sequence of the nitrogenous bases in the mRNA into a specific order of amino acids in a protein. Amino acids are the building blocks of proteins.

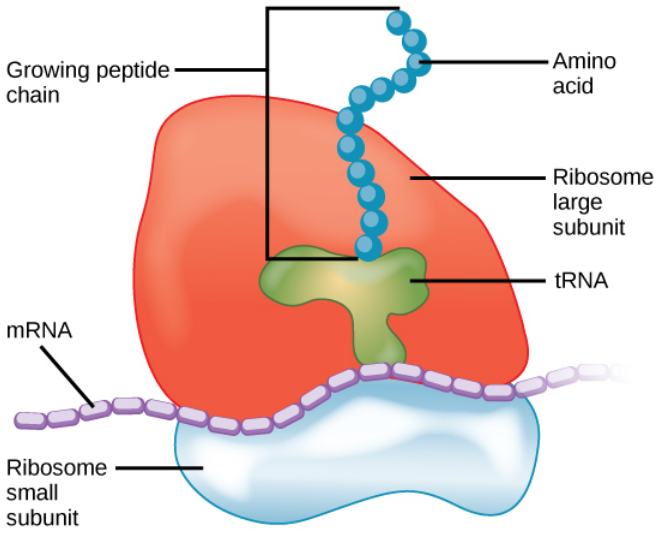


Figure 2.1.4.6: Ribosomes are made up of a large subunit (top) and a small subunit (bottom). During protein synthesis, ribosomes assemble amino acids into proteins.

Because protein synthesis is an essential function of all cells (including enzymes, hormones, antibodies, pigments, structural components, and surface receptors), ribosomes are found in practically every cell. Ribosomes are particularly abundant in cells that synthesize large amounts of protein. For example, the pancreas is responsible for creating several digestive enzymes and the cells that produce these enzymes contain many ribosomes. Thus, we see another example of form following function.

Video



In this 1-minute video, the structure and function of ribosomes are reviewed.

Mitochondria

Mitochondria (singular = mitochondrion) are often called the “powerhouses” or “energy factories” of a cell because they are responsible for making adenosine triphosphate (ATP), the cell’s main energy-carrying molecule. ATP represents the short-term stored energy of the cell. Cellular respiration is the process of making ATP using the chemical energy found in glucose and other nutrients. In mitochondria, this process uses oxygen and produces carbon dioxide as a waste product. In fact, the carbon dioxide that you exhale with every breath comes from the cellular reactions that produce carbon dioxide as a byproduct.

In keeping with our theme of form following function, it is important to point out that muscle cells have a very high concentration of mitochondria that produce ATP. Your muscle cells need a lot of energy to keep your body moving. When your cells don’t get enough oxygen, they do not make a lot of ATP. Instead, the small amount of ATP they make in the absence of oxygen is accompanied by the production of lactic acid.

Mitochondria are oval-shaped, double-membrane organelles (Figure 2.1.4.7) that have their own ribosomes and DNA. Each membrane is a phospholipid bilayer embedded with proteins. The inner layer has folds called cristae. The area surrounded by the folds is called the mitochondrial matrix. The cristae and the matrix have different roles in cellular respiration.

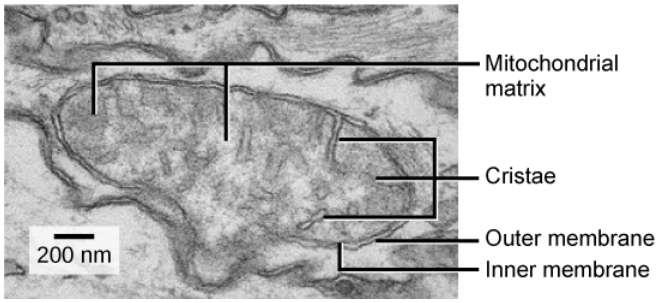


Figure 2.1.4.7: This electron micrograph shows a mitochondrion as viewed with a transmission electron microscope. This organelle has an outer membrane and an inner membrane. The inner membrane contains folds, called cristae, which increase its surface area. The space between the two membranes is called the intermembrane space, and the space inside the inner membrane is called the mitochondrial matrix. ATP synthesis takes place on the inner membrane. (credit: modification of work by Matthew Britton; scale-bar data from Matt Russell)

Video



In this 1-minute video, the structure and function of mitochondria are reviewed.

Peroxisomes

Peroxisomes are small, round organelles enclosed by single membranes. They carry out oxidation reactions that break down fatty acids and amino acids. They also detoxify many poisons that may enter the body. (Many of these oxidation reactions release hydrogen peroxide, H_2O_2, which would be damaging to cells; however, when these reactions are confined to peroxisomes, enzymes safely break down the H_2O_2 into oxygen and water.) For example, alcohol is detoxified by peroxisomes in liver cells. Glyoxysomes, which are specialized peroxisomes in plants, are responsible for converting stored fats into sugars.

Vesicles and Vacuoles

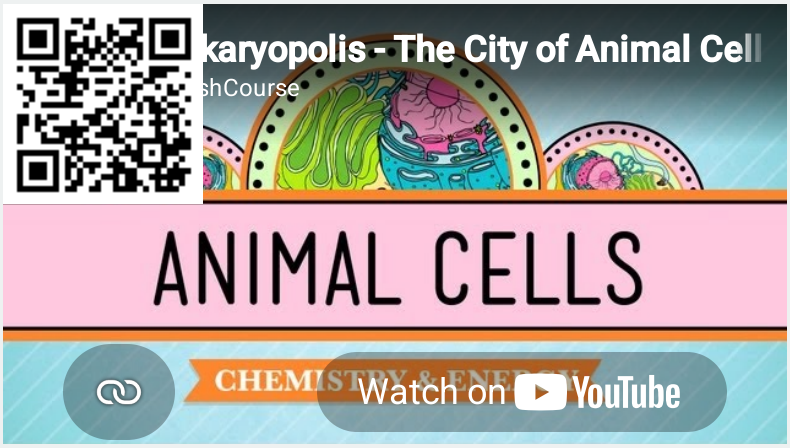
Vesicles and vacuoles are membrane-bound sacs that function in storage and transport. Other than the fact that vacuoles are somewhat larger than vesicles, there is a very subtle distinction between them: The membranes of vesicles can fuse with either the plasma membrane or other membrane systems within the cell. Additionally, some agents such as enzymes within plant vacuoles break down macromolecules. The membrane of a vacuole does not fuse with the membranes of other cellular components.

Animal Cells versus Plant Cells

At this point, you know that each eukaryotic cell has a plasma membrane, cytoplasm, a nucleus, ribosomes, mitochondria, peroxisomes, and in some, vacuoles, but there are some striking differences between animal and plant cells. While both animal and plant cells have microtubule organizing centers (MTOCs), animal cells also have centrioles associated with the MTOC: a complex

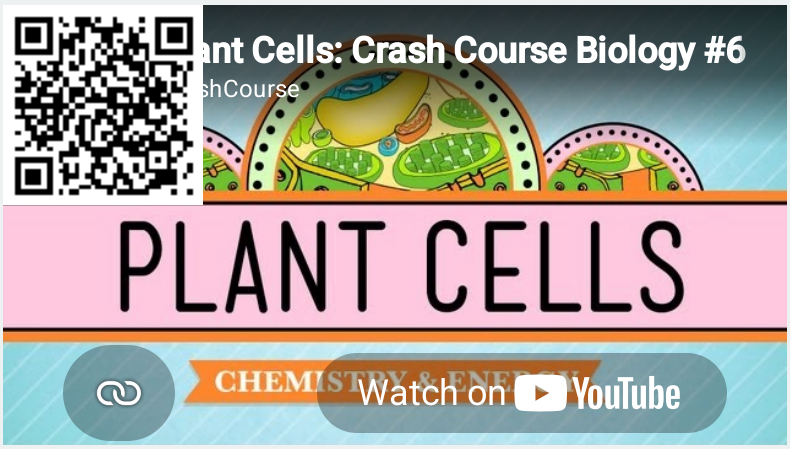
called the centrosome. Animal cells each have a centrosome and lysosomes, whereas plant cells do not. Plant cells have a cell wall, chloroplasts and other specialized plastids, and a large central vacuole, whereas animal cells do not.

Video



In this 11.5-minute video, Hank tells us about the animal cell...responsible for all the cool things that happen in our bodies.

Video



In this 10.5-minute video, Hank describes why plants are so amazing - discussing their evolution, and how their cells are both similar to & different from animal cells.

The Centrosome

The centrosome is a microtubule-organizing center found near the nuclei of animal cells. It contains a pair of centrioles, two structures that lie perpendicular to each other (Figure 2.1.4.8). Each centriole is a cylinder of nine triplets of microtubules.

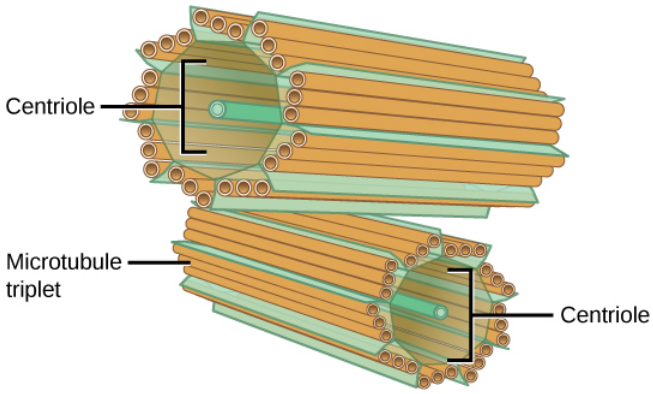


Figure 2.1.4.8: The centrosome consists of two centrioles that lie at right angles to each other. Each centriole is a cylinder made up of nine triplets of microtubules. Nontubulin proteins (indicated by the green lines) hold the microtubule triplets together.

The centrosome (the organelle where all microtubules originate) replicates itself before a cell divides, and the centrioles appear to have some role in pulling the duplicated chromosomes to opposite ends of the dividing cell. However, the exact function of the centrioles in cell division isn't clear, because cells that have had the centrosome removed can still divide, and plant cells, which lack centrosomes, are capable of cell division.

Lysosomes

Animal cells have another set of organelles not found in plant cells: lysosomes. The lysosomes are the cell's "garbage disposal." In plant cells, the digestive processes take place in vacuoles. Enzymes within the lysosomes aid the breakdown of proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles. These enzymes are active at a much lower pH than that of the cytoplasm. Therefore, the pH within lysosomes is more acidic than the pH of the cytoplasm. Many reactions that take place in the cytoplasm could not occur at a low pH, so again, the advantage of compartmentalizing the eukaryotic cell into organelles is apparent.

Video



In this 1-minute video, the structure and function of lysosomes are reviewed.

The Cell Wall

If you examine Figure 2.1.4.1b, the diagram of a plant cell, you will see a structure external to the plasma membrane called the cell wall. The cell wall is a rigid covering that protects the cell, provides structural support, and gives shape to the cell. Fungal and protistan cells also have cell walls. While the chief component of prokaryotic cell walls is peptidoglycan, the major organic molecule in the plant cell wall is cellulose (Figure 2.1.4.9), a polysaccharide made up of glucose units. Have you ever noticed that when you bite into a raw vegetable, like celery, it crunches? That's because you are tearing the rigid cell walls of the celery cells with your teeth.

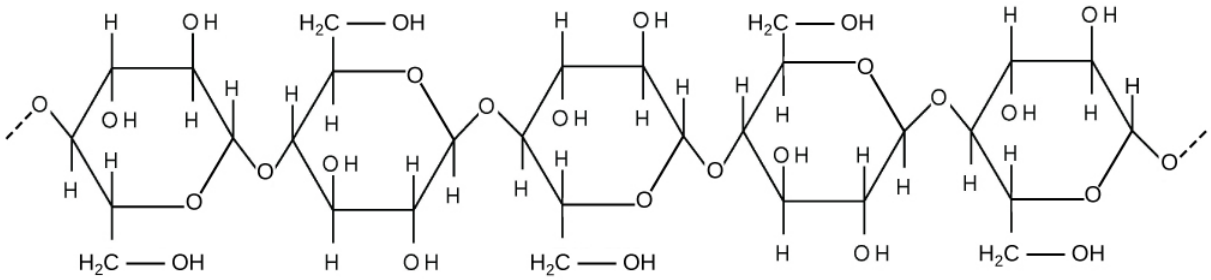


Figure 2.1.4.9: Cellulose is a long chain of β-glucose molecules connected by a 1-4 linkage. The dashed lines at each end of the figure indicate a series of many more glucose units. The size of the page makes it impossible to portray an entire cellulose molecule.

Chloroplasts

Like the mitochondria, chloroplasts have their own DNA and ribosomes, but chloroplasts have an entirely different function. Chloroplasts are plant cell organelles that carry out photosynthesis. Photosynthesis is the series of reactions that use carbon dioxide, water, and light energy to make glucose and oxygen. This is a major difference between plants and animals; plants (autotrophs) are able to make their own food, like sugars, while animals (heterotrophs) must ingest their food.

Like mitochondria, chloroplasts have outer and inner membranes, but within the space enclosed by a chloroplast's inner membrane is a set of interconnected and stacked fluid-filled membrane sacs called thylakoids (Figure 2.1.4.10). Each stack of thylakoids is called a granum (plural = grana). The fluid enclosed by the inner membrane that surrounds the grana is called the stroma.

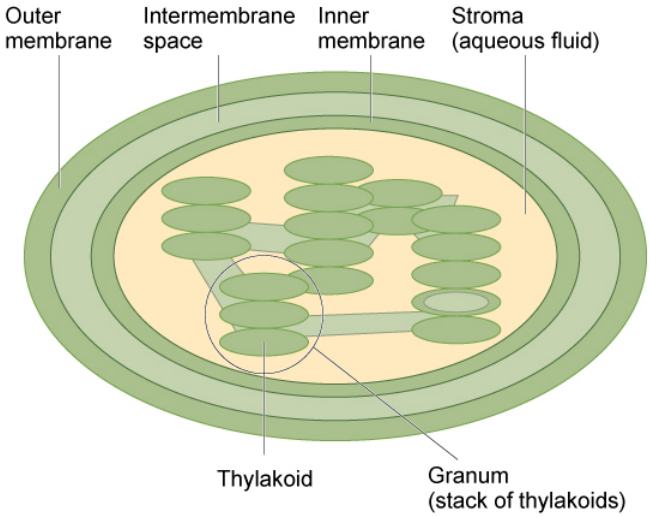


Figure 2.1.4.10: The chloroplast has an outer membrane, an inner membrane, and membrane structures called thylakoids that are stacked into grana. The space inside the thylakoid membranes is called the thylakoid space. The light harvesting reactions take place in the thylakoid membranes, and the synthesis of sugar takes place in the fluid inside the inner membrane, which is called the stroma. Chloroplasts also have their own genome, which is contained on a single circular chromosome.

The chloroplasts contain a green pigment called chlorophyll, which captures the light energy that drives the reactions of photosynthesis. Like plant cells, photosynthetic protists also have chloroplasts. Some bacteria perform photosynthesis, but their chlorophyll is not relegated to an organelle.

Video



In this 1-minute video, the structure and function of chloroplasts are reviewed.

Evolution Connection: Endosymbiosis

We have mentioned that both mitochondria and chloroplasts contain DNA and ribosomes. Have you wondered why? Strong evidence points to endosymbiosis as the explanation.

Symbiosis is a relationship in which organisms from two separate species depend on each other for their survival. Endosymbiosis (endo- = "within") is a mutually beneficial relationship in which one organism lives inside the other. Endosymbiotic relationships abound in nature. We have already mentioned that microbes that produce vitamin K live inside the human gut. This relationship is beneficial for us because we are unable to synthesize vitamin K. It is also beneficial for the microbes because they are protected from other organisms and from drying out, and they receive abundant food from the environment of the large intestine.

Scientists have long noticed that bacteria, mitochondria, and chloroplasts are similar in size. We also know that bacteria have DNA and ribosomes, just as mitochondria and chloroplasts do. Scientists believe that host cells and bacteria formed an endosymbiotic relationship when the host cells ingested both aerobic and autotrophic bacteria (cyanobacteria) but did not destroy them. Through many millions of years of evolution, these ingested bacteria became more specialized in their functions, with the aerobic bacteria becoming mitochondria and the autotrophic bacteria becoming chloroplasts.

The Central Vacuole

Previously, we mentioned vacuoles as essential components of plant cells. If you look at Figure 2.1.4.1b, you will see that plant cells each have a large central vacuole that occupies most of the area of the cell. The central vacuole plays a key role in regulating the cell's concentration of water in changing environmental conditions. Have you ever noticed that if you forget to water a plant for a few days, it wilts? That's because as the water concentration in the soil becomes lower than the water concentration in the plant, water moves out of the central vacuoles and cytoplasm. As the central vacuole shrinks, it leaves the cell wall unsupported. This loss of support to the cell walls of plant cells results in the wilted appearance of the plant.

The central vacuole also supports the expansion of the cell. When the central vacuole holds more water, the cell gets larger without having to invest a lot of energy in synthesizing new cytoplasm.

Summary

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. The plasma membrane is a phospholipid bilayer embedded with proteins. The nucleus's nucleolus is the site of ribosome assembly. Ribosomes are either found in the cytoplasm or attached to the cytoplasmic side of the plasma membrane or endoplasmic reticulum. They perform protein synthesis. Mitochondria participate in cellular respiration; they are responsible for the majority of ATP produced in the cell. Peroxisomes hydrolyze fatty acids, amino

acids, and some toxins. Vesicles and vacuoles are storage and transport compartments. In plant cells, vacuoles also help break down macromolecules.

Animal cells also have a centrosome and lysosomes. The centrosome has two bodies perpendicular to each other, the centrioles, and has an unknown purpose in cell division. Lysosomes are the digestive organelles of animal cells.

Plant cells and plant-like cells each have a cell wall, chloroplasts, and a central vacuole. The plant cell wall, whose primary component is cellulose, protects the cell, provides structural support, and gives shape to the cell. Photosynthesis takes place in chloroplasts. The central vacuole can expand without having to produce more cytoplasm.

Glossary

cell wall
rigid cell covering made of cellulose that protects the cell, provides structural support, and gives shape to the cell

central vacuole
large plant cell organelle that regulates the cell's storage compartment, holds water, and plays a significant role in cell growth as the site of macromolecule degradation

centrosome
region in animal cells made of two centrioles

chlorophyll
green pigment that captures the light energy that drives the light reactions of photosynthesis

chloroplast
plant cell organelle that carries out photosynthesis

chromatin
protein-DNA complex that serves as the building material of chromosomes

chromosome
structure within the nucleus that is made up of chromatin that contains DNA, the hereditary material

cytoplasm
entire region between the plasma membrane and the nuclear envelope, consisting of organelles suspended in the gel-like cytosol, the cytoskeleton, and various chemicals

cytosol
gel-like material of the cytoplasm in which cell structures are suspended

eukaryotic cell
cell that has a membrane-bound nucleus and several other membrane-bound compartments or sacs

lysosome
organelle in an animal cell that functions as the cell's digestive component; it breaks down proteins, polysaccharides, lipids, nucleic acids, and even worn-out organelles

mitochondria
(singular = mitochondrion) cellular organelles responsible for carrying out cellular respiration, resulting in the production of ATP, the cell's main energy-carrying molecule

nuclear envelope
double-membrane structure that constitutes the outermost portion of the nucleus

nucleolus
darkly staining body within the nucleus that is responsible for assembling the subunits of the ribosomes

nucleoplasm
semi-solid fluid inside the nucleus that contains the chromatin and nucleolus

nucleus
cell organelle that houses the cell's DNA and directs the synthesis of ribosomes and proteins

organelle
compartment or sac within a cell

peroxisome
small, round organelle that contains hydrogen peroxide, oxidizes fatty acids and amino acids, and detoxifies many poisons

plasma membrane
phospholipid bilayer with embedded (integral) or attached (peripheral) proteins, and separates the internal content of the cell from its surrounding environment

ribosome
cellular structure that carries out protein synthesis

vacuole
membrane-bound sac, somewhat larger than a vesicle, which functions in cellular storage and transport

vesicle
small, membrane-bound sac that functions in cellular storage and transport; its membrane is capable of fusing with the plasma membrane and the membranes of the endoplasmic reticulum and Golgi apparatus

---

This page titled 2.1.4: Eukaryotic Cells is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.3: Eukaryotic Cells** by OpenStax is licensed CC BY 4.0.

2.1.5: The Endomembrane System and Proteins

Learning Objectives

- List the components of the endomembrane system
- Recognize the relationship between the endomembrane system and its functions

The endomembrane system (endo = “within”) is a group of membranes and organelles (Figure 2.1.5.1) in eukaryotic cells that works together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, which we’ve already mentioned, and the endoplasmic reticulum and Golgi apparatus, which we will cover shortly. Although not technically *within* the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles. The endomembrane system does not include the membranes of either mitochondria or chloroplasts.

Art Connection

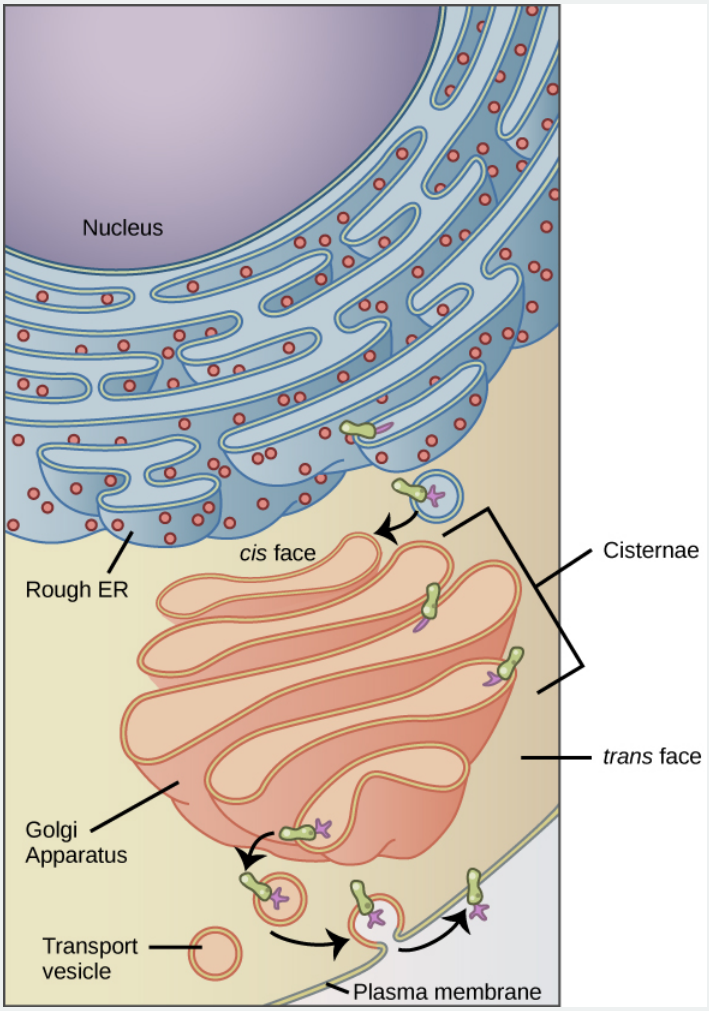


Figure 2.1.5.1: Membrane and secretory proteins are synthesized in the rough endoplasmic reticulum (RER). The RER also sometimes modifies proteins. In this illustration, a (green) integral membrane protein in the ER is modified by attachment of a (purple) carbohydrate. Vesicles with the integral protein bud from the ER and fuse with the cis face of the Golgi apparatus. As the protein passes along the Golgi’s cisternae, it is further modified by the addition of more carbohydrates. After its synthesis is complete, it exits as integral membrane protein of the vesicle that bud from the Golgi’s trans face and when the vesicle fuses with the cell membrane the protein becomes integral portion of that cell membrane. (credit: modification of work by Magnus Manske)

If a peripheral membrane protein were synthesized in the lumen (inside) of the ER, would it end up on the inside or outside of the plasma membrane?

The Endoplasmic Reticulum

The endoplasmic reticulum (ER) (Figure 2.1.5.1) is a series of interconnected membranous sacs and tubules that collectively modifies proteins and synthesizes lipids. However, these two functions are performed in separate areas of the ER: the rough ER and the smooth ER, respectively.

The hollow portion of the ER tubules is called the lumen or cisternal space. The membrane of the ER, which is a phospholipid bilayer embedded with proteins, is continuous with the nuclear envelope.

Video



In this 1-minute video, the structure and function of the endoplasmic reticulum are reviewed.

Rough ER

The rough endoplasmic reticulum (RER) is so named because the ribosomes attached to its cytoplasmic surface give it a studded appearance when viewed through an electron microscope (Figure 2.1.5.2).

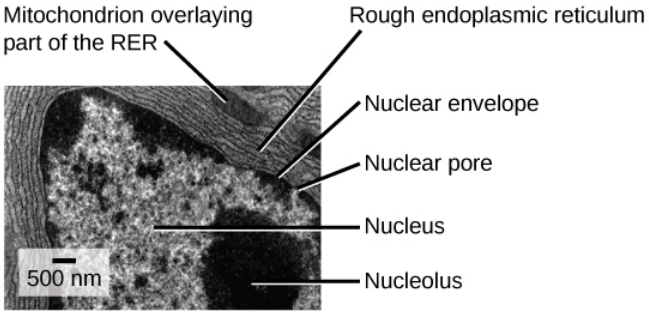


Figure 2.1.5.2: This transmission electron micrograph shows the rough endoplasmic reticulum and other organelles in a pancreatic cell. (credit: modification of work by Louisa Howard)

Ribosomes transfer their newly synthesized proteins into the lumen of the RER where they undergo structural modifications, such as folding or the acquisition of side chains. These modified proteins will be incorporated into cellular membranes—the membrane of the ER or those of other organelles—or secreted from the cell (such as protein hormones, enzymes). The RER also makes phospholipids for cellular membranes.

If the phospholipids or modified proteins are not destined to stay in the RER, they will reach their destinations via transport vesicles that bud from the RER's membrane (Figure 2.1.5.1).

Since the RER is engaged in modifying proteins (such as enzymes, for example) that will be secreted from the cell, you would be correct in assuming that the RER is abundant in cells that secrete proteins. This is the case with cells of the liver, for example.

Smooth ER

The smooth endoplasmic reticulum (SER) is continuous with the RER but has few or no ribosomes on its cytoplasmic surface (Figure 2.1.5.1). Functions of the SER include synthesis of carbohydrates, lipids, and steroid hormones; detoxification of medications and poisons; and storage of calcium ions.

In muscle cells, a specialized SER called the sarcoplasmic reticulum is responsible for storage of the calcium ions that are needed to trigger the coordinated contractions of the muscle cells.

Link to Learning



Video 2.1.5.1: You can watch an excellent animation of the endomembrane system here.

Career Connection: Cardiologist

Heart disease is the leading cause of death in the United States. This is primarily due to our sedentary lifestyle and our high trans-fat diets.

Heart failure is just one of many disabling heart conditions. Heart failure does not mean that the heart has stopped working. Rather, it means that the heart can't pump with sufficient force to transport oxygenated blood to all the vital organs. Left untreated, heart failure can lead to kidney failure and failure of other organs.

The wall of the heart is composed of cardiac muscle tissue. Heart failure occurs when the endoplasmic reticula of cardiac muscle cells do not function properly. As a result, an insufficient number of calcium ions are available to trigger a sufficient contractile force.

Cardiologists (cardi- = "heart"; -ologist = "one who studies") are doctors who specialize in treating heart diseases, including heart failure. Cardiologists can make a diagnosis of heart failure via physical examination, results from an electrocardiogram (ECG, a test that measures the electrical activity of the heart), a chest X-ray to see whether the heart is enlarged, and other tests. If heart failure is diagnosed, the cardiologist will typically prescribe appropriate medications and recommend a reduction in table salt intake and a supervised exercise program.

The Golgi Apparatus

We have already mentioned that vesicles can bud from the ER and transport their contents elsewhere, but where do the vesicles go? Before reaching their final destination, the lipids or proteins within the transport vesicles still need to be sorted, packaged, and tagged so that they wind up in the right place. Sorting, tagging, packaging, and distribution of lipids and proteins takes place in the Golgi apparatus (also called the Golgi body), a series of flattened membranes (Figure 2.1.5.3).

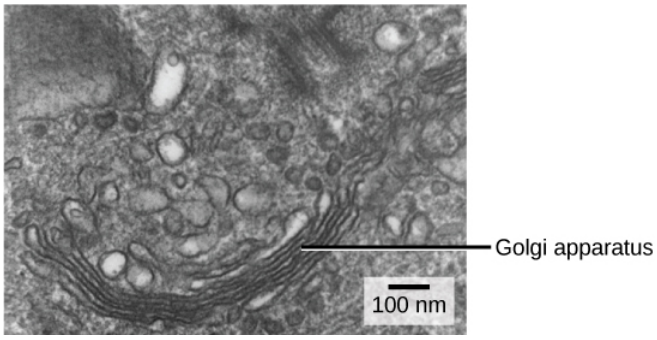


Figure 2.1.5.3: The Golgi apparatus in this white blood cell is visible as a stack of semicircular, flattened rings in the lower portion of the image. Several vesicles can be seen near the Golgi apparatus. (credit: modification of work by Louisa Howard)

The receiving side of the Golgi apparatus is called the *cis* face. The opposite side is called the *trans* face. The transport vesicles that formed from the ER travel to the *cis* face, fuse with it, and empty their contents into the lumen of the Golgi apparatus. As the proteins and lipids travel through the Golgi, they undergo further modifications that allow them to be sorted. The most frequent modification is the addition of short chains of sugar molecules. These newly modified proteins and lipids are then tagged with phosphate groups or other small molecules so that they can be routed to their proper destinations.

Finally, the modified and tagged proteins are packaged into secretory vesicles that bud from the *trans* face of the Golgi. While some of these vesicles deposit their contents into other parts of the cell where they will be used, other secretory vesicles fuse with the plasma membrane and release their contents outside the cell.

In another example of form following function, cells that engage in a great deal of secretory activity (such as cells of the salivary glands that secrete digestive enzymes or cells of the immune system that secrete antibodies) have an abundance of Golgi.

In plant cells, the Golgi apparatus has the additional role of synthesizing polysaccharides, some of which are incorporated into the cell wall and some of which are used in other parts of the cell.

Video



In this 1-minute video, the structure and function of the Golgi apparatus are reviewed.

Career Connection: Geneticist

Many diseases arise from genetic mutations that prevent the synthesis of critical proteins. One such disease is Lowe disease (also called oculocerebrorenal syndrome, because it affects the eyes, brain, and kidneys). In Lowe disease, there is a deficiency in an enzyme localized to the Golgi apparatus. Children with Lowe disease are born with cataracts, typically develop kidney disease after the first year of life, and may have impaired mental abilities.

Lowe disease is a genetic disease caused by a mutation on the X chromosome. The X chromosome is one of the two human sex chromosome, as these chromosomes determine a person's sex. Females possess two X chromosomes while males possess one

X and one Y chromosome. In females, the genes on only one of the two X chromosomes are expressed. Therefore, females who carry the Lowe disease gene on one of their X chromosomes have a 50/50 chance of having the disease. However, males only have one X chromosome and the genes on this chromosome are always expressed. Therefore, males will always have Lowe disease if their X chromosome carries the Lowe disease gene. The location of the mutated gene, as well as the locations of many other mutations that cause genetic diseases, has now been identified. Through prenatal testing, a woman can find out if the fetus she is carrying may be afflicted with one of several genetic diseases.

Geneticists analyze the results of prenatal genetic tests and may counsel pregnant women on available options. They may also conduct genetic research that leads to new drugs or foods, or perform DNA analyses that are used in forensic investigations.

Lysosomes

In addition to their role as the digestive component and organelle-recycling facility of animal cells, lysosomes are considered to be parts of the endomembrane system. Lysosomes also use their hydrolytic enzymes to destroy pathogens (disease-causing organisms) that might enter the cell. A good example of this occurs in a group of white blood cells called macrophages, which are part of your body's immune system. In a process known as phagocytosis or endocytosis, a section of the plasma membrane of the macrophage invaginates (folds in) and engulfs a pathogen. The invaginated section, with the pathogen inside, then pinches itself off from the plasma membrane and becomes a vesicle. The vesicle fuses with a lysosome. The lysosome's hydrolytic enzymes then destroy the pathogen (Figure 2.1.5.4).

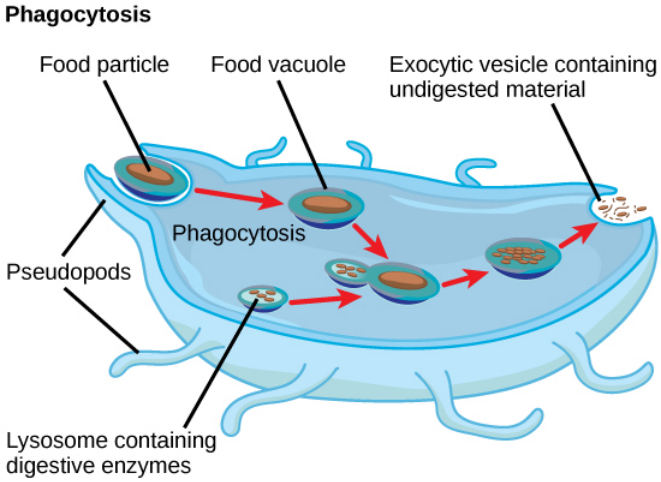


Figure 2.1.5.4: A macrophage has engulfed (phagocytized) a potentially pathogenic bacterium and then fuses with a lysosomes within the cell to destroy the pathogen. Other organelles are present in the cell but for simplicity are not shown.

Summary

The endomembrane system includes the nuclear envelope, lysosomes, vesicles, the ER, and Golgi apparatus, as well as the plasma membrane. These cellular components work together to modify, package, tag, and transport proteins and lipids that form the membranes.

The RER modifies proteins and synthesizes phospholipids used in cell membranes. The SER synthesizes carbohydrates, lipids, and steroid hormones; engages in the detoxification of medications and poisons; and stores calcium ions. Sorting, tagging, packaging, and distribution of lipids and proteins take place in the Golgi apparatus. Lysosomes are created by the budding of the membranes of the RER and Golgi. Lysosomes digest macromolecules, recycle worn-out organelles, and destroy pathogens.

Art Connections

Figure 2.1.5.1: If a peripheral membrane protein were synthesized in the lumen (inside) of the ER, would it end up on the inside or outside of the plasma membrane?

Answer

> It would end up on the outside. After the vesicle passes through the Golgi apparatus and fuses with the plasma membrane, it turns inside out.

Glossary

endomembrane system
: group of organelles and membranes in eukaryotic cells that work together modifying, packaging, and transporting lipids and proteins

endoplasmic reticulum (ER)
: series of interconnected membranous structures within eukaryotic cells that collectively modify proteins and synthesize lipids

Golgi apparatus
: eukaryotic organelle made up of a series of stacked membranes that sorts, tags, and packages lipids and proteins for distribution

rough endoplasmic reticulum (RER)
: region of the endoplasmic reticulum that is studded with ribosomes and engages in protein modification and phospholipid synthesis

smooth endoplasmic reticulum (SER)
: region of the endoplasmic reticulum that has few or no ribosomes on its cytoplasmic surface and synthesizes carbohydrates, lipids, and steroid hormones; detoxifies certain chemicals (like pesticides, preservatives, medications, and environmental pollutants), and stores calcium ions

---

This page titled 2.1.5: The Endomembrane System and Proteins is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.4: The Endomembrane System and Proteins** by OpenStax is licensed CC BY 4.0.

2.1.6: The Cytoskeleton

Skills to Develop

- Describe the cytoskeleton
- Compare the roles of microfilaments, intermediate filaments, and microtubules
- Compare and contrast cilia and flagella
- Summarize the differences among the components of prokaryotic cells, animal cells, and plant cells

If you were to remove all the organelles from a cell, would the plasma membrane and the cytoplasm be the only components left? No. Within the cytoplasm, there would still be ions and organic molecules, plus a network of protein fibers that help maintain the shape of the cell, secure some organelles in specific positions, allow cytoplasm and vesicles to move within the cell, and enable cells within multicellular organisms to move. Collectively, this network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, intermediate filaments, and microtubules (Figure 2.1.6.1). Here, we will examine each.

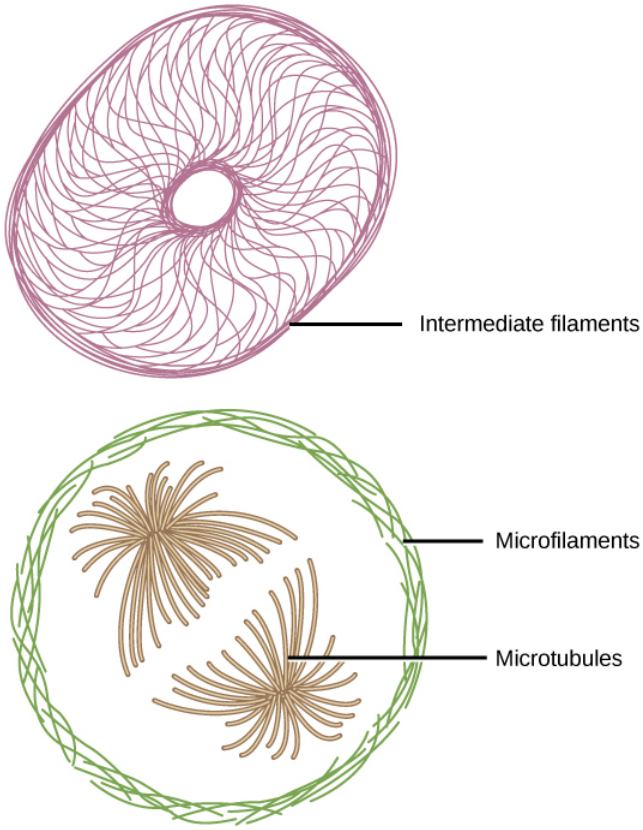


Figure 2.1.6.1: Microfilaments thicken the cortex around the inner edge of a cell; like rubber bands, they resist tension. Microtubules are found in the interior of the cell where they maintain cell shape by resisting compressive forces. Intermediate filaments are found throughout the cell and hold organelles in place.

Microfilaments

Of the three types of protein fibers in the cytoskeleton, microfilaments are the narrowest. They function in cellular movement, have a diameter of about 7 nm, and are made of two intertwined strands of a globular protein called actin (Figure 2.1.6.2). For this reason, microfilaments are also known as actin filaments.

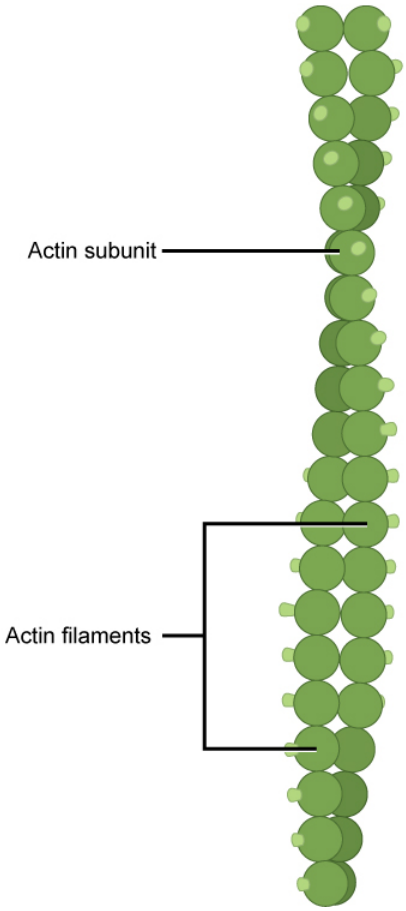


Figure 2.1.6.2: Microfilaments are made of two intertwined strands of actin.

Actin is powered by ATP to assemble its filamentous form, which serves as a track for the movement of a motor protein called myosin. This enables actin to engage in cellular events requiring motion, such as cell division in animal cells and cytoplasmic streaming, which is the circular movement of the cell cytoplasm in plant cells. Actin and myosin are plentiful in muscle cells. When your actin and myosin filaments slide past each other, your muscles contract.

Microfilaments also provide some rigidity and shape to the cell. They can depolymerize (disassemble) and reform quickly, thus enabling a cell to change its shape and move. White blood cells (your body's infection-fighting cells) make good use of this ability. They can move to the site of an infection and phagocytize the pathogen.

Link to Learning



Video 2.1.6.1: To see an example of a white blood cell in action, watch a short time-lapse video of the cell capturing two bacteria. It engulfs one and then moves on to the other.

Intermediate Filaments

Intermediate filaments are made of several strands of fibrous proteins that are wound together (Figure 2.1.6.3). These elements of the cytoskeleton get their name from the fact that their diameter, 8 to 10 nm, is between those of microfilaments and microtubules.



Figure 2.1.6.3: Intermediate filaments consist of several intertwined strands of fibrous proteins.

Intermediate filaments have no role in cell movement. Their function is purely structural. They bear tension, thus maintaining the shape of the cell, and anchor the nucleus and other organelles in place. Figure 2.1.6.1 shows how intermediate filaments create a supportive scaffolding inside the cell.

The intermediate filaments are the most diverse group of cytoskeletal elements. Several types of fibrous proteins are found in the intermediate filaments. You are probably most familiar with keratin, the fibrous protein that strengthens your hair, nails, and the epidermis of the skin.

Microtubules

As their name implies, microtubules are small hollow tubes. The walls of the microtubule are made of polymerized dimers of α-tubulin and β-tubulin, two globular proteins (Figure 2.1.6.4). With a diameter of about 25 nm, microtubules are the widest components of the cytoskeleton. They help the cell resist compression, provide a track along which vesicles move through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. Like microfilaments, microtubules can dissolve and reform quickly.

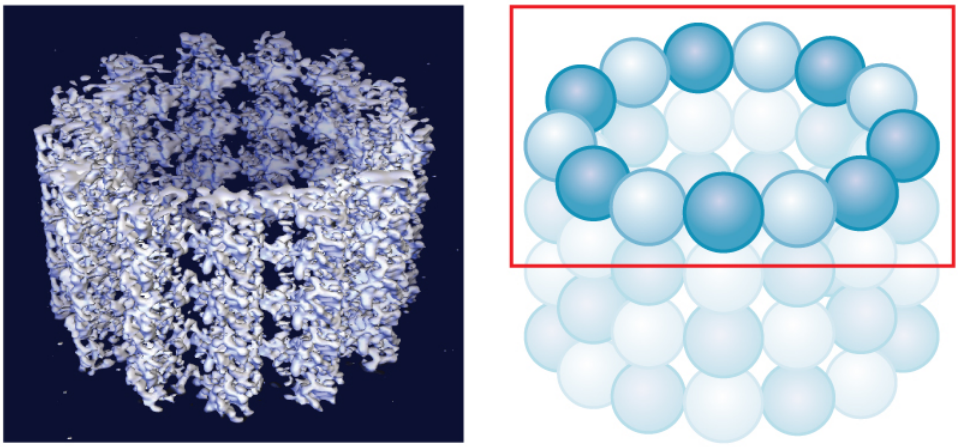


Figure 2.1.6.4: Microtubules are hollow. Their walls consist of 13 polymerized dimers of α-tubulin and β-tubulin (right image). The left image shows the molecular structure of the tube.

Microtubules are also the structural elements of flagella, cilia, and centrioles (the latter are the two perpendicular bodies of the centrosome). In fact, in animal cells, the centrosome is the microtubule-organizing center. In eukaryotic cells, flagella and cilia are quite different structurally from their counterparts in prokaryotes, as discussed below.

Flagella and Cilia

To refresh your memory, flagella (singular = flagellum) are long, hair-like structures that extend from the plasma membrane and are used to move an entire cell (for example, sperm, *Euglena*). When present, the cell has just one flagellum or a few flagella. When cilia (singular = cilium) are present, however, many of them extend along the entire surface of the plasma membrane. They are

short, hair-like structures that are used to move entire cells (such as paramecia) or substances along the outer surface of the cell (for example, the cilia of cells lining the Fallopian tubes that move the ovum toward the uterus, or cilia lining the cells of the respiratory tract that trap particulate matter and move it toward your nostrils.)

Despite their differences in length and number, flagella and cilia share a common structural arrangement of microtubules called a "9 + 2 array." This is an appropriate name because a single flagellum or cilium is made of a ring of nine microtubule doublets, surrounding a single microtubule doublet in the center (Figure 2.1.6.5).

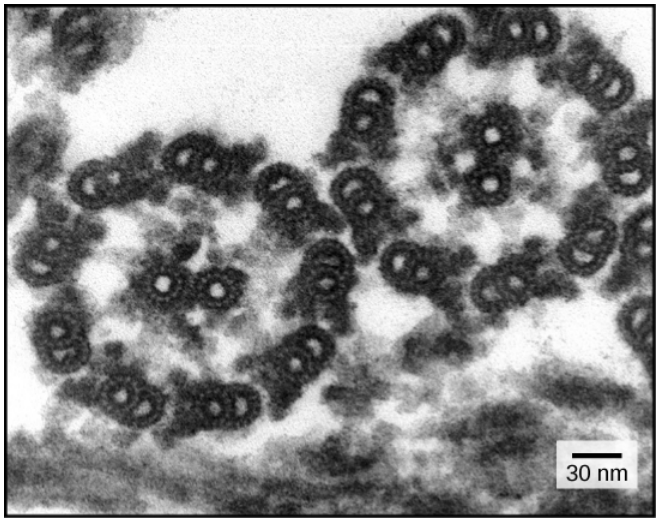


Figure 2.1.6.5: This transmission electron micrograph of two flagella shows the 9 + 2 array of microtubules: nine microtubule doublets surround a single microtubule doublet. (credit: modification of work by Dartmouth Electron Microscope Facility, Dartmouth College; scale-bar data from Matt Russell)

You have now completed a broad survey of the components of prokaryotic and eukaryotic cells. For a summary of cellular components in prokaryotic and eukaryotic cells, see Table 2.1.6.1.

Table 2.1.6.1: Cellular components in prokaryotic and eukaryotic cells.

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
Plasma membrane	Separates cell from external environment; controls passage of organic molecules, ions, water, oxygen, and wastes into and out of cell	Yes	Yes	Yes
Cytoplasm	Provides turgor pressure to plant cells as fluid inside the central vacuole; site of many metabolic reactions; medium in which organelles are found	Yes	Yes	Yes
Nucleolus	Darkened area within the nucleus where ribosomal subunits are synthesized.	No	Yes	Yes
Nucleus	Cell organelle that houses DNA and directs synthesis of ribosomes and proteins	No	Yes	Yes
Ribosomes	Protein synthesis	Yes	Yes	Yes
Mitochondria	ATP production/cellular respiration	No	Yes	Yes
Peroxisomes	Oxidizes and thus breaks down fatty acids and amino acids, and detoxifies poisons	No	Yes	Yes
Vesicles and vacuoles	Storage and transport; digestive function in plant cells	No	Yes	Yes
Centrosome	Unspecified role in cell division in animal cells; source of microtubules in animal cells	No	Yes	No
Lysosomes	Digestion of macromolecules; recycling of worn-out organelles	No	Yes	No
Cell wall	Protection, structural support and maintenance of cell shape	Yes, primarily peptidoglycan	No	Yes, primarily cellulose
Chloroplasts	Photosynthesis	No	No	Yes
Endoplasmic reticulum	Modifies proteins and	No	Yes	Yes

Cell Component	Function	Present in Prokaryotes?	Present in Animal Cells?	Present in Plant Cells?
	synthesizes lipids			
Golgi apparatus	Modifies, sorts, tags, packages, and distributes lipids and proteins	No	Yes	Yes
Cytoskeleton	Maintains cell's shape, secures organelles in specific positions, allows cytoplasm and vesicles to move within cell, and enables unicellular organisms to move independently	Yes	Yes	Yes
Flagella	Cellular locomotion	Some	Some	No, except for some plant sperm cells.
Cilia	Cellular locomotion, movement of particles along extracellular surface of plasma membrane, and filtration	Some	Some	No

Summary

The cytoskeleton has three different types of protein elements. From narrowest to widest, they are the microfilaments (actin filaments), intermediate filaments, and microtubules. Microfilaments are often associated with myosin. They provide rigidity and shape to the cell and facilitate cellular movements. Intermediate filaments bear tension and anchor the nucleus and other organelles in place. Microtubules help the cell resist compression, serve as tracks for motor proteins that move vesicles through the cell, and pull replicated chromosomes to opposite ends of a dividing cell. They are also the structural element of centrioles, flagella, and cilia.

Glossary

cilium

(plural = cilia) short, hair-like structure that extends from the plasma membrane in large numbers and is used to move an entire cell or move substances along the outer surface of the cell

cytoskeleton

network of protein fibers that collectively maintain the shape of the cell, secure some organelles in specific positions, allow cytoplasm and vesicles to move within the cell, and enable unicellular organisms to move independently

flagellum

(plural = flagella) long, hair-like structure that extends from the plasma membrane and is used to move the cell

intermediate filament

cytoskeletal component, composed of several intertwined strands of fibrous protein, that bears tension, supports cell-cell junctions, and anchors cells to extracellular structures

microfilament

narrowest element of the cytoskeleton system; it provides rigidity and shape to the cell and enables cellular movements

microtubule

widest element of the cytoskeleton system; it helps the cell resist compression, provides a track along which vesicles move through the cell, pulls replicated chromosomes to opposite ends of a dividing cell, and is the structural element of centrioles, flagella, and cilia

---

This page titled 2.1.6: The Cytoskeleton is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.5: The Cytoskeleton** by OpenStax is licensed CC BY 4.0.

2.1.7: Connections between Cells and Cellular Activities

Skills to Develop

- Describe the extracellular matrix
- List examples of the ways that plant cells and animal cells communicate with adjacent cells
- Summarize the roles of tight junctions, desmosomes, gap junctions, and plasmodesmata

You already know that a group of similar cells working together is called a tissue. As you might expect, if cells are to work together, they must communicate with each other, just as you need to communicate with others if you work on a group project. Let's take a look at how cells communicate with each other.

Extracellular Matrix of Animal Cells

Most animal cells release materials into the extracellular space. The primary components of these materials are proteins, and the most abundant protein is collagen. Collagen fibers are interwoven with carbohydrate-containing protein molecules called proteoglycans. Collectively, these materials are called the extracellular matrix (Figure 2.1.7.1). Not only does the extracellular matrix hold the cells together to form a tissue, but it also allows the cells within the tissue to communicate with each other. How can this happen?

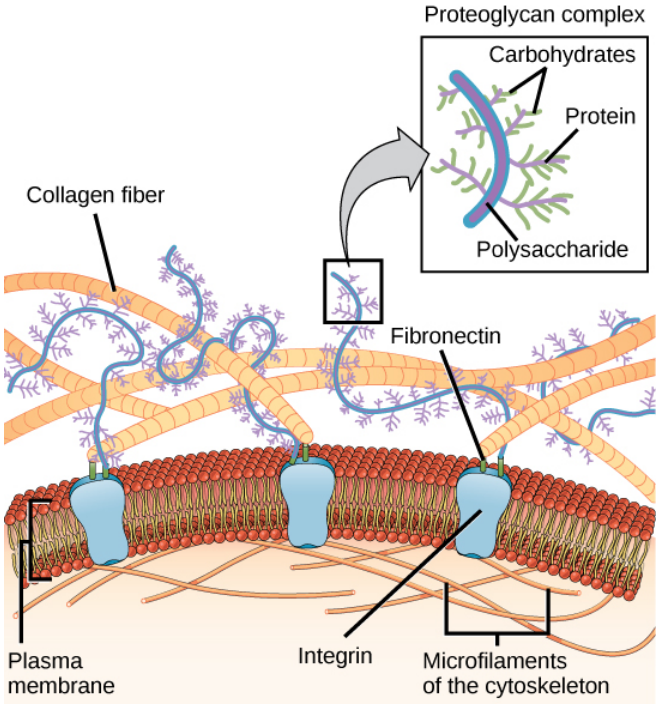


Figure 2.1.7.1: The extracellular matrix consists of a network of proteins and carbohydrates.

Cells have protein receptors on the extracellular surfaces of their plasma membranes. When a molecule within the matrix binds to the receptor, it changes the molecular structure of the receptor. The receptor, in turn, changes the conformation of the microfilaments positioned just inside the plasma membrane. These conformational changes induce chemical signals inside the cell that reach the nucleus and turn "on" or "off" the transcription of specific sections of DNA, which affects the production of associated proteins, thus changing the activities within the cell.

Blood clotting provides an example of the role of the extracellular matrix in cell communication. When the cells lining a blood vessel are damaged, they display a protein receptor called tissue factor. When tissue factor binds with another factor in the extracellular matrix, it causes platelets to adhere to the wall of the damaged blood vessel, stimulates the adjacent smooth muscle cells in the blood vessel to contract (thus constricting the blood vessel), and initiates a series of steps that stimulate the platelets to produce clotting factors.

Intercellular Junctions

Cells can also communicate with each other via direct contact, referred to as intercellular junctions. There are some differences in the ways that plant and animal cells do this. Plasmodesmata are junctions between plant cells, whereas animal cell contacts include tight junctions, gap junctions, and desmosomes.

Plasmodesmata

In general, long stretches of the plasma membranes of neighboring plant cells cannot touch one another because they are separated by the cell wall that surrounds each cell. How then, can a plant transfer water and other soil nutrients from its roots, through its stems, and to its leaves? Such transport uses the vascular tissues (xylem and phloem) primarily. There also exist structural modifications called plasmodesmata (singular = plasmodesma), numerous channels that pass between cell walls of adjacent plant cells, connect their cytoplasm, and enable materials to be transported from cell to cell, and thus throughout the plant (Figure 2.1.7.2).

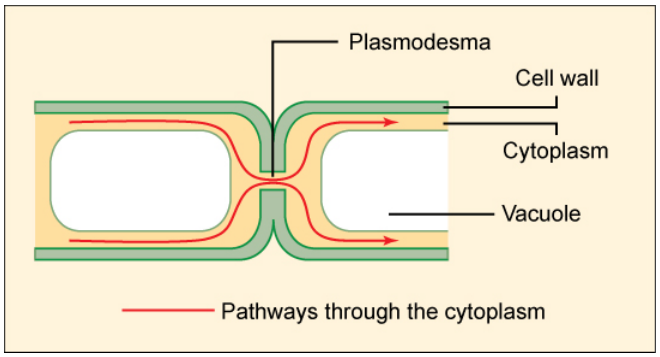


Figure 2.1.7.2: A plasmodesma is a channel between the cell walls of two adjacent plant cells. Plasmodesmata allow materials to pass from the cytoplasm of one plant cell to the cytoplasm of an adjacent cell.

Tight Junctions

A tight junction is a watertight seal between two adjacent animal cells (Figure 2.1.7.3). The cells are held tightly against each other by proteins (predominantly two proteins called claudins and occludins).

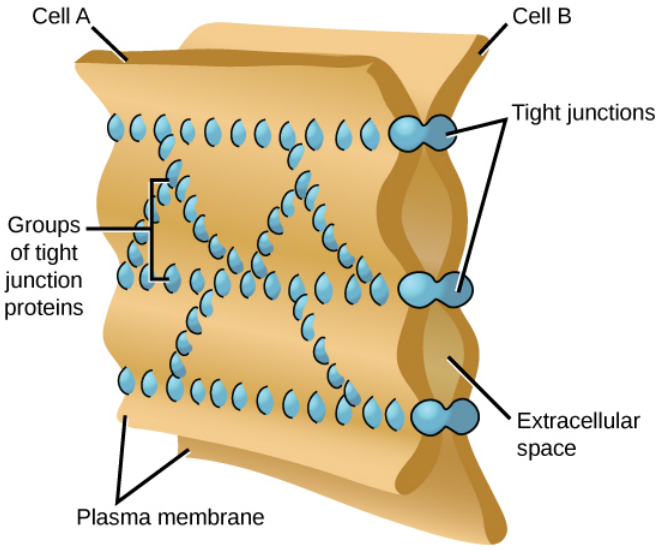


Figure 2.1.7.3: Tight junctions form watertight connections between adjacent animal cells. Proteins create tight junction adherence. (credit: modification of work by Mariana Ruiz Villareal)

This tight adherence prevents materials from leaking between the cells; tight junctions are typically found in epithelial tissues that line internal organs and cavities, and comprise most of the skin. For example, the tight junctions of the epithelial cells lining your urinary bladder prevent urine from leaking out into the extracellular space.

Desmosomes

Also found only in animal cells are desmosomes, which act like spot welds between adjacent epithelial cells (Figure 2.1.7.4). Short proteins called cadherins in the plasma membrane connect to intermediate filaments to create desmosomes. The cadherins join two adjacent cells together and maintain the cells in a sheet-like formation in organs and tissues that stretch, like the skin, heart, and muscles.

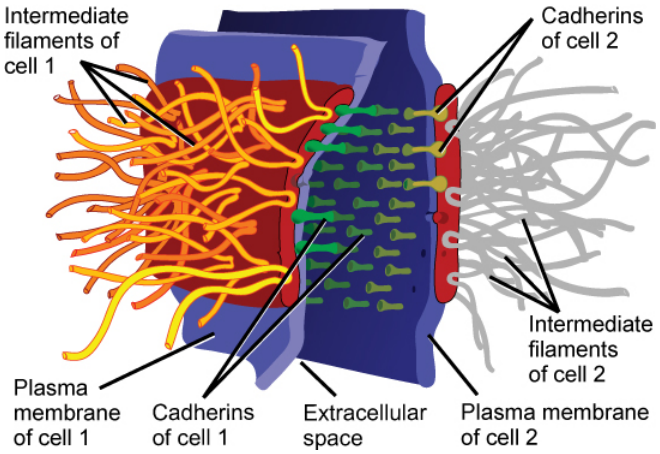


Figure 2.1.7.4: A desmosome forms a very strong spot weld between cells. It is created by the linkage of cadherins and intermediate filaments. (credit: modification of work by Mariana Ruiz Villareal)

Gap Junctions

Gap junctions in animal cells are like plasmodesmata in plant cells in that they are channels between adjacent cells that allow for the transport of ions, nutrients, and other substances that enable cells to communicate (Figure 2.1.7.5). Structurally, however, gap junctions and plasmodesmata differ.

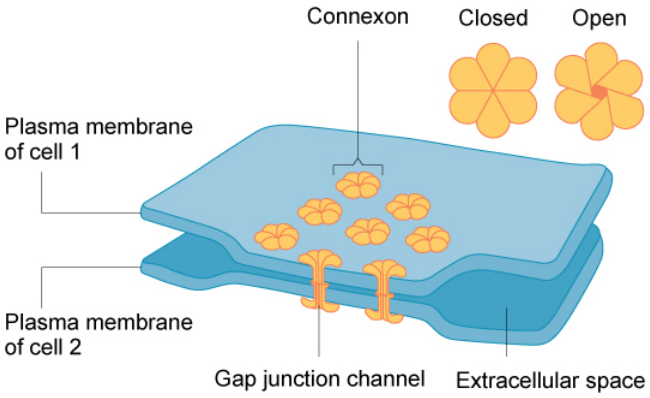


Figure 2.1.7.5: A gap junction is a protein-lined pore that allows water and small molecules to pass between adjacent animal cells. (credit: modification of work by Mariana Ruiz Villareal)

Gap junctions develop when a set of six proteins (called connexins) in the plasma membrane arrange themselves in an elongated donut-like configuration called a connexon. When the pores (“doughnut holes”) of connexons in adjacent animal cells align, a channel between the two cells forms. Gap junctions are particularly important in cardiac muscle: The electrical signal for the muscle to contract is passed efficiently through gap junctions, allowing the heart muscle cells to contract in tandem.

Summary

Animal cells communicate via their extracellular matrices and are connected to each other via tight junctions, desmosomes, and gap junctions. Plant cells are connected and communicate with each other via plasmodesmata.

When protein receptors on the surface of the plasma membrane of an animal cell bind to a substance in the extracellular matrix, a chain of reactions begins that changes activities taking place within the cell. Plasmodesmata are channels between adjacent plant cells, while gap junctions are channels between adjacent animal cells. However, their structures are quite different. A tight junction is a watertight seal between two adjacent cells, while a desmosome acts like a spot weld.

Glossary

desmosome
: linkages between adjacent epithelial cells that form when cadherins in the plasma membrane attach to intermediate filaments

extracellular matrix
: material (primarily collagen, glycoproteins, and proteoglycans) secreted from animal cells that provides mechanical protection and anchoring for the cells in the tissue

gap junction
: channel between two adjacent animal cells that allows ions, nutrients, and low molecular weight substances to pass between cells, enabling the cells to communicate

plasmodesma
: (plural = plasmodesmata) channel that passes between the cell walls of adjacent plant cells, connects their cytoplasm, and allows materials to be transported from cell to cell

tight junction
: firm seal between two adjacent animal cells created by protein adherence

---

This page titled 2.1.7: Connections between Cells and Cellular Activities is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.6: Connections between Cells and Cellular Activities** by OpenStax is licensed CC BY 4.0.

2.1.E: Cell Structure (Exercises)

4.1: Studying Cells

A cell is the smallest unit of a living thing. A living thing, whether made of one cell (like bacteria) or many cells (like a human), is called an organism. Thus, cells are the basic building blocks of all organisms. There are many types of cells, all grouped into one of two broad categories: prokaryotic and eukaryotic. For example, both animal and plant cells are classified as eukaryotic cells, whereas bacterial cells are classified as prokaryotic.

Review Questions

When viewing a specimen through a light microscope, scientists use _____ to distinguish the individual components of cells.

A. a beam of electrons
B. radioactive isotopes
C. special stains
D. high temperatures

Answer

C

The _____ is the basic unit of life.

A. organism
B. cell
C. tissue
D. organ

Answer

B

Free Response

In your everyday life, you have probably noticed that certain instruments are ideal for certain situations. For example, you would use a spoon rather than a fork to eat soup because a spoon is shaped for scooping, while soup would slip between the tines of a fork. The use of ideal instruments also applies in science. In what situation(s) would the use of a light microscope be ideal, and why?

Answer

A light microscope would be ideal when viewing a small living organism, especially when the cell has been stained to reveal details.

In what situation(s) would the use of a scanning electron microscope be ideal, and why?

Answer

A scanning electron microscope would be ideal when you want to view the minute details of a cell's surface, because its beam of electrons moves back and forth over the surface to convey the image.

In what situation(s) would a transmission electron microscope be ideal, and why?

Answer

A transmission electron microscope would be ideal for viewing the cell's internal structures, because many of the internal structures have membranes that are not visible by the light microscope.

What are the advantages and disadvantages of each of these types of microscopes?

Answer

The advantages of light microscopes are that they are easily obtained, and the light beam does not kill the cells. However, typical light microscopes are somewhat limited in the amount of detail they can reveal. Electron microscopes are ideal because you can view intricate details, but they are bulky and costly, and preparation for the microscopic examination kills the specimen.

4.2: Prokaryotic Cells

Cells fall into one of two broad categories: prokaryotic and eukaryotic. Only the predominantly single-celled organisms of the domains Bacteria and Archaea are classified as prokaryotes (pro- = "before"; -kary- = "nucleus"). Cells of animals, plants, fungi, and protists are all eukaryotes (ceu- = "true") and are made up of eukaryotic cells.

Review Questions

Prokaryotes depend on _____ to obtain some materials and to get rid of wastes.

A. ribosomes
B. flagella
C. cell division
D. diffusion

Answer

D

Bacteria that lack fimbriae are less likely to _____.

A. adhere to cell surfaces
B. swim through bodily fluids
C. synthesize proteins
D. retain the ability to divide

Answer

A

Free Response

Antibiotics are medicines that are used to fight bacterial infections. These medicines kill prokaryotic cells without harming human cells. What part or parts of the bacterial cell do you think antibiotics target? Why?

Answer

The cell wall would be targeted by antibiotics as well as the bacteria's ability to replicate. This would inhibit the bacteria's ability to reproduce, and it would compromise its defense mechanisms.

Explain why not all microbes are harmful.

Answer

Some microbes are beneficial. For instance, *E. coli* bacteria populate the human gut and help break down fiber in the diet. Some foods such as yogurt are formed by bacteria.

4.3: Eukaryotic Cells

Our natural world also utilizes the principle of form following function, especially in cell biology, and this will become clear as we explore eukaryotic cells. Unlike prokaryotic cells, eukaryotic cells have: 1) a membrane-bound nucleus; 2) numerous membrane-bound organelles such as the endoplasmic reticulum, Golgi apparatus, chloroplasts, mitochondria, and others; and 3) several, rod-shaped chromosomes. Because a eukaryotic cell's nucleus is surrounded by a membrane, it is has "true nucleus."

Review Questions

Which of the following is surrounded by two phospholipid bilayers?

A. the ribosomes
B. the vesicles
C. the cytoplasm
D. the nucleoplasm

Answer

D

Peroxisomes got their name because hydrogen peroxide is:

A. used in their detoxification reactions
B. produced during their oxidation reactions
C. incorporated into their membranes
D. a cofactor for the organelles' enzymes

Answer

B

In plant cells, the function of the lysosomes is carried out by _____.

A. vacuoles
B. peroxisomes
C. ribosomes
D. nuclei

Answer

A

Which of the following is found both in eukaryotic and prokaryotic cells?

A. nucleus
B. mitochondrion
C. vacuole
D. ribosomes

Answer

D

Free Response

You already know that ribosomes are abundant in red blood cells. In what other cells of the body would you find them in great abundance? Why?

Answer

Ribosomes are abundant in muscle cells as well because muscle cells are constructed of the proteins made by the ribosomes.

What are the structural and functional similarities and differences between mitochondria and chloroplasts?

Answer

Both are similar in that they are enveloped in a double membrane, both have an intermembrane space, and both make ATP. Both mitochondria and chloroplasts have DNA, and mitochondria have inner folds called cristae and a matrix, while chloroplasts have chlorophyll and accessory pigments in the thylakoids that form stacks (grana) and a stroma.

4.4: The Endomembrane System and Proteins

The endomembrane system is a group of membranes and organelles in eukaryotic cells that works together to modify, package, and transport lipids and proteins. It includes the nuclear envelope, lysosomes, and vesicles, which we've already mentioned, and the endoplasmic reticulum and Golgi apparatus. Although not technically within the cell, the plasma membrane is included in the endomembrane system because, as you will see, it interacts with the other endomembranous organelles.

Review Questions

Which of the following is not a component of the endomembrane system?

A. mitochondrion
B. Golgi apparatus
C. endoplasmic reticulum
D. lysosome

Answer

A

The process by which a cell engulfs a foreign particle is known as:

A. endosymbiosis
B. phagocytosis
C. hydrolysis
D. membrane synthesis

Answer

B

Which of the following is most likely to have the greatest concentration of smooth endoplasmic reticulum?

A. a cell that secretes enzymes
B. a cell that destroys pathogens
C. a cell that makes steroid hormones
D. a cell that engages in photosynthesis

Answer

C

Which of the following sequences correctly lists in order the steps involved in the incorporation of a proteinaceous molecule within a cell?

A. synthesis of the protein on the ribosome; modification in the Golgi apparatus; packaging in the endoplasmic reticulum; tagging in the vesicle
B. synthesis of the protein on the lysosome; tagging in the Golgi; packaging in the vesicle; distribution in the endoplasmic reticulum
C. synthesis of the protein on the ribosome; modification in the endoplasmic reticulum; tagging in the Golgi; distribution via the vesicle
D. synthesis of the protein on the lysosome; packaging in the vesicle; distribution via the Golgi; tagging in the endoplasmic reticulum

Answer

C

Free Response

In the context of cell biology, what do we mean by form follows function? What are at least two examples of this concept?

Answer

"Form follows function" refers to the idea that the function of a body part dictates the form of that body part. As an example, compare your arm to a bat's wing. While the bones of the two correspond, the parts serve different functions in each organism and their forms have adapted to follow that function.

In your opinion, is the nuclear membrane part of the endomembrane system? Why or why not? Defend your answer.

Answer

Since the external surface of the nuclear membrane is continuous with the rough endoplasmic reticulum, which is part of the endomembrane system, then it is correct to say that it is part of the system.

4.5: The Cytoskeleton

Within the cytoplasm, there are ions and organic molecules, plus a network of protein fibers that help maintain the shape of the cell, secure some organelles in specific positions, allow cytoplasm and vesicles to move within the cell, and enable cells within multicellular organisms to move. Collectively, this network of protein fibers is known as the cytoskeleton. There are three types of fibers within the cytoskeleton: microfilaments, intermediate filaments, and microtubules.

Review Questions

Which of the following have the ability to disassemble and reform quickly?

A. microfilaments and intermediate filaments
B. microfilaments and microtubules
C. intermediate filaments and microtubules
D. only intermediate filaments

Answer

B

Which of the following do not play a role in intracellular movement?

A. microfilaments and intermediate filaments
B. microfilaments and microtubules
C. intermediate filaments and microtubules
D. only intermediate filaments

Answer

D

Free Response

What are the similarities and differences between the structures of centrioles and flagella?

Answer

Centrioles and flagella are alike in that they are made up of microtubules. In centrioles, two rings of nine microtubule "triplets" are arranged at right angles to one another. This arrangement does not occur in flagella.

How do cilia and flagella differ?

Answer

Cilia and flagella are alike in that they are made up of microtubules. Cilia are short, hair-like structures that exist in large numbers and usually cover the entire surface of the plasma membrane. Flagella, in contrast, are long, hair-like structures; when flagella are present, a cell has just one or two.

4.6: Connections between Cells and Cellular Activities

You already know that a group of similar cells working together is called a tissue. As you might expect, if cells are to work together, they must communicate with each other, just as you need to communicate with others if you work on a group project. Let's take a look at how cells communicate with each other.

Review Questions

Which of the following are found only in plant cells?

A. gap junctions
B. desmosomes
C. plasmodesmata
D. tight junctions

Answer

C

The key components of desmosomes are cadherins and _____.

A. actin
B. microfilaments
C. intermediate filaments
D. microtubules

Answer

C

Free Response

How does the structure of a plasmodesma differ from that of a gap junction?

Answer

They differ because plant cell walls are rigid. Plasmodesmata, which a plant cell needs for transportation and communication, are able to allow movement of really large molecules. Gap junctions are necessary in animal cells for transportation and communication.

Explain how the extracellular matrix functions.

Answer

The extracellular matrix functions in support and attachment for animal tissues. It also functions in the healing and growth of the tissue.

This page titled 2.1.E: Cell Structure (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **4.E: Cell Structure (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

2.2: Structure and Function of Plasma Membranes

The plasma membrane, which is also called the cell membrane, has many functions, but the most basic one is to define the borders of the cell and keep the cell functional. The plasma membrane is selectively permeable. This means that the membrane allows some materials to freely enter or leave the cell, while other materials cannot move freely, but require the use of a specialized structure, and occasionally, even energy investment for crossing.

2.2.1: Prelude to Structure and Function of Plasma Membranes

2.2.2: Components and Structure

2.2.3: Passive Transport

2.2.4: Active Transport

2.2.5: Bulk Transport

2.2.E: Structure and Function of Plasma Membranes (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.2: Structure and Function of Plasma Membranes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

2.2.1: Prelude to Structure and Function of Plasma Membranes

The plasma membrane, which is also called the cell membrane, has many functions, but the most basic one is to define the borders of the cell and keep the cell functional. The plasma membrane is selectively permeable. This means that the membrane allows some materials to freely enter or leave the cell, while other materials cannot move freely, but require the use of a specialized structure, and occasionally, even energy investment for crossing.



Figure 2.2.1.1: Despite its seeming hustle and bustle, Grand Central Station functions with a high level of organization: People and objects move from one location to another, they cross or are contained within certain boundaries, and they provide a constant flow as part of larger activity. Analogously, a plasma membrane's functions involve movement within the cell and across boundaries in the process of intracellular and intercellular activities. (credit: modification of work by Randy Le'Moine).

This page titled 2.2.1: Prelude to Structure and Function of Plasma Membranes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.0: Prelude to Structure and Function of Plasma Membranes** by OpenStax is licensed CC BY 4.0.

2.2.2: Components and Structure

Learning Objectives

- Understand the fluid mosaic model of cell membranes
- Describe the functions of phospholipids, proteins, and carbohydrates in membranes
- Discuss membrane fluidity

A cell's plasma membrane defines the cell, outlines its borders, and determines the nature of its interaction with its environment (see Table 2.2.2.1 for a summary). Cells exclude some substances, take in others, and excrete still others, all in controlled quantities. The plasma membrane must be very flexible to allow certain cells, such as red blood cells and white blood cells, to change shape as they pass through narrow capillaries. These are the more obvious functions of a plasma membrane. In addition, the surface of the plasma membrane carries markers that allow cells to recognize one another, which is vital for tissue and organ formation during early development, and which later plays a role in the "self" versus "non-self" distinction of the immune response.

Among the most sophisticated functions of the plasma membrane is the ability to transmit signals by means of complex, integral proteins known as receptors. These proteins act both as receivers of extracellular inputs and as activators of intracellular processes. These membrane receptors provide extracellular attachment sites for effectors like hormones and growth factors, and they activate intracellular response cascades when their effectors are bound. Occasionally, receptors are hijacked by viruses (HIV, human immunodeficiency virus, is one example) that use them to gain entry into cells, and at times, the genes encoding receptors become mutated, causing the process of signal transduction to malfunction with disastrous consequences.

Video



Fluid Mosaic Model

The existence of the plasma membrane was identified in the 1890s, and its chemical components were identified in 1915. The principal components identified at that time were lipids and proteins. The first widely accepted model of the plasma membrane's structure was proposed in 1935 by Hugh Davson and James Danielli; it was based on the "railroad track" appearance of the plasma membrane in early electron micrographs. They theorized that the structure of the plasma membrane resembles a sandwich, with protein being analogous to the bread, and lipids being analogous to the filling. In the 1950s, advances in microscopy, notably transmission electron microscopy (TEM), allowed researchers to see that the core of the plasma membrane consisted of a double, rather than a single, layer. A new model that better explains both the microscopic observations and the function of that plasma membrane was proposed by S.J. Singer and Garth L. Nicolson in 1972.

The explanation proposed by Singer and Nicolson is called the fluid mosaic model. The model has evolved somewhat over time, but it still best accounts for the structure and functions of the plasma membrane as we now understand them. The fluid mosaic model describes the structure of the plasma membrane as a mosaic of components—including phospholipids, cholesterol, proteins, and carbohydrates—that gives the membrane a fluid character. Plasma membranes range from 5 to 10 nm in thickness. For comparison, human red blood cells, visible via light microscopy, are approximately 8 µm wide, or approximately 1,000 times wider than a plasma membrane. The membrane does look a bit like a sandwich (Figure 2.2.2.1).

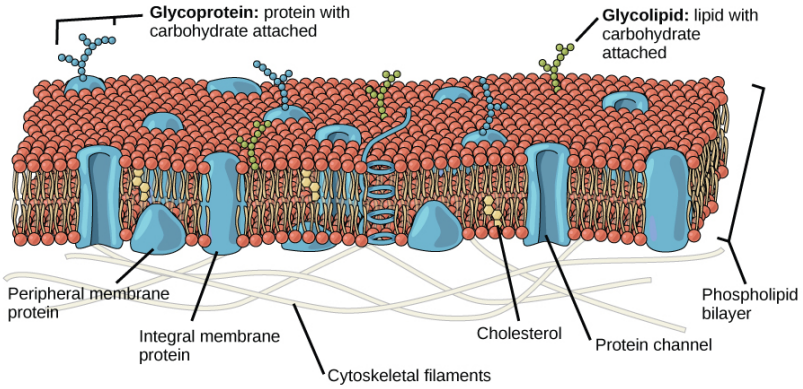


Figure 2.2.2.1: The fluid mosaic model of the plasma membrane describes the plasma membrane as a fluid combination of phospholipids, cholesterol, and proteins. Carbohydrates attached to lipids (glycolipids) and to proteins (glycoproteins) extend from the outward-facing surface of the membrane.

The principal components of a plasma membrane are lipids (phospholipids and cholesterol), proteins, and carbohydrates attached to some of the lipids and some of the proteins. A phospholipid is a molecule consisting of glycerol, two fatty acids, and a phosphate-linked head group. Cholesterol, another lipid composed of four fused carbon rings, is found alongside the phospholipids in the core of the membrane. The proportions of proteins, lipids, and carbohydrates in the plasma membrane vary with cell type, but for a typical human cell, protein accounts for about 50 percent of the composition by mass, lipids (of all types) account for about 40 percent of the composition by mass, with the remaining 10 percent of the composition by mass being carbohydrates. However, the concentration of proteins and lipids varies with different cell membranes. For example, myelin, an outgrowth of the membrane of specialized cells that insulates the axons of the peripheral nerves, contains only 18 percent protein and 76 percent lipid. The mitochondrial inner membrane contains 76 percent protein and only 24 percent lipid. The plasma membrane of human red blood cells is 30 percent lipid. Carbohydrates are present only on the exterior surface of the plasma membrane and are attached to proteins, forming glycoproteins, or attached to lipids, forming glycolipids.

Phospholipids

The main fabric of the membrane is composed of amphiphilic, phospholipid molecules. The hydrophilic or “water-loving” areas of these molecules (which look like a collection of balls in an artist’s rendition of the model) (Figure 2.2.2.1) are in contact with the aqueous fluid both inside and outside the cell. Hydrophobic, or water-hating molecules, tend to be non-polar. They interact with other non-polar molecules in chemical reactions, but generally do not interact with polar molecules. When placed in water, hydrophobic molecules tend to form a ball or cluster. The hydrophilic regions of the phospholipids tend to form hydrogen bonds with water and other polar molecules on both the exterior and interior of the cell. Thus, the membrane surfaces that face the interior and exterior of the cell are hydrophilic. In contrast, the interior of the cell membrane is hydrophobic and will not interact with water. Therefore, phospholipids form an excellent two-layer cell membrane that separates fluid within the cell from the fluid outside of the cell.

A phospholipid molecule (Figure 2.2.2.2) consists of a three-carbon glycerol backbone with two fatty acid molecules attached to carbons 1 and 2, and a phosphate-containing group attached to the third carbon. This arrangement gives the overall molecule an area described as its head (the phosphate-containing group), which has a polar character or negative charge, and an area called the tail (the fatty acids), which has no charge. The head can form hydrogen bonds, but the tail cannot. A molecule with this arrangement of a positively or negatively charged area and an uncharged, or non-polar, area is referred to as amphiphilic or “dual-loving.”

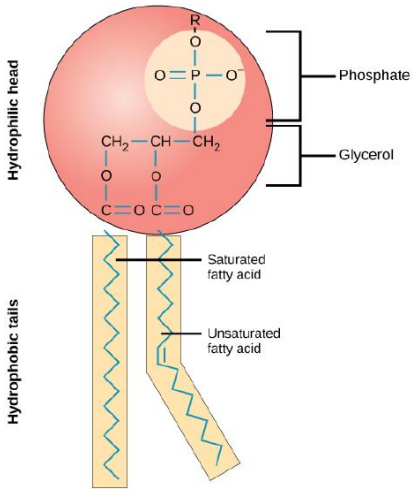


Figure 2.2.2.2: This phospholipid molecule is composed of a hydrophilic head and two hydrophobic tails. The hydrophilic head group consists of a phosphate-containing group attached to a glycerol molecule. The hydrophobic tails, each containing either a saturated or an unsaturated fatty acid, are long hydrocarbon chains.

This characteristic is vital to the structure of a plasma membrane because, in water, phospholipids tend to become arranged with their hydrophobic tails facing each other and their hydrophilic heads facing out. In this way, they form a lipid bilayer—a barrier composed of a double layer of phospholipids that separates the water and other materials on one side of the barrier from the water and other materials on the other side. In fact, phospholipids heated in an aqueous solution tend to spontaneously form small spheres or droplets (called micelles or liposomes), with their hydrophilic heads forming the exterior and their hydrophobic tails on the inside (Figure 2.2.2.3).

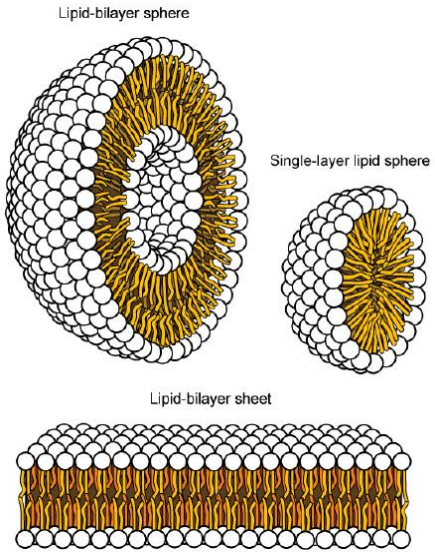


Figure 2.2.2.3: In an aqueous solution, phospholipids tend to arrange themselves with their polar heads facing outward and their hydrophobic tails facing inward. (credit: modification of work by Mariana Ruiz Villareal)

Proteins

Proteins make up the second major component of plasma membranes. Integral proteins (some specialized types are called integrins) are, as their name suggests, integrated completely into the membrane structure, and their hydrophobic membrane-spanning regions interact with the hydrophobic region of the the phospholipid bilayer (Figure 2.2.2.1). Single-pass integral membrane proteins usually have a hydrophobic transmembrane segment that consists of 20–25 amino acids. Some span only part of the membrane—associating with a single layer—while others stretch from one side of the membrane to the other, and are exposed on either side. Some complex proteins are composed of up to 12 segments of a single protein, which are extensively folded and embedded in the membrane (Figure 2.2.2.4). This type of protein has a hydrophilic region or regions, and one or several mildly hydrophobic regions. This arrangement of regions of the protein tends to orient the protein alongside the phospholipids, with the hydrophobic region of

the protein adjacent to the tails of the phospholipids and the hydrophilic region or regions of the protein protruding from the membrane and in contact with the cytosol or extracellular fluid.

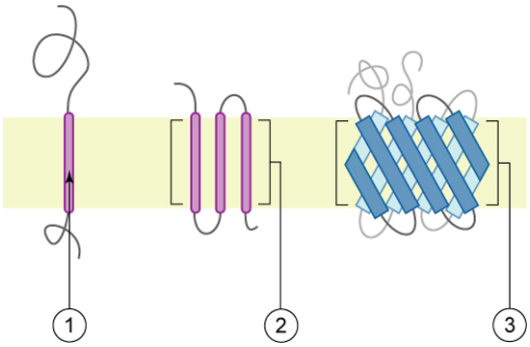


Figure 2.2.2.4: Integral membranes proteins may have one or more alpha-helices that span the membrane (examples 1 and 2), or they may have beta-sheets that span the membrane (example 3). (credit: "Foobar"/Wikimedia Commons)

Peripheral proteins are found on the exterior and interior surfaces of membranes, attached either to integral proteins or to phospholipids. Peripheral proteins, along with integral proteins, may serve as enzymes, as structural attachments for the fibers of the cytoskeleton, or as part of the cell's recognition sites. These are sometimes referred to as "cell-specific" proteins. The body recognizes its own proteins and attacks foreign proteins associated with invasive pathogens.

Carbohydrates

Carbohydrates are the third major component of plasma membranes. They are always found on the exterior surface of cells and are bound either to proteins (forming glycoproteins) or to lipids (forming glycolipids) (Figure 2.2.2.1). These carbohydrate chains may consist of 2–60 monosaccharide units and can be either straight or branched. Along with peripheral proteins, carbohydrates form specialized sites on the cell surface that allow cells to recognize each other. These sites have unique patterns that allow the cell to be recognized, much the way that the facial features unique to each person allow him or her to be recognized. This recognition function is very important to cells, as it allows the immune system to differentiate between body cells (called "self") and foreign cells or tissues (called "non-self"). Similar types of glycoproteins and glycolipids are found on the surfaces of viruses and may change frequently, preventing immune cells from recognizing and attacking them.

These carbohydrates on the exterior surface of the cell—the carbohydrate components of both glycoproteins and glycolipids—are collectively referred to as the glycocalyx (meaning "sugar coating"). The glycocalyx is highly hydrophilic and attracts large amounts of water to the surface of the cell. This aids in the interaction of the cell with its watery environment and in the cell's ability to obtain substances dissolved in the water. As discussed above, the glycocalyx is also important for cell identification, self/non-self determination, and embryonic development, and is used in cell-cell attachments to form tissues.

Evolution Connection: How Viruses Infect Specific Organs

Glycoprotein and glycolipid patterns on the surfaces of cells give many viruses an opportunity for infection. HIV and hepatitis viruses infect only specific organs or cells in the human body. HIV is able to penetrate the plasma membranes of a subtype of lymphocytes called T-helper cells, as well as some monocytes and central nervous system cells. The hepatitis virus attacks liver cells.

These viruses are able to invade these cells, because the cells have binding sites on their surfaces that are specific to and compatible with certain viruses (Figure 2.2.2.5). Other recognition sites on the virus's surface interact with the human immune system, prompting the body to produce antibodies. Antibodies are made in response to the antigens or proteins associated with invasive pathogens, or in response to foreign cells, such as might occur with an organ transplant. These same sites serve as places for antibodies to attach and either destroy or inhibit the activity of the virus. Unfortunately, these recognition sites on HIV change at a rapid rate because of mutations, making the production of an effective vaccine against the virus very difficult, as the virus evolves and adapts. A person infected with HIV will quickly develop different populations, or variants, of the virus that are distinguished by differences in these recognition sites. This rapid change of surface markers decreases the effectiveness of the person's immune system in attacking the virus, because the antibodies will not recognize the new variations of the

surface patterns. In the case of HIV, the problem is compounded by the fact that the virus specifically infects and destroys cells involved in the immune response, further incapacitating the host.

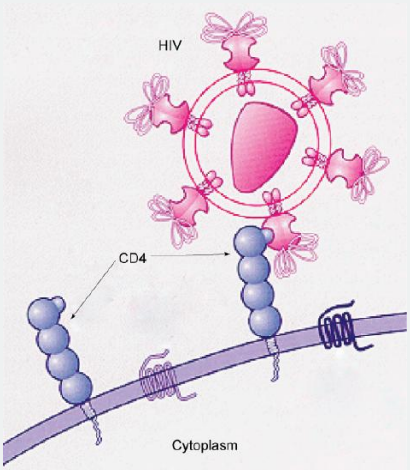


Figure 2.2.2.5: HIV binds to the CD4 receptor, a glycoprotein on the surfaces of T cells. (credit: modification of work by NIH, NIAID)

Membrane Fluidity

The mosaic characteristic of the membrane, described in the fluid mosaic model, helps to illustrate its nature. The integral proteins and lipids exist in the membrane as separate but loosely attached molecules. These resemble the separate, multicolored tiles of a mosaic picture, and they float, moving somewhat with respect to one another. The membrane is not like a balloon, however, that can expand and contract; rather, it is fairly rigid and can burst if penetrated or if a cell takes in too much water. However, because of its mosaic nature, a very fine needle can easily penetrate a plasma membrane without causing it to burst, and the membrane will flow and self-seal when the needle is extracted.

The mosaic characteristics of the membrane explain some but not all of its fluidity. There are two other factors that help maintain this fluid characteristic. One factor is the nature of the phospholipids themselves. In their saturated form, the fatty acids in phospholipid tails are saturated with bound hydrogen atoms. There are no double bonds between adjacent carbon atoms. This results in tails that are relatively straight. In contrast, unsaturated fatty acids do not contain a maximal number of hydrogen atoms, but they do contain some double bonds between adjacent carbon atoms; a double bond results in a bend in the string of carbons of approximately 30 degrees (Figure 2.2.2.2).

Thus, if saturated fatty acids, with their straight tails, are compressed by decreasing temperatures, they press in on each other, making a dense and fairly rigid membrane. If unsaturated fatty acids are compressed, the “kinks” in their tails elbow adjacent phospholipid molecules away, maintaining some space between the phospholipid molecules. This “elbow room” helps to maintain fluidity in the membrane at temperatures at which membranes with saturated fatty acid tails in their phospholipids would “freeze” or solidify. The relative fluidity of the membrane is particularly important in a cold environment. A cold environment tends to compress membranes composed largely of saturated fatty acids, making them less fluid and more susceptible to rupturing. Many organisms (fish are one example) are capable of adapting to cold environments by changing the proportion of unsaturated fatty acids in their membranes in response to the lowering of the temperature.

Link to Learning



Visit this site to see animations of the fluidity and mosaic quality of membranes.

Animals have an additional membrane constituent that assists in maintaining fluidity. Cholesterol, which lies alongside the phospholipids in the membrane, tends to dampen the effects of temperature on the membrane. Thus, this lipid functions as a buffer, preventing lower temperatures from inhibiting fluidity and preventing increased temperatures from increasing fluidity too much. Thus, cholesterol extends, in both directions, the range of temperature in which the membrane is appropriately fluid and consequently functional. Cholesterol also serves other functions, such as organizing clusters of transmembrane proteins into lipid rafts.

Table 2.2.2.1: The Components and Functions of the Plasma Membrane.

Component	Location
Phospholipid	Main fabric of the membrane
Cholesterol	Attached between phospholipids and between the two phospholipid layers
Integral proteins (for example, integrins)	Embedded within the phospholipid layer(s). May or may not penetrate through both layers
Peripheral proteins	On the inner or outer surface of the phospholipid bilayer; not embedded within the phospholipids
Carbohydrates (components of glycoproteins and glycolipids)	Generally attached to proteins on the outside membrane layer

Career Connection: Immunologist

The variations in peripheral proteins and carbohydrates that affect a cell's recognition sites are of prime interest in immunology. These changes are taken into consideration in vaccine development. Many infectious diseases, such as smallpox, polio, diphtheria, and tetanus, were conquered by the use of vaccines.

Immunologists are the physicians and scientists who research and develop vaccines, as well as treat and study allergies or other immune problems. Some immunologists study and treat autoimmune problems (diseases in which a person's immune system attacks his or her own cells or tissues, such as lupus) and immunodeficiencies, whether acquired (such as acquired immunodeficiency syndrome, or AIDS) or hereditary (such as severe combined immunodeficiency, or SCID). Immunologists are called in to help treat organ transplantation patients, who must have their immune systems suppressed so that their bodies will not reject a transplanted organ. Some immunologists work to understand natural immunity and the effects of a person's

environment on it. Others work on questions about how the immune system affects diseases such as cancer. In the past, the importance of having a healthy immune system in preventing cancer was not at all understood.

To work as an immunologist, a PhD or MD is required. In addition, immunologists undertake at least 2–3 years of training in an accredited program and must pass an examination given by the American Board of Allergy and Immunology. Immunologists must possess knowledge of the functions of the human body as they relate to issues beyond immunization, and knowledge of pharmacology and medical technology, such as medications, therapies, test materials, and surgical procedures.

Note



Summary

The modern understanding of the plasma membrane is referred to as the fluid mosaic model. The plasma membrane is composed of a bilayer of phospholipids, with their hydrophobic, fatty acid tails in contact with each other. The landscape of the membrane is studded with proteins, some of which span the membrane. Some of these proteins serve to transport materials into or out of the cell. Carbohydrates are attached to some of the proteins and lipids on the outward-facing surface of the membrane, forming complexes that function to identify the cell to other cells. The fluid nature of the membrane is due to temperature, the configuration of the fatty acid tails (some kinked by double bonds), the presence of cholesterol embedded in the membrane, and the mosaic nature of the proteins and protein-carbohydrate combinations, which are not firmly fixed in place. Plasma membranes enclose and define the borders of cells, but rather than being a static bag, they are dynamic and constantly in flux.

Glossary

amphiphilic
: molecule possessing a polar or charged area and a nonpolar or uncharged area capable of interacting with both hydrophilic and hydrophobic environments

fluid mosaic model
: describes the structure of the plasma membrane as a mosaic of components including phospholipids, cholesterol, proteins, glycoproteins, and glycolipids (sugar chains attached to proteins or lipids, respectively), resulting in a fluid character (fluidity)

glycolipid
: combination of carbohydrates and lipids

glycoprotein
: combination of carbohydrates and proteins

hydrophilic
: molecule with the ability to bond with water; “water-loving”

hydrophobic

molecule that does not have the ability to bond with water; “water-hating”

integral protein

protein integrated into the membrane structure that interacts extensively with the hydrocarbon chains of membrane lipids and often spans the membrane; these proteins can be removed only by the disruption of the membrane by detergents

peripheral protein

protein found at the surface of a plasma membrane either on its exterior or interior side; these proteins can be removed (washed off of the membrane) by a high-salt wash

---

This page titled 2.2.2: Components and Structure is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.1: Components and Structure** by OpenStax is licensed CC BY 4.0.

2.2.3: Passive Transport

Learning Objectives

- Explain why and how passive transport occurs
- Understand the processes of osmosis and diffusion
- Define tonicity and describe its relevance to passive transport

Plasma membranes must allow certain substances to enter and leave a cell, and prevent some harmful materials from entering and some essential materials from leaving. In other words, plasma membranes are selectively permeable—they allow some substances to pass through, but not others. If they were to lose this selectivity, the cell would no longer be able to sustain itself, and it would be destroyed. Some cells require larger amounts of specific substances than do other cells; they must have a way of obtaining these materials from extracellular fluids. This may happen passively, as certain materials move back and forth, or the cell may have special mechanisms that facilitate transport. Some materials are so important to a cell that it spends some of its energy, hydrolyzing adenosine triphosphate (ATP), to obtain these materials. Red blood cells use some of their energy doing just that. All cells spend the majority of their energy to maintain an imbalance of sodium and potassium ions between the interior and exterior of the cell.

The most direct forms of membrane transport are passive. Passive transport is a naturally occurring phenomenon and does not require the cell to exert any of its energy to accomplish the movement. In passive transport, substances move from an area of higher concentration to an area of lower concentration. A physical space in which there is a range of concentrations of a single substance is said to have a concentration gradient.

Selective Permeability

Plasma membranes are asymmetric: the interior of the membrane is not identical to the exterior of the membrane. In fact, there is a considerable difference between the array of phospholipids and proteins between the two leaflets that form a membrane. On the interior of the membrane, some proteins serve to anchor the membrane to fibers of the cytoskeleton. There are peripheral proteins on the exterior of the membrane that bind elements of the extracellular matrix. Carbohydrates, attached to lipids or proteins, are also found on the exterior surface of the plasma membrane. These carbohydrate complexes help the cell bind substances that the cell needs in the extracellular fluid. This adds considerably to the selective nature of plasma membranes (Figure 2.2.3.1).

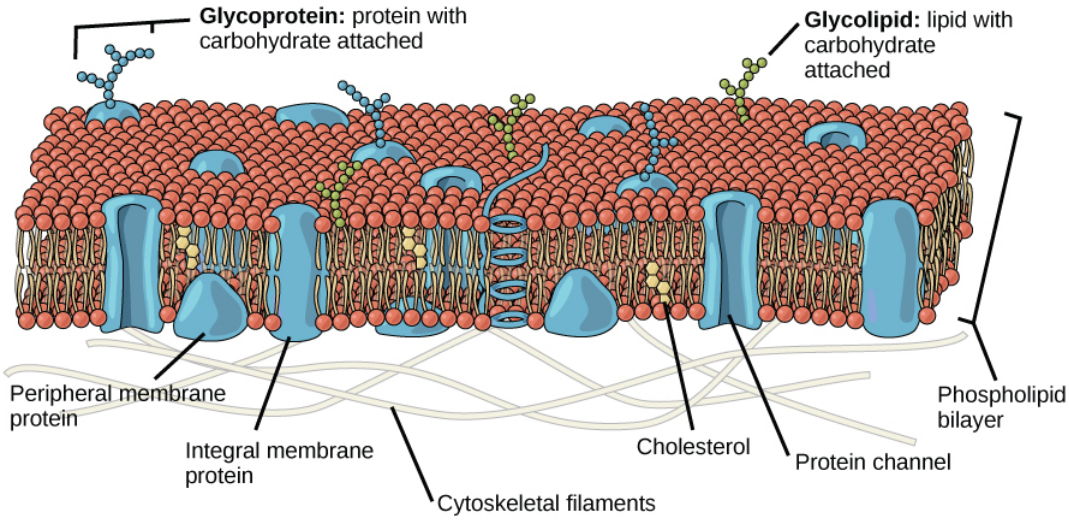


Figure 2.2.3.1: The exterior surface of the plasma membrane is not identical to the interior surface of the same membrane.

Recall that plasma membranes are amphiphilic: They have hydrophilic and hydrophobic regions. This characteristic helps the movement of some materials through the membrane and hinders the movement of others. Lipid-soluble material with a low molecular weight can easily slip through the hydrophobic lipid core of the membrane. Substances such as the fat-soluble vitamins A, D, E, and K readily pass through the plasma membranes in the digestive tract and other tissues. Fat-soluble drugs and hormones

also gain easy entry into cells and are readily transported into the body's tissues and organs. Molecules of oxygen and carbon dioxide have no charge and so pass through membranes by simple diffusion.

Polar substances present problems for the membrane. While some polar molecules connect easily with the outside of a cell, they cannot readily pass through the lipid core of the plasma membrane. Additionally, while small ions could easily slip through the spaces in the mosaic of the membrane, their charge prevents them from doing so. Ions such as sodium, potassium, calcium, and chloride must have special means of penetrating plasma membranes. Simple sugars and amino acids also need help with transport across plasma membranes, achieved by various transmembrane proteins (channels).

Diffusion

Diffusion is a passive process of transport. A single substance tends to move from an area of high concentration to an area of low concentration until the concentration is equal across a space. You are familiar with diffusion of substances through the air. For example, think about someone opening a bottle of ammonia in a room filled with people. The ammonia gas is at its highest concentration in the bottle; its lowest concentration is at the edges of the room. The ammonia vapor will diffuse, or spread away, from the bottle, and gradually, more and more people will smell the ammonia as it spreads. Materials move within the cell's cytosol by diffusion, and certain materials move through the plasma membrane by diffusion (Figure 2.2.3.2). Diffusion expends no energy. On the contrary, concentration gradients are a form of potential energy, dissipated as the gradient is eliminated.

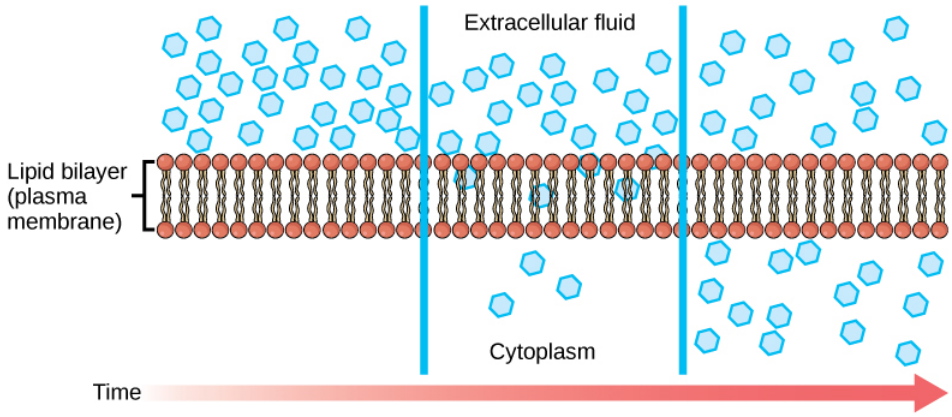


Figure 2.2.3.2: Diffusion through a permeable membrane moves a substance from an area of high concentration (extracellular fluid, in this case) down its concentration gradient (into the cytoplasm). (credit: modification of work by Mariana Ruiz Villareal)

Each separate substance in a medium, such as the extracellular fluid, has its own concentration gradient, independent of the concentration gradients of other materials. In addition, each substance will diffuse according to that gradient. Within a system, there will be different rates of diffusion of the different substances in the medium.

Video



Factors That Affect Diffusion

Molecules move constantly in a random manner, at a rate that depends on their mass, their environment, and the amount of thermal energy they possess, which in turn is a function of temperature. This movement accounts for the diffusion of molecules through whatever medium in which they are localized. A substance will tend to move into any space available to it until it is evenly distributed throughout it. After a substance has diffused completely through a space, removing its concentration gradient, molecules will still move around in the space, but there will be no *net* movement of the number of molecules from one area to another. This lack of a concentration gradient in which there is no net movement of a substance is known as dynamic equilibrium. While diffusion will go forward in the presence of a concentration gradient of a substance, several factors affect the rate of diffusion.

- Extent of the concentration gradient: The greater the difference in concentration, the more rapid the diffusion. The closer the distribution of the material gets to equilibrium, the slower the rate of diffusion becomes.
- Mass of the molecules diffusing: Heavier molecules move more slowly; therefore, they diffuse more slowly. The reverse is true for lighter molecules.
- Temperature: Higher temperatures increase the energy and therefore the movement of the molecules, increasing the rate of diffusion. Lower temperatures decrease the energy of the molecules, thus decreasing the rate of diffusion.
- Solvent density: As the density of a solvent increases, the rate of diffusion decreases. The molecules slow down because they have a more difficult time getting through the denser medium. If the medium is less dense, diffusion increases. Because cells primarily use diffusion to move materials within the cytoplasm, any increase in the cytoplasm's density will inhibit the movement of the materials. An example of this is a person experiencing dehydration. As the body's cells lose water, the rate of diffusion decreases in the cytoplasm, and the cells' functions deteriorate. Neurons tend to be very sensitive to this effect. Dehydration frequently leads to unconsciousness and possibly coma because of the decrease in diffusion rate within the cells.
- Solubility: As discussed earlier, nonpolar or lipid-soluble materials pass through plasma membranes more easily than polar materials, allowing a faster rate of diffusion.
- Surface area and thickness of the plasma membrane: Increased surface area increases the rate of diffusion, whereas a thicker membrane reduces it.
- Distance travelled: The greater the distance that a substance must travel, the slower the rate of diffusion. This places an upper limitation on cell size. A large, spherical cell will die because nutrients or waste cannot reach or leave the center of the cell, respectively. Therefore, cells must either be small in size, as in the case of many prokaryotes, or be flattened, as with many single-celled eukaryotes.

A variation of diffusion is the process of filtration. In filtration, material moves according to its concentration gradient through a membrane; sometimes the rate of diffusion is enhanced by pressure, causing the substances to filter more rapidly. This occurs in the kidney, where blood pressure forces large amounts of water and accompanying dissolved substances, or solutes, out of the blood and into the renal tubules. The rate of diffusion in this instance is almost totally dependent on pressure. One of the effects of high blood pressure is the appearance of protein in the urine, which is "squeezed through" by the abnormally high pressure.

Facilitated transport

In facilitated transport, also called facilitated diffusion, materials diffuse across the plasma membrane with the help of membrane proteins. A concentration gradient exists that would allow these materials to diffuse into the cell without expending cellular energy. However, these materials are ions are polar molecules that are repelled by the hydrophobic parts of the cell membrane. Facilitated transport proteins shield these materials from the repulsive force of the membrane, allowing them to diffuse into the cell.

The material being transported is first attached to protein or glycoprotein receptors on the exterior surface of the plasma membrane. This allows the material that is needed by the cell to be removed from the extracellular fluid. The substances are then passed to specific integral proteins that facilitate their passage. Some of these integral proteins are collections of beta pleated sheets that form a pore or channel through the phospholipid bilayer. Others are carrier proteins which bind with the substance and aid its diffusion through the membrane.

Channels

The integral proteins involved in facilitated transport are collectively referred to as transport proteins, and they function as either channels for the material or carriers. In both cases, they are transmembrane proteins. Channels are specific for the substance that is being transported. Channel proteins have hydrophilic domains exposed to the intracellular and extracellular fluids; they additionally

have a hydrophilic channel through their core that provides a hydrated opening through the membrane layers (Figure 2.2.3.3). Passage through the channel allows polar compounds to avoid the nonpolar central layer of the plasma membrane that would otherwise slow or prevent their entry into the cell. Aquaporins are channel proteins that allow water to pass through the membrane at a very high rate.

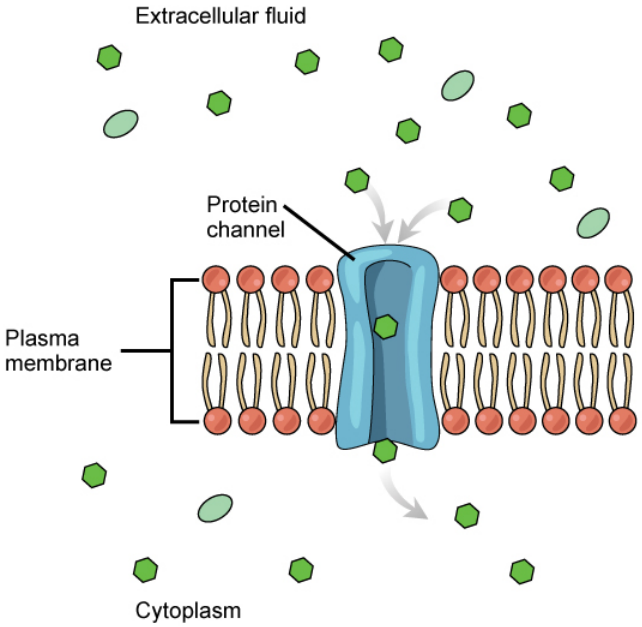
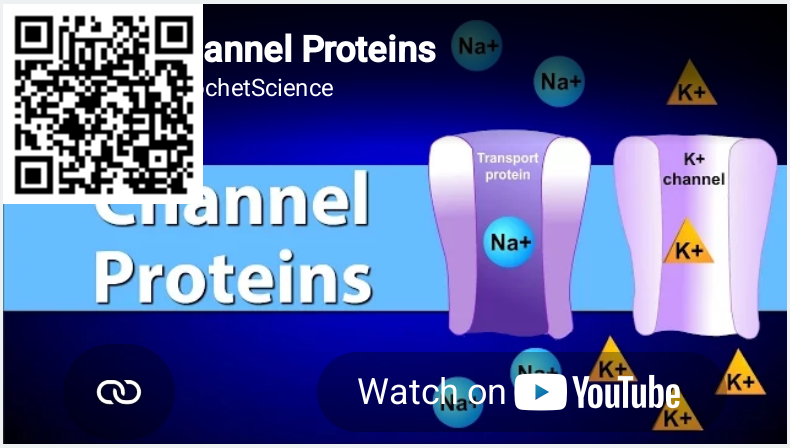


Figure 2.2.3.3: Facilitated transport moves substances down their concentration gradients. They may cross the plasma membrane with the aid of channel proteins. (credit: modification of work by Mariana Ruiz Villareal)

Channel proteins are either open at all times or they are “gated,” which controls the opening of the channel. The attachment of a particular ion to the channel protein may control the opening, or other mechanisms or substances may be involved. In some tissues, sodium and chloride ions pass freely through open channels, whereas in other tissues a gate must be opened to allow passage. An example of this occurs in the kidney, where both forms of channels are found in different parts of the renal tubules. Cells involved in the transmission of electrical impulses, such as nerve and muscle cells, have gated channels for sodium, potassium, and calcium in their membranes. Opening and closing of these channels changes the relative concentrations on opposing sides of the membrane of these ions, resulting in the facilitation of electrical transmission along membranes (in the case of nerve cells) or in muscle contraction (in the case of muscle cells).

Video



Carrier Proteins

Another type of protein embedded in the plasma membrane is a carrier protein. This aptly named protein binds a substance and, in doing so, triggers a change of its own shape, moving the bound molecule from the outside of the cell to its interior (Figure 2.2.3.4); depending on the gradient, the material may move in the opposite direction. Carrier proteins are typically specific for a single substance. This selectivity adds to the overall selectivity of the plasma membrane. The exact mechanism for the change of shape is poorly understood. Proteins can change shape when their hydrogen bonds are affected, but this may not fully explain this mechanism. Each carrier protein is specific to one substance, and there are a finite number of these proteins in any membrane. This can cause problems in transporting enough of the material for the cell to function properly. When all of the proteins are bound to their ligands, they are saturated and the rate of transport is at its maximum. Increasing the concentration gradient at this point will not result in an increased rate of transport.

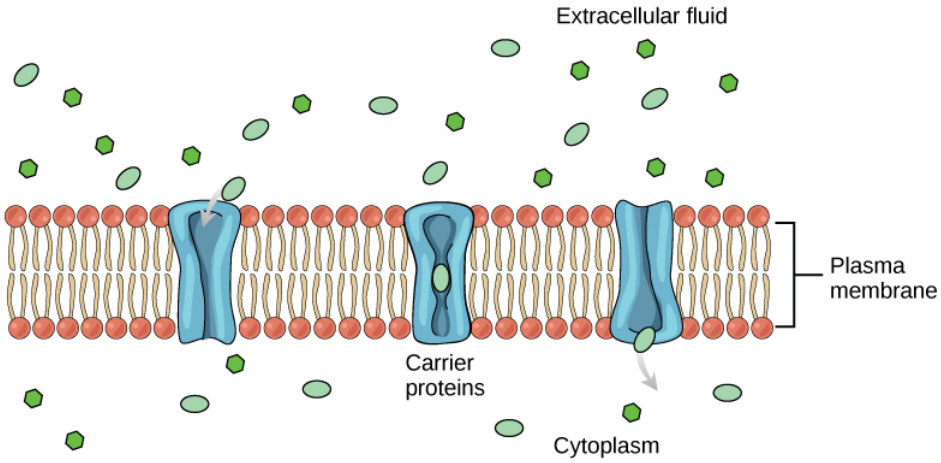


Figure 2.2.3.4: Some substances are able to move down their concentration gradient across the plasma membrane with the aid of carrier proteins. Carrier proteins change shape as they move molecules across the membrane. (credit: modification of work by Mariana Ruiz Villareal)

An example of this process occurs in the kidney. Glucose, water, salts, ions, and amino acids needed by the body are filtered in one part of the kidney. This filtrate, which includes glucose, is then reabsorbed in another part of the kidney. Because there are only a finite number of carrier proteins for glucose, if more glucose is present than the proteins can handle, the excess is not transported and it is excreted from the body in the urine. In a diabetic individual, this is described as “spilling glucose into the urine.” A different group of carrier proteins called glucose transport proteins, or GLUTs, are involved in transporting glucose and other hexose sugars through plasma membranes within the body.

Channel and carrier proteins transport material at different rates. Channel proteins transport much more quickly than do carrier proteins. Channel proteins facilitate diffusion at a rate of tens of millions of molecules per second, whereas carrier proteins work at a rate of a thousand to a million molecules per second.

Osmosis

Osmosis is the movement of water through a semipermeable membrane according to the concentration gradient of water across the membrane, which is inversely proportional to the concentration of solutes. While diffusion transports material across membranes and within cells, osmosis transports *only water* across a membrane and the membrane limits the diffusion of solutes in the water. Not surprisingly, the aquaporins that facilitate water movement play a large role in osmosis, most prominently in red blood cells and the membranes of kidney tubules.

Mechanism

Osmosis is a special case of diffusion. Water, like other substances, moves from an area of high concentration to one of low concentration. An obvious question is what makes water move at all? Imagine a beaker with a semipermeable membrane separating the two sides or halves (Figure 2.2.3.5). On both sides of the membrane the water level is the same, but there are different concentrations of a dissolved substance, or solute, that cannot cross the membrane (otherwise the concentrations on each side

would be balanced by the solute crossing the membrane). If the volume of the solution on both sides of the membrane is the same, but the concentrations of solute are different, then there are different amounts of water, the solvent, on either side of the membrane.

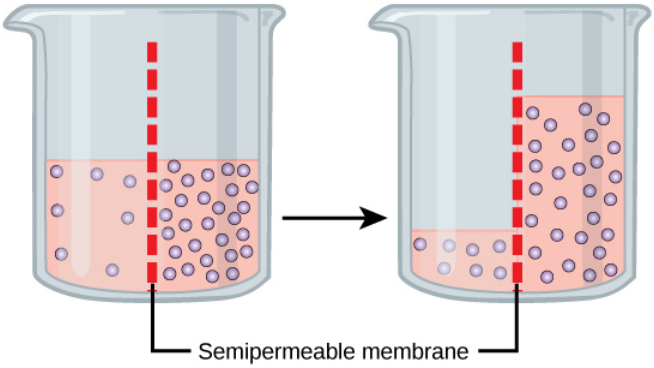


Figure 2.2.3.5: In osmosis, water always moves from an area of higher water concentration to one of lower concentration. In the diagram shown, the solute cannot pass through the selectively permeable membrane, but the water can.

To illustrate this, imagine two full glasses of water. One has a single teaspoon of sugar in it, whereas the second one contains one-quarter cup of sugar. If the total volume of the solutions in both cups is the same, which cup contains more water? Because the large amount of sugar in the second cup takes up much more space than the teaspoon of sugar in the first cup, the first cup has more water in it.

Returning to the beaker example, recall that it has a mixture of solutes on either side of the membrane. A principle of diffusion is that the molecules move around and will spread evenly throughout the medium if they can. However, only the material capable of getting through the membrane will diffuse through it. In this example, the solute cannot diffuse through the membrane, but the water can. Water has a concentration gradient in this system. Thus, water will diffuse down its concentration gradient, crossing the membrane to the side where it is less concentrated. This diffusion of water through the membrane—osmosis—will continue until the concentration gradient of water goes to zero or until the hydrostatic pressure of the water balances the osmotic pressure. Osmosis proceeds constantly in living systems.

Tonicity

Tonicity describes how an extracellular solution can change the volume of a cell by affecting osmosis. A solution's tonicity often directly correlates with the osmolarity of the solution. Osmolarity describes the total solute concentration of the solution. A solution with low osmolarity has a greater number of water molecules relative to the number of solute particles; a solution with high osmolarity has fewer water molecules with respect to solute particles. In a situation in which solutions of two different osmolarities are separated by a membrane permeable to water, though not to the solute, water will move from the side of the membrane with lower osmolarity (and more water) to the side with higher osmolarity (and less water). This effect makes sense if you remember that the solute cannot move across the membrane, and thus the only component in the system that can move—the water—moves along its own concentration gradient. An important distinction that concerns living systems is that osmolarity measures the number of particles (which may be molecules) in a solution. Therefore, a solution that is cloudy with cells may have a lower osmolarity than a solution that is clear, if the second solution contains more dissolved molecules than there are cells.

Hypotonic Solutions

Three terms—hypotonic, isotonic, and hypertonic—are used to relate the osmolarity of a cell to the osmolarity of the extracellular fluid that contains the cells. In a hypotonic situation, the extracellular fluid has lower osmolarity than the fluid inside the cell, and water enters the cell. (In living systems, the point of reference is always the cytoplasm, so the prefix *hypo-* means that the extracellular fluid has a lower concentration of solutes, or a lower osmolarity, than the cell cytoplasm.) It also means that the extracellular fluid has a higher concentration of water in the solution than does the cell. In this situation, water will follow its concentration gradient and enter the cell.

Hypertonic Solutions

As for a hypertonic solution, the prefix *hyper-* refers to the extracellular fluid having a higher osmolarity than the cell's cytoplasm; therefore, the fluid contains less water than the cell does. Because the cell has a relatively higher concentration of water, water will

leave the cell.

Isotonic Solutions

In an isotonic solution, the extracellular fluid has the same osmolarity as the cell. If the osmolarity of the cell matches that of the extracellular fluid, there will be no net movement of water into or out of the cell, although water will still move in and out. Blood cells and plant cells in hypertonic, isotonic, and hypotonic solutions take on characteristic appearances (Figure 2.2.3.6).

Art Connection

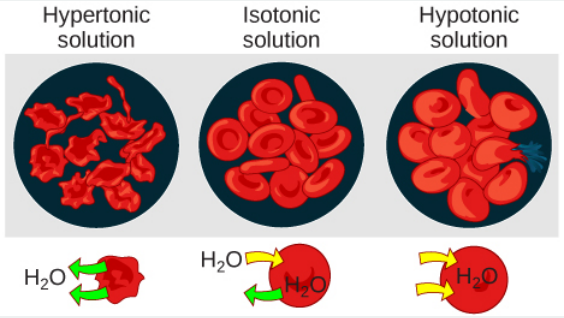


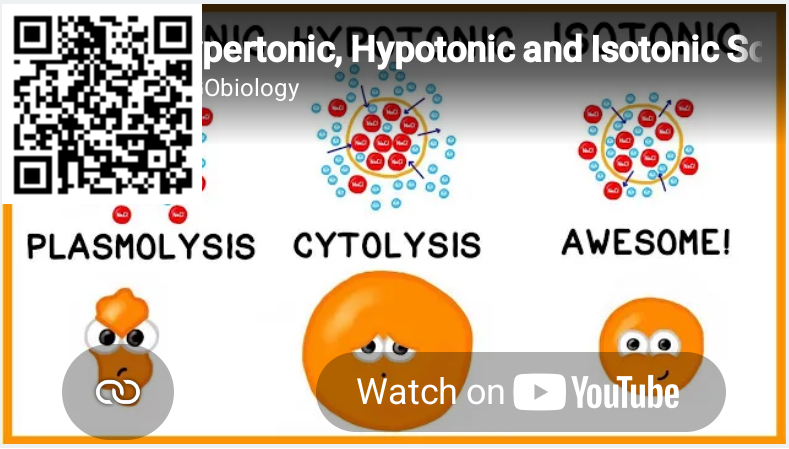
Figure 2.2.3.6: Osmotic pressure changes the shape of red blood cells in hypertonic, isotonic, and hypotonic solutions. (credit: Mariana Ruiz Villareal)

Figure 2.2.3.6: A doctor injects a patient with what the doctor thinks is an isotonic saline solution. The patient dies, and an autopsy reveals that many red blood cells have been destroyed. Do you think the solution the doctor injected was really isotonic?

Answer

No, it must have been hypotonic as a hypotonic solution would cause water to enter the cells, thereby making them burst.

Video



Tonicity in Living Systems

In a hypotonic environment, water enters a cell, and the cell swells. In an isotonic condition, the relative concentrations of solute and solvent are equal on both sides of the membrane. There is no net water movement; therefore, there is no change in the size of the cell. In a hypertonic solution, water leaves a cell and the cell shrinks. If either the hypo- or hyper- condition goes to excess, the cell's functions become compromised, and the cell may be destroyed.

A red blood cell will burst, or lyse, when it swells beyond the plasma membrane's capability to expand. Remember, the membrane resembles a mosaic, with discrete spaces between the molecules composing it. If the cell swells, and the spaces between the lipids and proteins become too large, the cell will break apart.

In contrast, when excessive amounts of water leave a red blood cell, the cell shrinks, or crenates. This has the effect of concentrating the solutes left in the cell, making the cytosol denser and interfering with diffusion within the cell. The cell's ability to function will be compromised and may also result in the death of the cell.

Various living things have ways of controlling the effects of osmosis—a mechanism called osmoregulation. Some organisms, such as plants, fungi, bacteria, and some protists, have cell walls that surround the plasma membrane and prevent cell lysis in a hypotonic solution. The plasma membrane can only expand to the limit of the cell wall, so the cell will not lyse. In fact, the cytoplasm in plants is always slightly hypertonic to the cellular environment, and water will always enter a cell if water is available. This inflow of water produces turgor pressure, which stiffens the cell walls of the plant (Figure 2.2.3.8). In nonwoody plants, turgor pressure supports the plant. Conversly, if the plant is not watered, the extracellular fluid will become hypertonic, causing water to leave the cell. In this condition, the cell does not shrink because the cell wall is not flexible. However, the cell membrane detaches from the wall and constricts the cytoplasm. This is called plasmolysis. Plants lose turgor pressure in this condition and wilt (Figure 2.2.3.9).

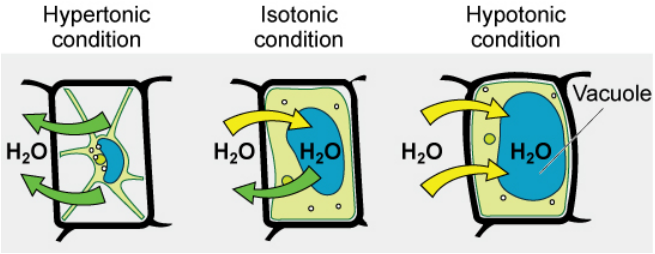


Figure 2.2.3.7: The turgor pressure within a plant cell depends on the tonicity of the solution that it is bathed in. (credit: modification of work by Mariana Ruiz Villareal)



Figure 2.2.3.8: Without adequate water, the plant on the left has lost turgor pressure, visible in its wilting; the turgor pressure is restored by watering it (right). (credit: Victor M. Vicente Selvas)

Tonicity is a concern for all living things. For example, paramecia and amoebas, which are protists that lack cell walls, have contractile vacuoles. This vesicle collects excess water from the cell and pumps it out, keeping the cell from lysing as it takes on water from its environment.

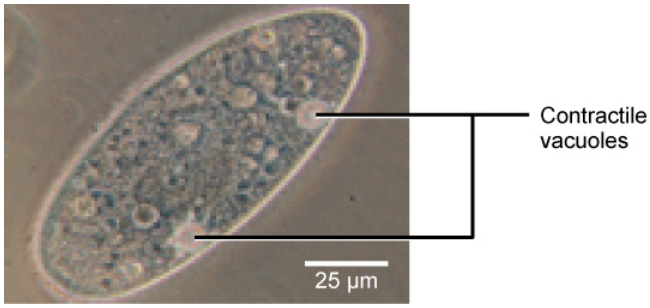
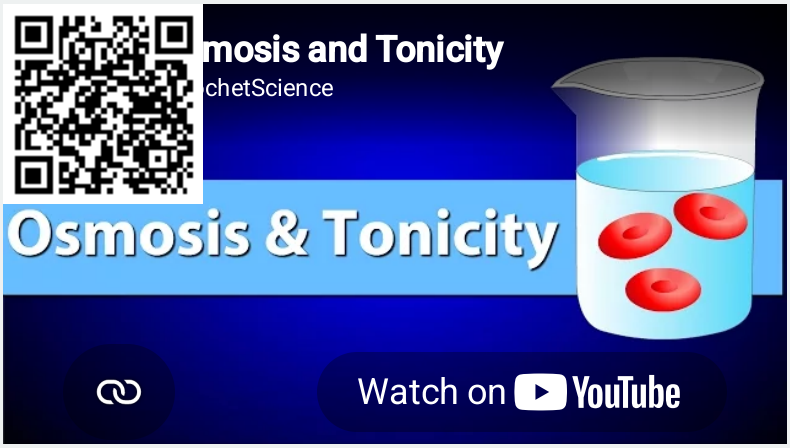


Figure 2.2.3.9: A paramecium's contractile vacuole, here visualized using bright field light microscopy at 480x magnification, continuously pumps water out of the organism's body to keep it from bursting in a hypotonic medium. (credit: modification of work by NIH; scale-bar data from Matt Russell)

Many marine invertebrates have internal salt levels matched to their environments, making them isotonic with the water in which they live. Fish, however, must spend approximately five percent of their metabolic energy maintaining osmotic homeostasis. Freshwater fish live in an environment that is hypotonic to their cells. These fish actively take in salt through their gills and excrete diluted urine to rid themselves of excess water. Saltwater fish live in the reverse environment, which is hypertonic to their cells, and they secrete salt through their gills and excrete highly concentrated urine.

In vertebrates, the kidneys regulate the amount of water in the body. Osmoreceptors are specialized cells in the brain that monitor the concentration of solutes in the blood. If the levels of solutes increase beyond a certain range, a hormone is released that retards water loss through the kidney and dilutes the blood to safer levels. Animals also have high concentrations of albumin, which is produced by the liver, in their blood. This protein is too large to pass easily through plasma membranes and is a major factor in controlling the osmotic pressures applied to tissues.

Video



Summary

The passive forms of transport, diffusion and osmosis, move materials of small molecular weight across membranes. Substances diffuse from areas of high concentration to areas of lower concentration, and this process continues until the substance is evenly distributed in a system. In solutions containing more than one substance, each type of molecule diffuses according to its own concentration gradient, independent of the diffusion of other substances. Many factors can affect the rate of diffusion, including concentration gradient, size of the particles that are diffusing, temperature of the system, and so on.

In living systems, diffusion of substances into and out of cells is mediated by the plasma membrane. Some materials diffuse readily through the membrane, but others are hindered, and their passage is made possible by specialized proteins, such as channels and transporters. The chemistry of living things occurs in aqueous solutions, and balancing the concentrations of those solutions is an ongoing problem. In living systems, diffusion of some substances would be slow or difficult without membrane proteins that facilitate transport.

Glossary

aquaporin
channel protein that allows water through the membrane at a very high rate

carrier protein
membrane protein that moves a substance across the plasma membrane by changing its own shape

channel protein
membrane protein that allows a substance to pass through its hollow core across the plasma membrane

concentration gradient
area of high concentration adjacent to an area of low concentration

diffusion
passive process of transport of low-molecular weight material according to its concentration gradient

facilitated transport

process by which material moves down a concentration gradient (from high to low concentration) using integral membrane proteins

hypertonic
situation in which extracellular fluid has a higher osmolarity than the fluid inside the cell, resulting in water moving out of the cell

hypotonic
situation in which extracellular fluid has a lower osmolarity than the fluid inside the cell, resulting in water moving into the cell

isotonic
situation in which the extracellular fluid has the same osmolarity as the fluid inside the cell, resulting in no net movement of water into or out of the cell

osmolarity
total amount of substances dissolved in a specific amount of solution

osmosis
transport of water through a semipermeable membrane according to the concentration gradient of water across the membrane that results from the presence of solute that cannot pass through the membrane

passive transport
method of transporting material through a membrane that does not require energy

plasmolysis
detaching of the cell membrane from the cell wall and constriction of the cell membrane when a plant cell is in a hypertonic solution

selectively permeable
characteristic of a membrane that allows some substances through but not others

solute
substance dissolved in a liquid to form a solution

tonicity
amount of solute in a solution

transport protein
membrane protein that facilitates passage of a substance across a membrane by binding it

---

This page titled 2.2.3: Passive Transport is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.2: Passive Transport** by OpenStax is licensed CC BY 4.0.

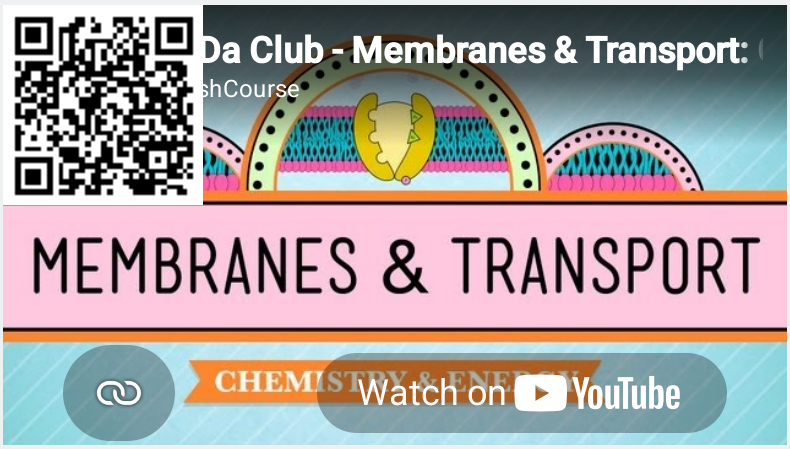
2.2.4: Active Transport

Learning Objectives

- Understand how electrochemical gradients affect ions
- Distinguish between primary active transport and secondary active transport

Active transport mechanisms require the use of the cell's energy, usually in the form of adenosine triphosphate (ATP). If a substance must move into the cell against its concentration gradient—that is, if the concentration of the substance inside the cell is greater than its concentration in the extracellular fluid (and vice versa)—the cell must use energy to move the substance. Some active transport mechanisms move small-molecular weight materials, such as ions, through the membrane. Other mechanisms transport much larger molecules.

Video



Electrochemical Gradient

We have discussed simple concentration gradients—differential concentrations of a substance across a space or a membrane—but in living systems, gradients are more complex. Because ions move into and out of cells and because cells contain proteins that do not move across the membrane and are mostly negatively charged, there is also an electrical gradient, a difference of charge, across the plasma membrane. The interior of living cells is electrically negative with respect to the extracellular fluid in which they are bathed, and at the same time, cells have higher concentrations of potassium (K^+) and lower concentrations of sodium (Na^+) than does the extracellular fluid. So in a living cell, the concentration gradient of Na^+ tends to drive it into the cell, and the electrical gradient of Na^+ (a positive ion) also tends to drive it inward to the negatively charged interior. The situation is more complex, however, for other elements such as potassium. The electrical gradient of K^+, a positive ion, also tends to drive it into the cell, but the concentration gradient of K^+ tends to drive K^+ *out* of the cell (Figure 2.2.4.1). The combined gradient of concentration and electrical charge that affects an ion is called its electrochemical gradient.

Art Connection

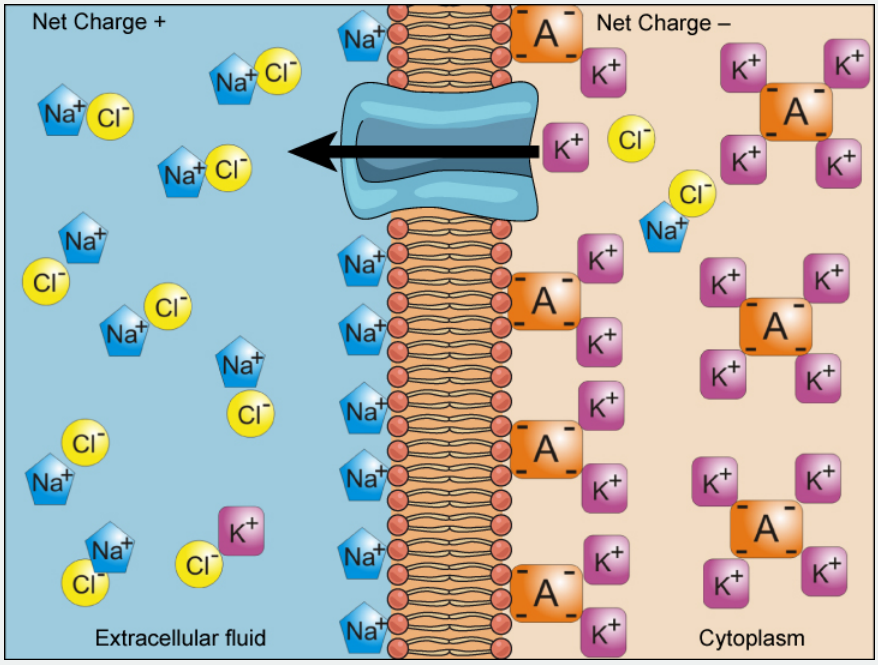


Figure 2.2.4.1: Electrochemical gradients arise from the combined effects of concentration gradients and electrical gradients. (credit: “Synaptitude”/Wikimedia Commons)

Figure 2.2.4.1: Injection of a potassium solution into a person’s blood is lethal; this is used in capital punishment and euthanasia. Why do you think a potassium solution injection is lethal?

Answer

Cells typically have a high concentration of potassium in the cytoplasm and are bathed in a high concentration of sodium. Injection of potassium dissipates this electrochemical gradient. In heart muscle, the sodium/potassium potential is responsible for transmitting the signal that causes the muscle to contract. When this potential is dissipated, the signal can’t be transmitted, and the heart stops beating. Potassium injections are also used to stop the heart from beating during surgery.

Moving Against a Gradient

To move substances against a concentration or electrochemical gradient, the cell must use energy. This energy is harvested from ATP generated through the cell’s metabolism. Active transport mechanisms, collectively called pumps, work against electrochemical gradients. Small substances constantly pass through plasma membranes. Active transport maintains concentrations of ions and other substances needed by living cells in the face of these passive movements. Much of a cell’s supply of metabolic energy may be spent maintaining these processes. (Most of a red blood cell’s metabolic energy is used to maintain the imbalance between exterior and interior sodium and potassium levels required by the cell.) Because active transport mechanisms depend on a cell’s metabolism for energy, they are sensitive to many metabolic poisons that interfere with the supply of ATP.

Two mechanisms exist for the transport of small-molecular weight material and small molecules. Primary active transport moves ions across a membrane and creates a difference in charge across that membrane, which is directly dependent on ATP. Secondary active transport describes the movement of material that is due to the electrochemical gradient established by primary active transport that does not directly require ATP.

Carrier Proteins for Active Transport

An important membrane adaption for active transport is the presence of specific carrier proteins or pumps to facilitate movement: there are three types of these proteins or transporters (Figure 2.2.4.2). A uniporter carries one specific ion or molecule. A symporter carries two different ions or molecules, both in the same direction. An antiporter also carries two different ions or molecules, but in different directions. All of these transporters can also transport small, uncharged organic molecules like glucose. These three types of carrier proteins are also found in facilitated diffusion, but they do not require ATP to work in that process. Some examples of

pumps for active transport are Na^+-K^+ ATPase, which carries sodium and potassium ions, and H^+-K^+ ATPase, which carries hydrogen and potassium ions. Both of these are antiporter carrier proteins. Two other carrier proteins are Ca^{2+} ATPase and H^+ ATPase, which carry only calcium and only hydrogen ions, respectively. Both are pumps.

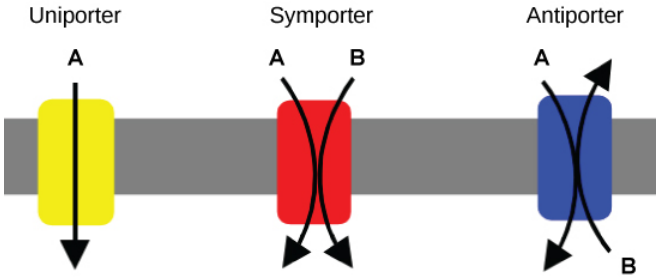


Figure 2.2.4.2: A uniporter carries one molecule or ion. A symporter carries two different molecules or ions, both in the same direction. An antiporter also carries two different molecules or ions, but in different directions. (credit: modification of work by "Lupask"/Wikimedia Commons)

Primary Active Transport

The primary active transport that functions with the active transport of sodium and potassium allows secondary active transport to occur. The second transport method is still considered active because it depends on the use of energy as does primary transport (Figure 2.2.4.3).

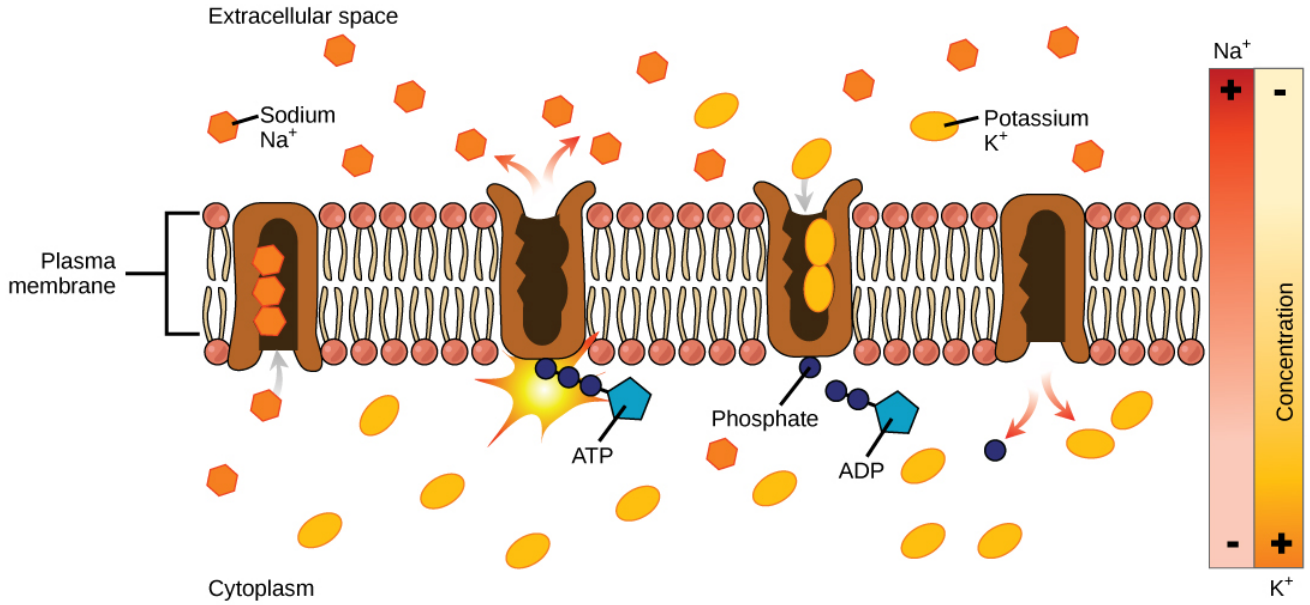


Figure 2.2.4.3: Primary active transport moves ions across a membrane, creating an electrochemical gradient (electrogenic transport). (credit: modification of work by Mariana Ruiz Villareal)

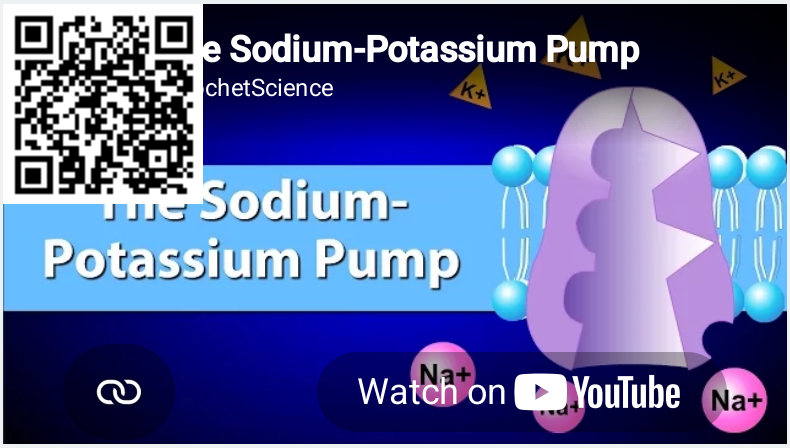
One of the most important pumps in animals cells is the sodium-potassium pump (Na^+-K^+ ATPase), which maintains the electrochemical gradient (and the correct concentrations of Na^+ and K^+) in living cells. The sodium-potassium pump moves K^+ into the cell while moving Na^+ out at the same time, at a ratio of three Na^+ for every two K^+ ions moved in. The Na^+-K^+ ATPase exists in two forms, depending on its orientation to the interior or exterior of the cell and its affinity for either sodium or potassium ions. The process consists of the following six steps.

1. With the enzyme oriented towards the interior of the cell, the carrier has a high affinity for sodium ions. Three ions bind to the protein.
2. ATP is hydrolyzed by the protein carrier and a low-energy phosphate group attaches to it.
3. As a result, the carrier changes shape and re-orients itself towards the exterior of the membrane. The protein's affinity for sodium decreases and the three sodium ions leave the carrier.

4. The shape change increases the carrier's affinity for potassium ions, and two such ions attach to the protein. Subsequently, the low-energy phosphate group detaches from the carrier.
5. With the phosphate group removed and potassium ions attached, the carrier protein repositions itself towards the interior of the cell.
6. The carrier protein, in its new configuration, has a decreased affinity for potassium, and the two ions are released into the cytoplasm. The protein now has a higher affinity for sodium ions, and the process starts again.

Several things have happened as a result of this process. At this point, there are more sodium ions outside of the cell than inside and more potassium ions inside than out. For every three ions of sodium that move out, two ions of potassium move in. This results in the interior being slightly more negative relative to the exterior. This difference in charge is important in creating the conditions necessary for the secondary process. The sodium-potassium pump is, therefore, an electrogenic pump (a pump that creates a charge imbalance), creating an electrical imbalance across the membrane and contributing to the membrane potential.

Link to Learning



Visit the site to see a simulation of active transport in a sodium-potassium ATPase.

Secondary Active Transport (Co-transport)

Secondary active transport brings sodium ions, and possibly other compounds, into the cell. As sodium ion concentrations build outside of the plasma membrane because of the action of the primary active transport process, an electrochemical gradient is created. If a channel protein exists and is open, the sodium ions will be pulled through the membrane. This movement is used to transport other substances that can attach themselves to the transport protein through the membrane (Figure 2.2.4.4). Many amino acids, as well as glucose, enter a cell this way. This secondary process is also used to store high-energy hydrogen ions in the mitochondria of plant and animal cells for the production of ATP. The potential energy that accumulates in the stored hydrogen ions is translated into kinetic energy as the ions surge through the channel protein ATP synthase, and that energy is used to convert ADP into ATP.

Art Connection

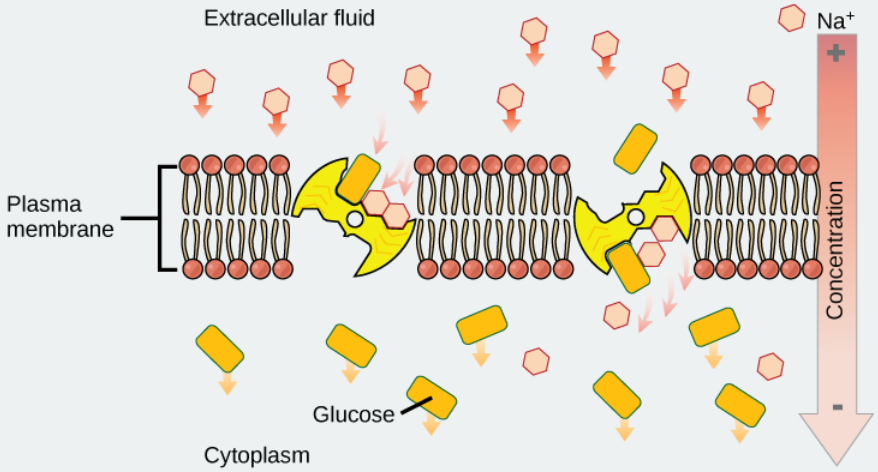


Figure 2.2.4.4: An electrochemical gradient, created by primary active transport, can move other substances against their concentration gradients, a process called co-transport or secondary active transport. (credit: modification of work by Mariana Ruiz Villareal)

Figure 2.2.4.4: If the pH outside the cell decreases, would you expect the amount of amino acids transported into the cell to increase or decrease?

Answer

A decrease in pH means an increase in positively charged H^+ ions, and an increase in the electrical gradient across the membrane. The transport of amino acids into the cell will increase.

Summary

The combined gradient that affects an ion includes its concentration gradient and its electrical gradient. A positive ion, for example, might tend to diffuse into a new area, down its concentration gradient, but if it is diffusing into an area of net positive charge, its diffusion will be hampered by its electrical gradient. When dealing with ions in aqueous solutions, a combination of the electrochemical and concentration gradients, rather than just the concentration gradient alone, must be considered. Living cells need certain substances that exist inside the cell in concentrations greater than they exist in the extracellular space. Moving substances up their electrochemical gradients requires energy from the cell. Active transport uses energy stored in ATP to fuel this transport. Active transport of small molecular-sized materials uses integral proteins in the cell membrane to move the materials: These proteins are analogous to pumps. Some pumps, which carry out primary active transport, couple directly with ATP to drive their action. In co-transport (or secondary active transport), energy from primary transport can be used to move another substance into the cell and up its concentration gradient.

Glossary

active transport
method of transporting material that requires energy

antiporter
transporter that carries two ions or small molecules in different directions

electrochemical gradient
gradient produced by the combined forces of an electrical gradient and a chemical gradient

electrogenic pump
pump that creates a charge imbalance

primary active transport

active transport that moves ions or small molecules across a membrane and may create a difference in charge across that membrane

pump
active transport mechanism that works against electrochemical gradients

secondary active transport
movement of material that is due to the electrochemical gradient established by primary active transport

symporter
transporter that carries two different ions or small molecules, both in the same direction

transporter
specific carrier proteins or pumps that facilitate movement

uniporter
transporter that carries one specific ion or molecule

This page titled 2.2.4: Active Transport is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.3: Active Transport** by OpenStax is licensed CC BY 4.0.

2.2.5: Bulk Transport

Learning Objectives

- Describe endocytosis, including phagocytosis, pinocytosis, and receptor-mediated endocytosis
- Understand the process of exocytosis

In addition to moving small ions and molecules through the membrane, cells also need to remove and take in larger molecules and particles (see Table 2.2.5.1 for examples). Some cells are even capable of engulfing entire unicellular microorganisms. You might have correctly hypothesized that the uptake and release of large particles by the cell requires energy. A large particle, however, cannot pass through the membrane, even with energy supplied by the cell.

Endocytosis

Endocytosis is a type of active transport that moves particles, such as large molecules, parts of cells, and even whole cells, into a cell. There are different variations of endocytosis, but all share a common characteristic: The plasma membrane of the cell invaginates, forming a pocket around the target particle. The pocket pinches off, resulting in the particle being contained in a newly created intracellular vesicle formed from the plasma membrane.

Phagocytosis

Phagocytosis (the condition of "cell eating") is the process by which large particles, such as cells or relatively large particles, are taken in by a cell. For example, when microorganisms invade the human body, a type of white blood cell called a neutrophil will remove the invaders through this process, surrounding and engulfing the microorganism, which is then destroyed by the neutrophil (Figure 2.2.5.1).

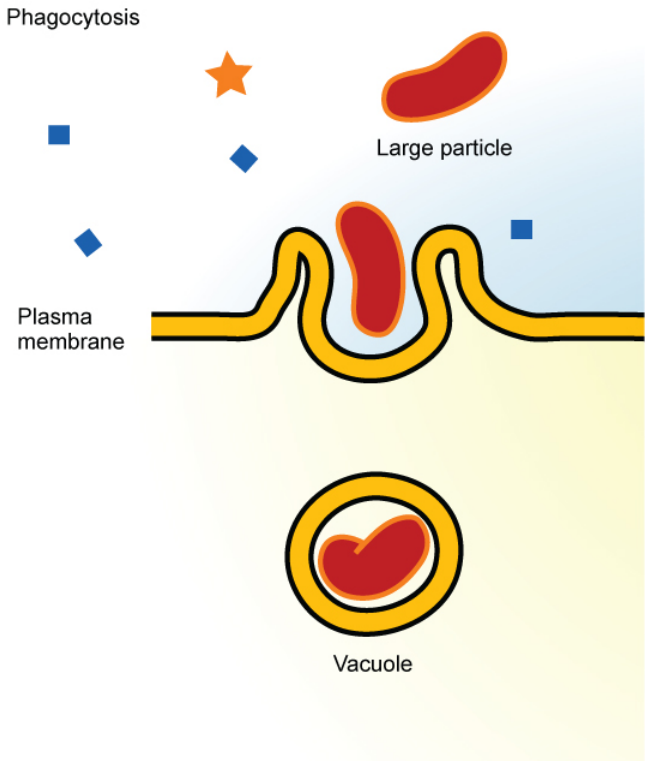


Figure 2.2.5.1: In phagocytosis, the cell membrane surrounds the particle and engulfs it. (credit: Mariana Ruiz Villareal)

In preparation for phagocytosis, a portion of the inward-facing surface of the plasma membrane becomes coated with a protein called clathrin, which stabilizes this section of the membrane. The coated portion of the membrane then extends from the body of the cell and surrounds the particle, eventually enclosing it. Once the vesicle containing the particle is enclosed within the cell, the clathrin disengages from the membrane and the vesicle merges with a lysosome for the breakdown of the material in the newly

formed compartment (endosome). When accessible nutrients from the degradation of the vesicular contents have been extracted, the newly formed endosome merges with the plasma membrane and releases its contents into the extracellular fluid. The endosomal membrane again becomes part of the plasma membrane.

Pinocytosis

A variation of endocytosis is called pinocytosis. This literally means “cell drinking” and was named at a time when the assumption was that the cell was purposefully taking in extracellular fluid. In reality, this is a process that takes in molecules, including water, which the cell needs from the extracellular fluid. Pinocytosis results in a much smaller vesicle than does phagocytosis, and the vesicle does not need to merge with a lysosome (Figure 2.2.5.2).

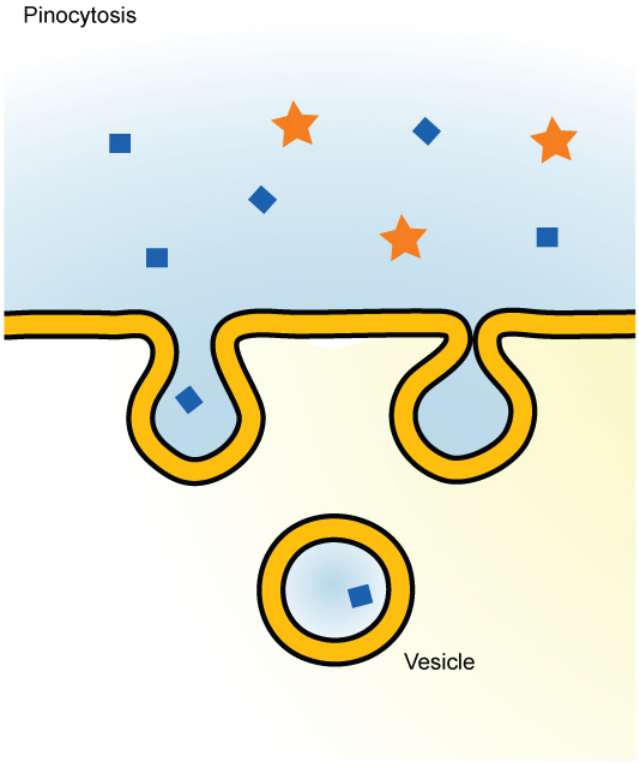


Figure 2.2.5.2: In pinocytosis, the cell membrane invaginates, surrounds a small volume of fluid, and pinches off. (credit: Mariana Ruiz Villareal)

A variation of pinocytosis is called potocytosis. This process uses a coating protein, called caveolin, on the cytoplasmic side of the plasma membrane, which performs a similar function to clathrin. The cavities in the plasma membrane that form the vacuoles have membrane receptors and lipid rafts in addition to caveolin. The vacuoles or vesicles formed in caveolae (singular caveola) are smaller than those in pinocytosis. Potocytosis is used to bring small molecules into the cell and to transport these molecules through the cell for their release on the other side of the cell, a process called transcytosis.

Receptor-mediated Endocytosis

A targeted variation of endocytosis employs receptor proteins in the plasma membrane that have a specific binding affinity for certain substances (Figure 2.2.5.3).

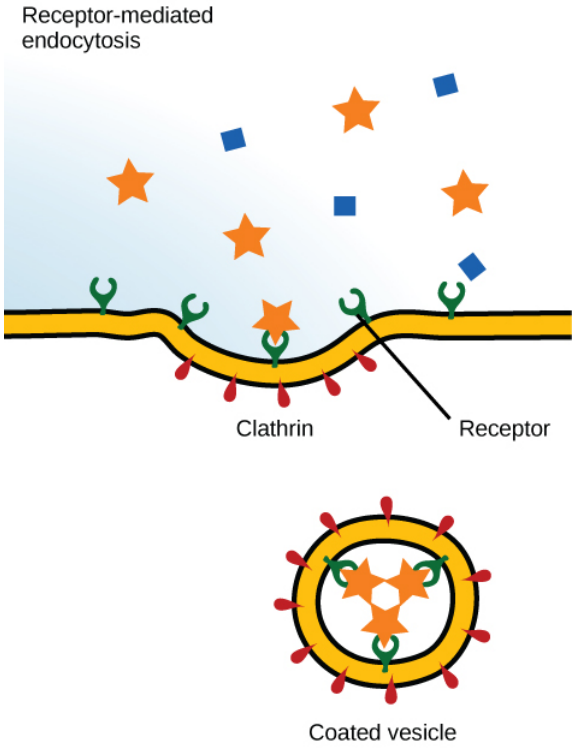
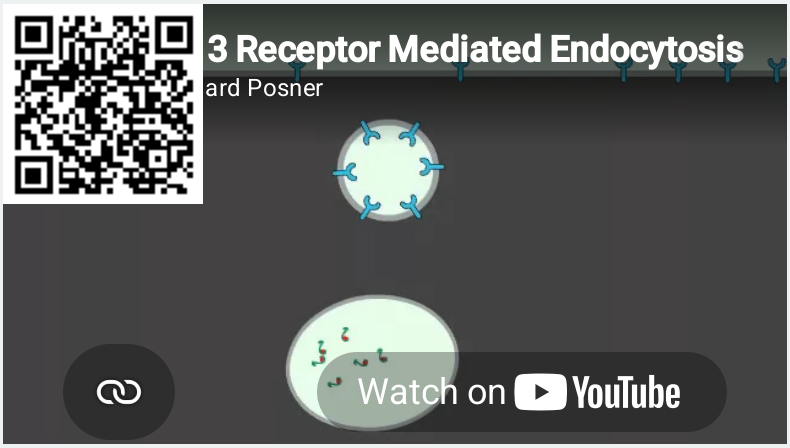


Figure 2.2.5.3: In receptor-mediated endocytosis, uptake of substances by the cell is targeted to a single type of substance that binds to the receptor on the external surface of the cell membrane. (credit: modification of work by Mariana Ruiz Villareal)

In receptor-mediated endocytosis, as in phagocytosis, clathrin is attached to the cytoplasmic side of the plasma membrane. If uptake of a compound is dependent on receptor-mediated endocytosis and the process is ineffective, the material will not be removed from the tissue fluids or blood. Instead, it will stay in those fluids and increase in concentration. Some human diseases are caused by the failure of receptor-mediated endocytosis. For example, the form of cholesterol termed low-density lipoprotein or LDL (also referred to as “bad” cholesterol) is removed from the blood by receptor-mediated endocytosis. In the human genetic disease familial hypercholesterolemia, the LDL receptors are defective or missing entirely. People with this condition have life-threatening levels of cholesterol in their blood, because their cells cannot clear LDL particles from their blood.

Although receptor-mediated endocytosis is designed to bring specific substances that are normally found in the extracellular fluid into the cell, other substances may gain entry into the cell at the same site. Flu viruses, diphtheria, and cholera toxin all have sites that cross-react with normal receptor-binding sites and gain entry into cells.

Link to Learning



Video 2.2.5.1: See receptor-mediated endocytosis in action, and click on different parts for a focused animation.

Exocytosis

The reverse process of moving material into a cell is the process of exocytosis. Exocytosis is the opposite of the processes discussed above in that its purpose is to expel material from the cell into the extracellular fluid. Waste material is enveloped in a membrane and fuses with the interior of the plasma membrane. This fusion opens the membranous envelope on the exterior of the cell, and the waste material is expelled into the extracellular space (Figure 2.2.5.4). Other examples of cells releasing molecules via exocytosis include the secretion of proteins of the extracellular matrix and secretion of neurotransmitters into the synaptic cleft by synaptic vesicles.

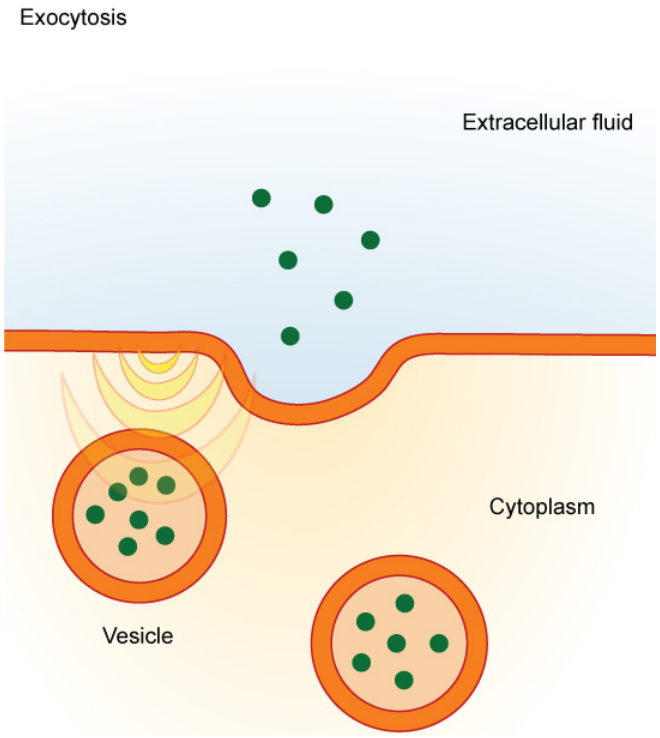


Figure 2.2.5.4: In exocytosis, vesicles containing substances fuse with the plasma membrane. The contents are then released to the exterior of the cell. (credit: modification of work by Mariana Ruiz Villareal)

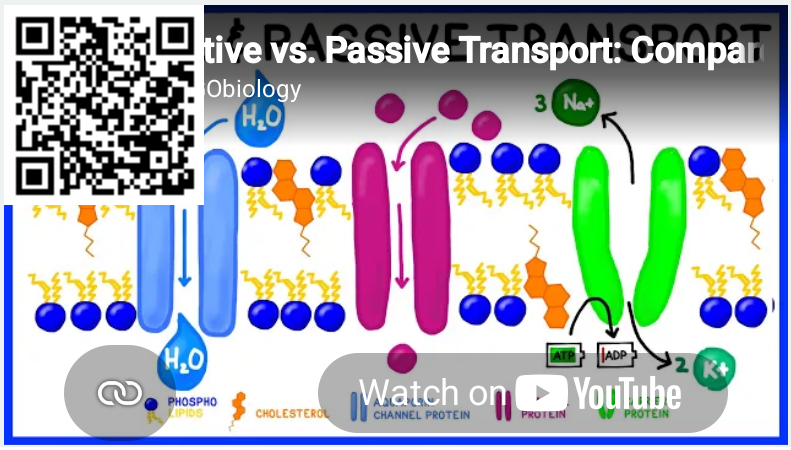
Table 2.2.5.1: Methods of transport, Energy requirements and types of Material transported.

Transport Method	Active/Passive	Material Transported
Diffusion	Passive	Small-molecular weight material
Osmosis	Passive	Water
Facilitated transport/diffusion	Passive	Sodium, potassium, calcium, glucose
Primary active transport	Active	Sodium, potassium, calcium
Secondary active transport	Active	Amino acids, lactose
Phagocytosis	Active	Large macromolecules, whole cells, or cellular structures
Pinocytosis and potocytosis	Active	Small molecules (liquids/water)
Receptor-mediated endocytosis	Active	Large quantities of macromolecules

Video



Video



Summary

Active transport methods require the direct use of ATP to fuel the transport. Large particles, such as macromolecules, parts of cells, or whole cells, can be engulfed by other cells in a process called phagocytosis. In phagocytosis, a portion of the membrane invaginates and flows around the particle, eventually pinching off and leaving the particle entirely enclosed by an envelope of plasma membrane. Vesicle contents are broken down by the cell, with the particles either used as food or dispatched. Pinocytosis is a similar process on a smaller scale. The plasma membrane invaginates and pinches off, producing a small envelope of fluid from outside the cell. Pinocytosis imports substances that the cell needs from the extracellular fluid. The cell expels waste in a similar but reverse manner: it pushes a membranous vacuole to the plasma membrane, allowing the vacuole to fuse with the membrane and incorporate itself into the membrane structure, releasing its contents to the exterior.

Glossary

caveolin

protein that coats the cytoplasmic side of the plasma membrane and participates in the process of liquid update by potocytosis

clathrin

protein that coats the inward-facing surface of the plasma membrane and assists in the formation of specialized structures, like coated pits, for phagocytosis

endocytosis

type of active transport that moves substances, including fluids and particles, into a cell

exocytosis
process of passing bulk material out of a cell

pinocytosis
a variation of endocytosis that imports macromolecules that the cell needs from the extracellular fluid

potocytosis
variation of pinocytosis that uses a different coating protein (caveolin) on the cytoplasmic side of the plasma membrane

receptor-mediated endocytosis
variation of endocytosis that involves the use of specific binding proteins in the plasma membrane for specific molecules or particles, and clathrin-coated pits that become clathrin-coated vesicles

---

This page titled 2.2.5: Bulk Transport is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.4: Bulk Transport** by OpenStax is licensed CC BY 4.0.

2.2.E: Structure and Function of Plasma Membranes (Exercises)

5.1: Components and Structure

Among the most sophisticated functions of the plasma membrane is the ability to transmit signals by means of complex, integral proteins known as receptors. These proteins act both as receivers of extracellular inputs and as activators of intracellular processes. These membrane receptors provide extracellular attachment sites for effectors like hormones and growth factors, and they activate intracellular response cascades when their effectors are bound.

Review Questions

Which plasma membrane component can be either found on its surface or embedded in the membrane structure?

A. protein
B. cholesterol
C. carbohydrate
D. phospholipid

Answer

A

Which characteristic of a phospholipid contributes to the fluidity of the membrane?

A. its head
B. cholesterol
C. a saturated fatty acid tail
D. double bonds in the fatty acid tail

Answer

D

What is the primary function of carbohydrates attached to the exterior of cell membranes?

A. identification of the cell
B. flexibility of the membrane
C. strengthening the membrane
D. channels through membrane

Answer

A

Free Response

Why is it advantageous for the cell membrane to be fluid in nature?

Answer

The fluid characteristic of the cell membrane allows greater flexibility to the cell than it would if the membrane were rigid. It also allows the motion of membrane components, required for some types of membrane transport.

Why do phospholipids tend to spontaneously orient themselves into something resembling a membrane?

Answer

The hydrophobic, nonpolar regions must align with each other in order for the structure to have minimal potential energy and, consequently, higher stability. The fatty acid tails of the phospholipids cannot mix with water, but the phosphate “head” of the molecule can. Thus, the head orients to water, and the tail to other lipids.

5.2: Passive Transport

Plasma membranes must allow certain substances to enter and leave a cell, and prevent some harmful materials from entering and some essential materials from leaving. In other words, plasma membranes are selectively permeable—they allow some substances to pass through, but not others. If they were to lose this selectivity, the cell would no longer be able to sustain itself, and it would be destroyed. Some cells require larger amounts of specific substances than do other cells.

Review Questions

Water moves via osmosis _____.

A. throughout the cytoplasm
B. from an area with a high concentration of other solutes to a lower one
C. from an area with a high concentration of water to one of lower concentration
D. from an area with a low concentration of water to one of higher concentration

Answer

C

The principal force driving movement in diffusion is the _____.

A. temperature
B. particle size
C. concentration gradient
D. membrane surface area

Answer

C

What problem is faced by organisms that live in fresh water?

A. Their bodies tend to take in too much water.
B. They have no way of controlling their tonicity.
C. Only salt water poses problems for animals that live in it.
D. Their bodies tend to lose too much water to their environment.

Answer

A

Free Response

Discuss why the following affect the rate of diffusion: molecular size, temperature, solution density, and the distance that must be traveled.

Answer

Heavy molecules move more slowly than lighter ones. It takes more energy in the medium to move them along. Increasing or decreasing temperature increases or decreases the energy in the medium, affecting molecular movement. The denser a solution is, the harder it is for molecules to move through it, causing diffusion to slow down due to friction. Living cells

require a steady supply of nutrients and a steady rate of waste removal. If the distance these substances need to travel is too great, diffusion cannot move nutrients and waste materials efficiently to sustain life.

Why does water move through a membrane?

Answer

Water moves through a membrane in osmosis because there is a concentration gradient across the membrane of solute and solvent. The solute cannot effectively move to balance the concentration on both sides of the membrane, so water moves to achieve this balance.

Both of the regular intravenous solutions administered in medicine, normal saline and lactated Ringer's solution, are isotonic. Why is this important?

Answer

Injection of isotonic solutions ensures that there will be no perturbation of the osmotic balance, and no water taken from tissues or added to them from the blood.

5.3: Active Transport

Active transport mechanisms require the use of the cell's energy, usually in the form of adenosine triphosphate (ATP). If a substance must move into the cell against its concentration gradient—that is, if the concentration of the substance inside the cell is greater than its concentration in the extracellular fluid (and vice versa)—the cell must use energy to move the substance. Some active transport mechanisms move small-molecular weight materials, such as ions, through the membrane.

Review Questions

Active transport must function continuously because _____.

A. plasma membranes wear out
B. not all membranes are amphiphilic
C. facilitated transport opposes active transport
D. diffusion is constantly moving solutes in opposite directions

Answer

D

How does the sodium-potassium pump make the interior of the cell negatively charged?

A. by expelling anions
B. by pulling in anions
C. by expelling more cations than are taken in
D. by taking in and expelling an equal number of cations

Answer

C

What is the combination of an electrical gradient and a concentration gradient called?

A. potential gradient
B. electrical potential
C. concentration potential
D. electrochemical gradient

Answer

D

Free Response

Where does the cell get energy for active transport processes?

Answer

The cell harvests energy from ATP produced by its own metabolism to power active transport processes, such as the activity of pumps.

How does the sodium-potassium pump contribute to the net negative charge of the interior of the cell?

Answer

The sodium-potassium pump forces out three (positive) Na^+ ions for every two (positive) K^+ ions it pumps in, thus the cell loses a positive charge at every cycle of the pump.

5.4: Bulk Transport

In addition to moving small ions and molecules through the membrane, cells also need to remove and take in larger molecules and particles (see Table 5.4.1 for examples). Some cells are even capable of engulfing entire unicellular microorganisms. You might have correctly hypothesized that the uptake and release of large particles by the cell requires energy. A large particle, however, cannot pass through the membrane, even with energy supplied by the cell.

Review Questions

What happens to the membrane of a vesicle after exocytosis?

A. It leaves the cell.
B. It is disassembled by the cell.
C. It fuses with and becomes part of the plasma membrane.
D. It is used again in another exocytosis event.

Answer

C

Which transport mechanism can bring whole cells into a cell?

A. pinocytosis
B. phagocytosis
C. facilitated transport
D. primary active transport

Answer

B

In what important way does receptor-mediated endocytosis differ from phagocytosis?

A. It transports only small amounts of fluid.
B. It does not involve the pinching off of membrane.
C. It brings in only a specifically targeted substance.
D. It brings substances into the cell, while phagocytosis removes substances.

Answer

C

Free Response

Why is it important that there are different types of proteins in plasma membranes for the transport of materials into and out of a cell?

Answer

The proteins allow a cell to select what compound will be transported, meeting the needs of the cell and not bringing in anything else.

Why do ions have a difficult time getting through plasma membranes despite their small size?

Answer

Ions are charged, and consequently, they are hydrophilic and cannot associate with the lipid portion of the membrane. Ions must be transported by carrier proteins or ion channels.

This page titled 2.2.E: Structure and Function of Plasma Membranes (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.E: Structure and Function of Plasma Membranes (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

2.3: Metabolism

Cellular processes 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? This chapter will discuss different forms of energy and the physical laws that govern energy transfer. This chapter will also describe how cells use energy and replenish it, and how chemical reactions in the cell are performed with great efficiency.

2.3.1: Prelude to Metabolism
2.3.2: Energy and Metabolism
2.3.3: Potential, Kinetic, Free, and Activation Energy
2.3.4: The Laws of Thermodynamics
2.3.5: ATP- Adenosine Triphosphate
2.3.6: Enzymes
2.3.E: Metabolism (Exercises)

This page titled 2.3: Metabolism is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

2.3.1: Prelude to Metabolism

Virtually every task performed by living organisms requires energy. Energy is needed to perform heavy labor and exercise, but humans also use a great deal of energy while thinking, and even during sleep. In fact, the living cells of every organism constantly use energy. Nutrients and other molecules are imported, metabolized (broken down) and possibly synthesized into new molecules, modified if needed, transported around the cell, and may be distributed to the entire organism. For example, the large proteins that make up muscles are actively built from smaller molecules. Complex carbohydrates are broken 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 for both the synthesis and breakdown of molecules. Additionally, signaling molecules such as hormones and neurotransmitters are transported between cells. Pathogenic bacteria and viruses are ingested and broken down by cells. 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.



Figure 2.3.1.1: A hummingbird needs energy to maintain prolonged periods of flight. The bird obtains its energy from taking in food and transforming the nutrients into energy through a series of biochemical reactions. The flight muscles in birds are extremely efficient in energy production. (credit: modification of work by Cory Zanker)

The cellular processes 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? This chapter will discuss different forms of energy and the physical laws that govern energy transfer. This chapter will also describe how cells use energy and replenish it, and how chemical reactions in the cell are performed with great efficiency.

This page titled 2.3.1: Prelude to Metabolism is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.0: Prelude to Metabolism** by OpenStax is licensed CC BY 4.0.

2.3.2: Energy and Metabolism

Skills to Develop

- Explain what metabolic pathways are and describe the two major types of metabolic pathways
- Discuss how chemical reactions play a role in energy transfer

Scientists use the term bioenergetics to discuss the concept of energy flow (Figure 2.3.2.1) through living systems, such as cells. Cellular processes such as the building and breaking down of 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 has been used, cells must continually produce more energy to replenish that used by the many energy-requiring chemical reactions that constantly take place. All of the chemical reactions that take place inside cells, including those that use energy and those that release energy, are the cell's metabolism.

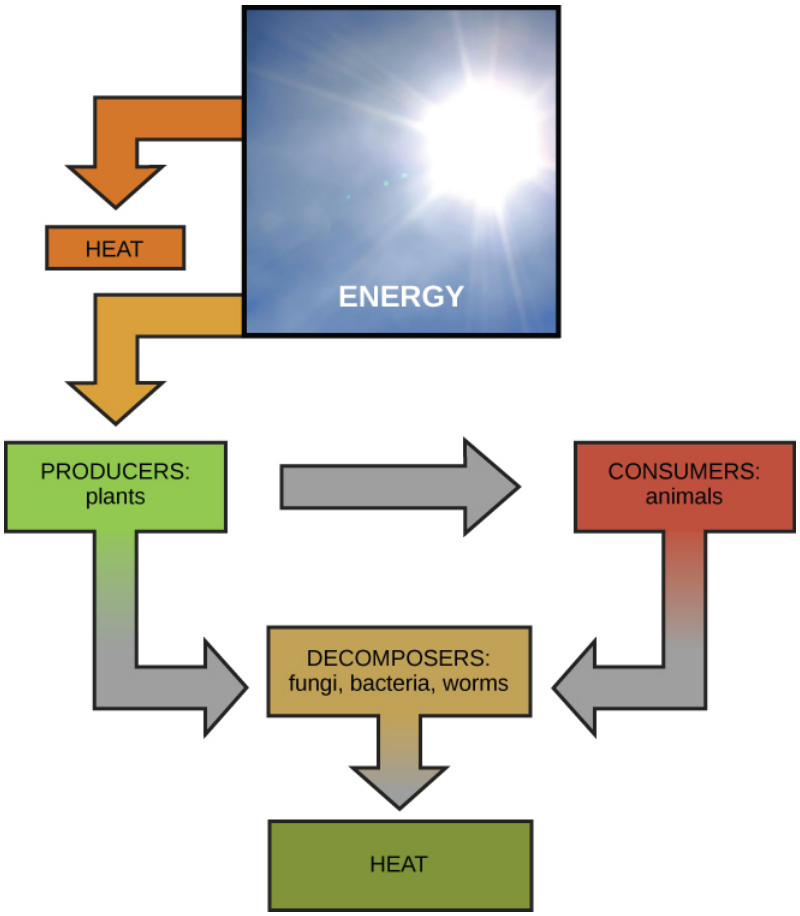


Figure 2.3.2.1: Most life forms on earth get their energy from the sun. Plants use photosynthesis to capture sunlight, and herbivores eat those plants to obtain energy. Carnivores eat the herbivores, and decomposers digest plant and animal matter.

Metabolism of Carbohydrates

The metabolism of sugar (a simple carbohydrate) 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 a great deal of energy stored within their bonds. The breakdown of glucose, a simple sugar, is described by the equation:

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

Carbohydrates that are consumed have their origins in photosynthesizing organisms like plants (Figure 6.1.2). 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 input of energy to proceed. The synthesis of glucose is described by this equation (notice that it is the reverse of the previous equation):

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

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

Solar energy is required to synthesize a molecule of glucose during the reactions of photosynthesis. In photosynthesis, light energy from the sun is initially transformed into chemical energy that is temporally stored in the energy carrier molecules ATP and NADPH (nicotinamide adenine dinucleotide phosphate). The stored energy in ATP and NADPH is then used later in photosynthesis to build one molecule of glucose from six molecules of CO_2. This process is analogous to eating breakfast in the morning to acquire energy for your body that can be used later in the day. Under ideal conditions, energy from 18 molecules of ATP is required to synthesize one molecule of glucose during the reactions of photosynthesis. Glucose molecules can also be combined with and converted into other types of sugars. When sugars are consumed, molecules of glucose eventually make their way into each living cell of the organism. Inside the cell, each sugar molecule is broken 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 is used to make high-energy ATP molecules, which can be used to perform work, powering many chemical reactions in the cell. The amount of energy needed to make one molecule of glucose from six molecules of carbon dioxide is 18 molecules of ATP and 12 molecules of NADPH (each one of which is energetically equivalent to three molecules of ATP), or a total of 54 molecule equivalents required for the synthesis of one molecule of glucose. This process is a fundamental and efficient way for cells to generate the molecular energy that they require.



Figure 2.3.2.2: 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 originally produced by plants. (credit “acorn”: modification of work by Noel Reynolds; credit “squirrel”: modification of work by Dawn Huczek)

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 synthesized sugar from smaller molecules, and the other pathway broke sugar down into smaller molecules. These two opposite processes—the first requiring energy and the second producing energy—are referred to as anabolic (building) and catabolic (breaking down) pathways, respectively. Consequently, metabolism is composed of building (anabolism) and degradation (catabolism).

Evolution Connection: Evolution of Metabolic Pathways

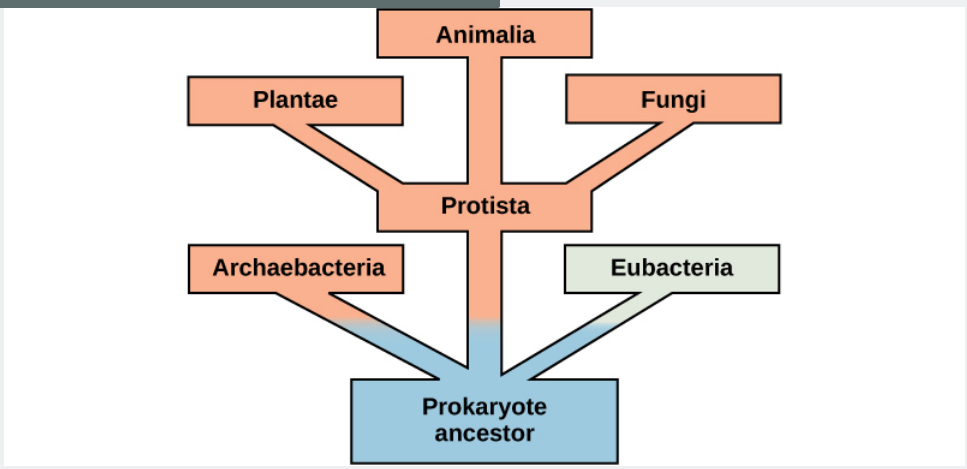


Figure 2.3.2.3: This tree shows the evolution of the various branches of life. The vertical dimension is time. Early life forms, in blue, used anaerobic metabolism to obtain energy from their surroundings.

There is more to the complexity of metabolism than understanding the metabolic pathways alone. Metabolic complexity varies from organism to organism. Photosynthesis is the primary pathway in which photosynthetic organisms like plants (the majority of global synthesis is done by planktonic algae) harvest the sun's energy and convert it into carbohydrates. The by-product of photosynthesis is oxygen, required by some cells to carry out cellular respiration. During cellular respiration, oxygen aids in the catabolic breakdown of carbon compounds, like carbohydrates. Among the products of this catabolism are CO2 and ATP. In addition, some eukaryotes perform catabolic processes without oxygen (fermentation); that is, they perform or use anaerobic metabolism.

Organisms probably evolved anaerobic metabolism to survive (living organisms came into existence about 3.8 billion years ago, when the atmosphere lacked oxygen). Despite the differences between organisms and the complexity of metabolism, researchers have found that all branches of life share some of the same metabolic pathways, suggesting that all organisms evolved from the same ancient common ancestor (Figure 2.3.2.3). Evidence indicates that over time, the pathways diverged, adding specialized enzymes to allow organisms to better adapt to their environment, thus increasing their chance to survive. However, the underlying principle remains that all organisms must harvest energy from their environment and convert it to ATP to carry out cellular functions.

Anabolic and Catabolic Pathways

Anabolic pathways require an input of energy to synthesize complex molecules from simpler ones. Synthesizing sugar from CO_2 is one example. Other examples are the synthesis of large proteins from amino acid building blocks, and the synthesis of new DNA strands from nucleic acid building blocks. These biosynthetic processes are critical to the life of the cell, take place constantly, and demand energy provided by ATP and other high-energy molecules like NADH (nicotinamide adenine dinucleotide) and NADPH (Figure 2.3.2.4).

ATP is an important molecule for cells to have in sufficient supply at all times. The breakdown of sugars illustrates how a single molecule of glucose can store enough energy to make a great deal of ATP, 36 to 38 molecules. This is a catabolic pathway. Catabolic pathways involve the degradation (or breakdown) of complex molecules into simpler ones. Molecular energy stored in the bonds of complex molecules is released in catabolic pathways and harvested in such a way that it can be used to produce ATP. Other energy-storing molecules, such as fats, are also broken down through similar catabolic reactions to release energy and make ATP (Figure 2.3.2.4).

It is important to know that the chemical reactions of metabolic pathways don't take place spontaneously. Each reaction step is facilitated, or catalyzed, by a protein called an enzyme. Enzymes are important for catalyzing all types of biological reactions—those that require energy as well as those that release energy.

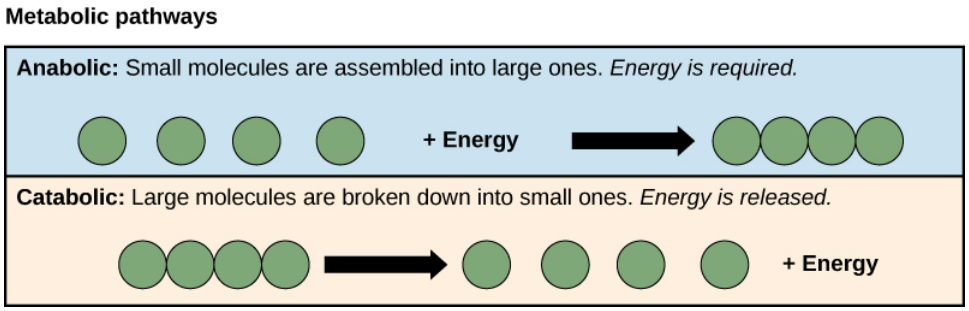


Figure 2.3.2.4: Anabolic pathways are those that require energy to synthesize larger molecules. Catabolic pathways are those that generate energy by breaking down larger molecules. Both types of pathways are required for maintaining the cell's energy balance.

Video



Just the first 5 minutes!

Summary

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 the breaking down of complex chemicals into simpler ones, such as the breakdown of large macromolecules. This process is referred to as catabolism, and such reactions are associated with a release of energy. On the other end of the spectrum, anabolism refers to metabolic processes that build complex molecules out of simpler ones, such as the synthesis of macromolecules. Anabolic processes require energy. Glucose synthesis and glucose breakdown are examples of anabolic and catabolic pathways, respectively.

Glossary

anabolic

(also, anabolism) pathways that require an input of energy to synthesize complex molecules from simpler ones

bioenergetics

study of energy flowing through living systems

catabolic

(also, catabolism) pathways in which complex molecules are broken down into simpler ones

metabolism

all the chemical reactions that take place inside cells, including anabolism and catabolism

This page titled 2.3.2: Energy and Metabolism is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.1: Energy and Metabolism** by OpenStax is licensed CC BY 4.0.

2.3.3: Potential, Kinetic, Free, and Activation Energy

Learning Objectives

- Define “energy”
- Explain the difference between kinetic and potential energy
- Discuss the concepts of free energy and activation energy
- Describe endergonic and exergonic reactions

Energy is defined as the ability to do work. As you’ve learned, energy exists in different forms. For example, electrical energy, light energy, and heat energy are all different types of energy. While these are all familiar types of energy that one can see or feel, there is another type of energy that is much less tangible. This energy is associated with something as simple as an object held above the ground. In order to appreciate the way energy flows into and out of biological systems, it is important to understand more about the different types of energy that exist in the physical world.

Types of Energy

When an object is in motion, there is energy associated with that object. In the example of an airplane in flight, there is a great deal of energy associated with the motion of the airplane. This is because moving objects are capable of enacting a change, or doing work. Think of a wrecking ball. Even a slow-moving wrecking ball can do a great deal of damage to other objects. However, a wrecking ball that is not in motion is incapable of performing work. Energy associated with objects in motion is called kinetic energy. A speeding bullet, a walking person, the rapid movement of molecules in the air (which produces heat), and electromagnetic radiation like light all have kinetic energy.

Now what if that same motionless wrecking ball is lifted two stories above a car with a crane? If the suspended wrecking ball is unmoving, is there energy associated with it? The answer is yes. The suspended wrecking ball has energy associated with it that is fundamentally different from the kinetic energy of objects in motion. This form of energy results from the fact that there is the *potential* for the wrecking ball to do work. If it is released, indeed it would do work. Because this type of energy refers to the potential to do work, it is called potential energy. Objects transfer their energy between kinetic and potential in the following way: As the wrecking ball hangs motionless, it has 0 kinetic and 100 percent potential energy. Once it is released, its kinetic energy begins to increase because it builds speed due to gravity. At the same time, as it nears the ground, it loses potential energy. Somewhere mid-fall it has 50 percent kinetic and 50 percent potential energy. Just before it hits the ground, the ball has nearly lost its potential energy and has near-maximal kinetic energy. Other examples of potential energy include the energy of water held behind a dam (Figure 2.3.3.1), or a person about to skydive out of an airplane.



Figure 2.3.3.1: Water behind a dam has potential energy. Moving water, such as in a waterfall or a rapidly flowing river, has kinetic energy. (credit “dam”: modification of work by "Pascal"/Flickr; credit “waterfall”: modification of work by Frank Gualtieri)

Potential energy is not only associated with the location of matter (such as a child sitting on a tree branch), but also with the structure of matter. A spring on the ground has potential energy if it is compressed; so does a rubber band that is pulled taut. The very existence of living cells relies heavily on structural potential energy. On a chemical level, the bonds that hold the atoms of

molecules together have potential energy. Remember that anabolic cellular pathways require energy to synthesize complex molecules from simpler ones, and catabolic pathways release energy when complex molecules are broken down. The fact that energy can be released by the breakdown of certain chemical bonds implies that those bonds have potential energy. In fact, there is potential energy stored within the bonds of all the food molecules we eat, which is eventually harnessed for use. This is because these bonds can release energy when broken. The type of potential energy that exists within chemical bonds, and is released when those bonds are broken, is called chemical energy (Figure 2.3.3.2). Chemical energy is responsible for providing living cells with energy from food. The release of energy is brought about by breaking the molecular bonds within fuel molecules.

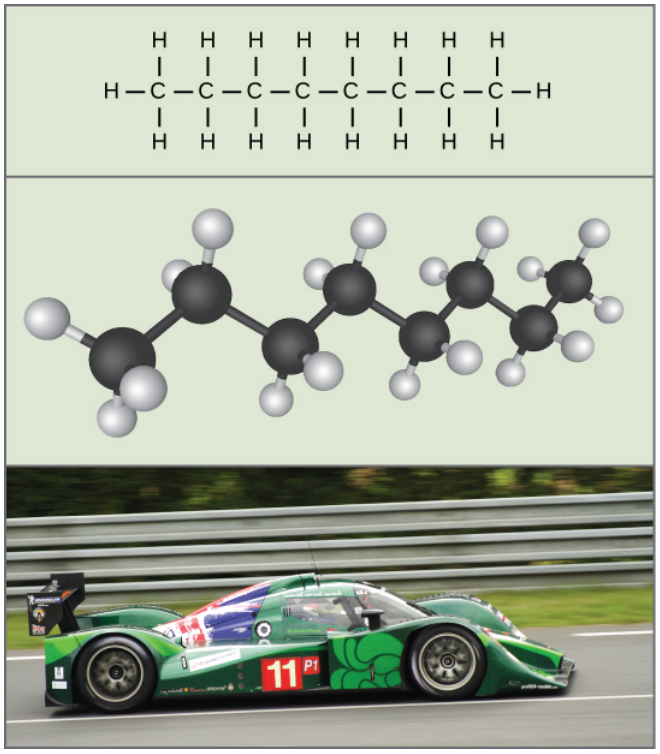


Figure 2.3.3.2: The molecules in gasoline (octane, the chemical formula shown) contain chemical energy within the chemical bonds. This energy is transformed into kinetic energy that allows a car to race on a racetrack. (credit “car”: modification of work by Russell Trow)

Free Energy

After learning that chemical reactions release energy when energy-storing bonds are broken, an important next question is how is the energy associated with chemical reactions quantified and expressed? How can the energy released from one reaction be compared to that of another reaction? A measurement of free energy is used to quantitate these energy transfers. Free energy is called Gibbs free energy (abbreviated with the letter G) after Josiah Willard Gibbs, the scientist who developed the measurement. Recall that according to the second law of thermodynamics, all energy transfers involve the loss of some amount of energy in an unusable form such as heat, resulting in entropy. Gibbs free energy specifically refers to the energy associated with a chemical reaction that is available after entropy is accounted for. In other words, Gibbs free energy is usable energy, or energy that is available to do work.

Video



Endergonic Reactions and Exergonic Reactions

If energy is released during a chemical reaction, then the resulting value from the above equation will be a negative number. In other words, reactions that release energy have a $\Delta G < 0$. A negative ΔG also means that the products of the reaction have less free energy than the reactants, because they gave off some free energy during the reaction. Reactions that have a negative ΔG and consequently release free energy are called exergonic reactions. Think: *ex*ergonic means energy is *ex*iting the system. These reactions are also referred to as spontaneous reactions, because they can occur without the addition of energy into the system. Understanding which chemical reactions are spontaneous and release free energy is extremely useful for biologists, because these reactions can be harnessed to perform work inside the cell. An important distinction must be drawn between the term spontaneous and the idea of a chemical reaction that occurs immediately. Contrary to the everyday use of the term, a spontaneous reaction is not one that suddenly or quickly occurs. The rusting of iron is an example of a spontaneous reaction that occurs slowly, little by little, over time.

If a chemical reaction requires an input of energy rather than releasing energy, then the ΔG for that reaction will be a positive value. In this case, the products have more free energy than the reactants. Thus, the products of these reactions can be thought of as energy-storing molecules. These chemical reactions are called endergonic reactions, and they are non-spontaneous. An endergonic reaction will not take place on its own without the addition of free energy.

Let's revisit the example of the synthesis and breakdown of the food molecule, glucose. Remember that the building of complex molecules, such as sugars, from simpler ones is an anabolic process and requires energy. Therefore, the chemical reactions involved in anabolic processes are endergonic reactions. On the other hand, the catabolic process of breaking sugar down into simpler molecules releases energy in a series of exergonic reactions. Like the example of rust above, the breakdown of sugar involves spontaneous reactions, but these reactions don't occur instantaneously. Figure 2.3.3.3 shows some other examples of endergonic and exergonic reactions. Later sections will provide more information about what else is required to make even spontaneous reactions happen more efficiently.

Art Connection



(a)



(b)



(c)



(d)

Figure 2.3.3.3: Shown are some examples of endergonic processes (ones that require energy) and exergonic processes (ones that release energy). These include (a) a compost pile decomposing, (b) a chick hatching from a fertilized egg, (c) sand art being destroyed, and (d) a ball rolling down a hill. (credit a: modification of work by Natalie Maynor; credit b: modification of work by USDA; credit c: modification of work by "Athlex"/Flickr; credit d: modification of work by Harry Malsch)

Look at each of the processes shown, and decide if it is endergonic or exergonic. In each case, does enthalpy increase or decrease, and does entropy increase or decrease?

Answer

A compost pile decomposing is an exergonic process; enthalpy increases (energy is released) and entropy increases (large molecules are broken down into smaller ones). A baby developing from a fertilized egg is an endergonic process; enthalpy decreases (energy is absorbed) and entropy decreases. Sand art being destroyed is an exergonic process; there is no change in enthalpy, but entropy increases. A ball rolling downhill is an exergonic process; enthalpy decreases (energy is released), but there is no change in enthalpy.

An important concept in the study of metabolism and energy is that of chemical equilibrium. Most chemical reactions are reversible. They can proceed in both directions, releasing energy into their environment in one direction, and absorbing it from the environment in the other direction (Figure 2.3.3.4). The same is true for the chemical reactions involved in cell metabolism, such as the breaking down and building up of proteins into and from individual amino acids, respectively. Reactants within a closed system will undergo chemical reactions in both directions until a state of equilibrium is reached. This state of equilibrium is one of the lowest possible free energy and a state of maximal entropy. Energy must be put into the system to push the reactants and products away from a state of equilibrium. Either reactants or products must be added, removed, or changed. If a cell were a closed system,

its chemical reactions would reach equilibrium, and it would die because there would be insufficient free energy left to perform the work needed to maintain life. In a living cell, chemical reactions are constantly moving towards equilibrium, but never reach it. This is because a living cell is an open system. Materials pass in and out, the cell recycles the products of certain chemical reactions into other reactions, and chemical equilibrium is never reached. In this way, living organisms are in a constant energy-requiring, uphill battle against equilibrium and entropy. This constant supply of energy ultimately comes from sunlight, which is used to produce nutrients in the process of photosynthesis.

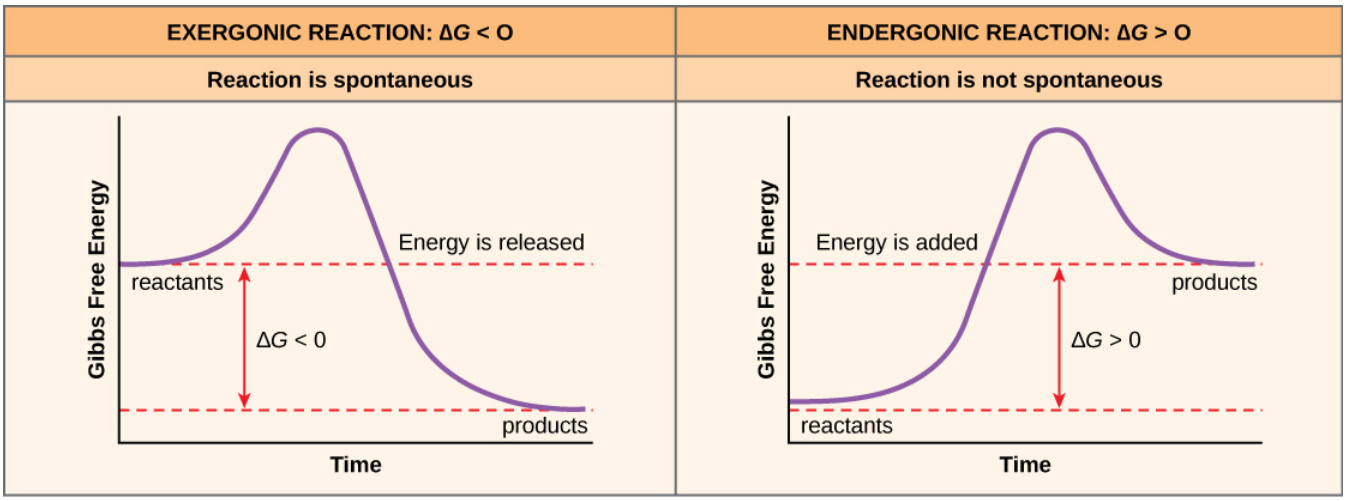


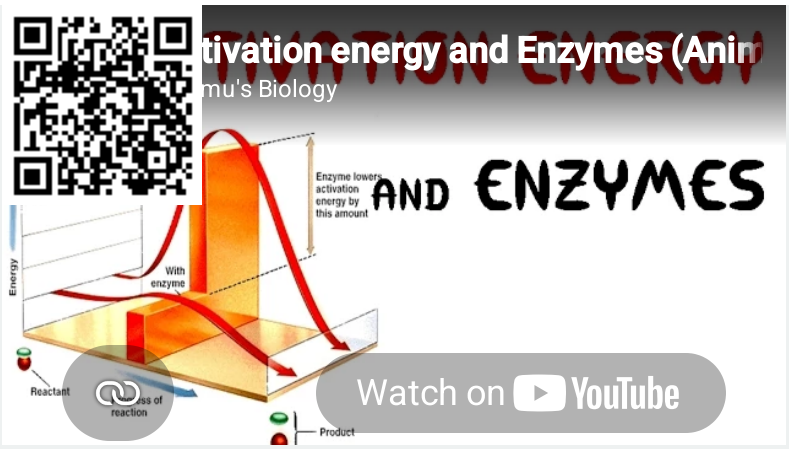
Figure 2.3.3.4: Exergonic and endergonic reactions result in changes in Gibbs free energy. Exergonic reactions release energy; endergonic reactions require energy to proceed.

Activation Energy

There is another important concept that must be considered regarding endergonic and exergonic reactions. Even exergonic reactions require a small amount of energy input to get going before they can proceed with their energy-releasing steps. These reactions have a net release of energy, but still require some energy in the beginning. This small amount of energy input necessary for all chemical reactions to occur is called the activation energy (or free energy of activation) and is abbreviated E_A (Figure 2.3.3.5).

Why would an energy-releasing, negative ΔG reaction actually require some energy to proceed? The reason lies in the steps that take place during a chemical reaction. During chemical reactions, certain chemical bonds are broken and new ones are formed. For example, when a glucose molecule is broken down, bonds between the carbon atoms of the molecule are broken. Since these are energy-storing bonds, they release energy when broken. However, to get them into a state that allows the bonds to break, the molecule must be somewhat contorted. A small energy input is required to achieve this contorted state. This contorted state is called the transition state, and it is a high-energy, unstable state. For this reason, reactant molecules don't last long in their transition state, but very quickly proceed to the next steps of the chemical reaction. Free energy diagrams illustrate the energy profiles for a given reaction. Whether the reaction is exergonic or endergonic determines whether the products in the diagram will exist at a lower or higher energy state than both the reactants and the products. However, regardless of this measure, the transition state of the reaction exists at a higher energy state than the reactants, and thus, E_A is always positive.

Link to Learning



Watch an animation of the move from free energy to transition state at this site.

Where does the activation energy required by chemical reactants come from? The source of the activation energy needed to push reactions forward is typically heat energy from the surroundings. Heat energy (the total bond energy of reactants or products in a chemical reaction) speeds up the motion of molecules, increasing the frequency and force with which they collide; it also moves atoms and bonds within the molecule slightly, helping them reach their transition state. For this reason, heating up a system will cause chemical reactants within that system to react more frequently. Increasing the pressure on a system has the same effect. Once reactants have absorbed enough heat energy from their surroundings to reach the transition state, the reaction will proceed.

The activation energy of a particular reaction determines the rate at which it will proceed. The higher the activation energy, the slower the chemical reaction will be. The example of iron rusting illustrates an inherently slow reaction. This reaction occurs slowly over time because of its high E_A. Additionally, the burning of many fuels, which is strongly exergonic, will take place at a negligible rate unless their activation energy is overcome by sufficient heat from a spark. Once they begin to burn, however, the chemical reactions release enough heat to continue the burning process, supplying the activation energy for surrounding fuel molecules. Like these reactions outside of cells, the activation energy for most cellular reactions is too high for heat energy to overcome at efficient rates. In other words, in order for important cellular reactions to occur at appreciable rates (number of reactions per unit time), their activation energies must be lowered (Figure 2.3.3.12.3.3.5); this is referred to as catalysis. This is a very good thing as far as living cells are concerned. Important macromolecules, such as proteins, DNA, and RNA, store considerable energy, and their breakdown is exergonic. If cellular temperatures alone provided enough heat energy for these exergonic reactions to overcome their activation barriers, the essential components of a cell would disintegrate.

Art Connection

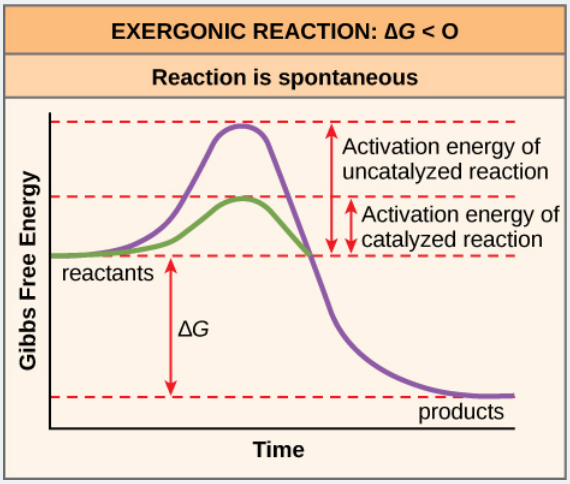


Figure 2.3.3.5: Activation energy is the energy required for a reaction to proceed, and it is lower if the reaction is catalyzed. The horizontal axis of this diagram describes the sequence of events in time.

If no activation energy were required to break down sucrose (table sugar), would you be able to store it in a sugar bowl?

Answer

No. We can store chemical energy because of the need to overcome the barrier to its breakdown.

Summary

Energy comes in many different forms. Objects in motion do physical work, and kinetic energy is the energy of objects in motion. Objects that are not in motion may have the potential to do work, and thus, have potential energy. Molecules also have potential energy because the breaking of molecular bonds has the potential to release energy. Living cells depend on the harvesting of potential energy from molecular bonds to perform work. Free energy is a measure of energy that is available to do work. The free energy of a system changes during energy transfers such as chemical reactions, and this change is referred to as ΔG.

The ΔG of a reaction can be negative or positive, meaning that the reaction releases energy or consumes energy, respectively. A reaction with a negative ΔG that gives off energy is called an exergonic reaction. One with a positive ΔG that requires energy input is called an endergonic reaction. Exergonic reactions are said to be spontaneous, because their products have less energy than their reactants. The products of endergonic reactions have a higher energy state than the reactants, and so these are nonspontaneous reactions. However, all reactions (including spontaneous -ΔG reactions) require an initial input of energy in order to reach the transition state, at which they'll proceed. This initial input of energy is called the activation energy.

Glossary

activation energy
energy necessary for reactions to occur

chemical energy
potential energy in chemical bonds that is released when those bonds are broken

endergonic
describes chemical reactions that require energy input

enthalpy
total energy of a system

exergonic
describes chemical reactions that release free energy

free energy
Gibbs free energy is the usable energy, or energy that is available to do work.

heat energy
total bond energy of reactants or products in a chemical reaction

kinetic energy
type of energy associated with objects or particles in motion

potential energy
type of energy that has the potential to do work; stored energy

transition state
high-energy, unstable state (an intermediate form between the substrate and the product) occurring during a chemical reaction

This page titled 2.3.3: Potential, Kinetic, Free, and Activation Energy is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.2: Potential, Kinetic, Free, and Activation Energy** by OpenStax is licensed CC BY 4.0.

2.3.4: The Laws of Thermodynamics

Skills to Develop

- Discuss the concept of entropy
- Explain the first and second laws of thermodynamics

Thermodynamics refers to the study of energy and energy transfer involving physical matter. The matter and its environment relevant to a particular case of energy transfer are classified as a system, and everything outside of that system is called the surroundings. For instance, when heating a pot of water on the stove, the system includes the stove, the pot, and the water. Energy is transferred within the system (between the stove, pot, and water). There are two types of systems: open and closed. An open system is one in which energy can be transferred between the system and its surroundings. The stovetop system is open because heat can be lost into the air. A closed system is one that cannot transfer energy to its surroundings.

Biological organisms are open systems. Energy is exchanged between them and their surroundings, as they consume energy-storing molecules and release energy to the environment by doing work. Like all things in the physical world, energy is subject to the laws of physics. The laws of thermodynamics govern the transfer of energy in and among all systems in the universe.

The First Law of Thermodynamics

The first law of thermodynamics deals with the total amount of energy in the universe. It states that this total amount of energy is constant. In other words, there has always been, and always will be, exactly the same amount of energy in the universe. Energy exists in many different forms. According to the first law of thermodynamics, energy may be transferred from place to place or transformed into different forms, but it cannot be created or destroyed. The transfers and transformations of energy take place around us all the time. Light bulbs transform electrical energy into light energy. Gas stoves transform chemical energy from natural gas into heat energy. Plants perform one of the most biologically useful energy transformations on earth: that of converting the energy of sunlight into the chemical energy stored within organic molecules (Figure 2.3.b.1). Some examples of energy transformations are shown in Figure 2.3.4.1.

The challenge for all living organisms is to obtain energy from their surroundings in forms that they can transfer or transform into usable energy to do work. Living cells have evolved to meet this challenge very well. Chemical energy stored within organic molecules such as sugars and fats is transformed through a series of cellular chemical reactions into energy within molecules of ATP. Energy in ATP molecules is easily accessible to do work. Examples of the types of work that cells need to do include building complex molecules, transporting materials, powering the beating motion of cilia or flagella, contracting muscle fibers to create movement, and reproduction.

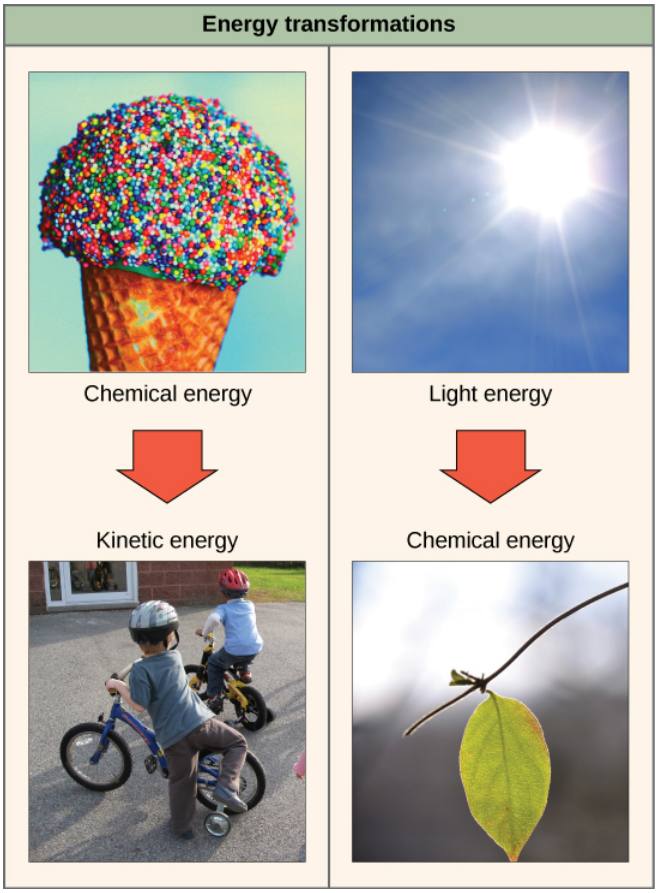


Figure 2.3.4.1: Shown are two examples of energy being transferred from one system to another and transformed from one form to another. Humans can convert the chemical energy in food, like this ice cream cone, into kinetic energy (the energy of movement to ride a bicycle). Plants can convert electromagnetic radiation (light energy) from the sun into chemical energy. (credit “ice cream”: modification of work by D. Sharon Pruitt; credit “kids on bikes”: modification of work by Michelle Riggen-Ransom; credit “leaf”: modification of work by Cory Zanker)

The Second Law of Thermodynamics

A living cell’s primary tasks of obtaining, transforming, and using energy to do work may seem simple. However, the second law of thermodynamics explains why these tasks are harder than they appear. None of the energy transfers we’ve discussed, along with all energy transfers and transformations in the universe, is completely efficient. In every energy transfer, some amount of energy is lost in a form that is unusable. In most cases, this form is heat energy. Thermodynamically, heat energy is defined as the energy transferred from one system to another that is not doing work. For example, when an airplane flies through the air, some of the energy of the flying plane is lost as heat energy due to friction with the surrounding air. This friction actually heats the air by temporarily increasing the speed of air molecules. Likewise, some energy is lost as heat energy during cellular metabolic reactions. This is good for warm-blooded creatures like us, because heat energy helps to maintain our body temperature. Strictly speaking, no energy transfer is completely efficient, because some energy is lost in an unusable form.

An important concept in physical systems is that of order and disorder (also known as randomness). The more energy that is lost by a system to its surroundings, the less ordered and more random the system is. Scientists refer to the measure of randomness or disorder within a system as entropy. High entropy means high disorder and low energy (Figure 2.3.4.2). To better understand entropy, think of a student’s bedroom. If no energy or work were put into it, the room would quickly become messy. It would exist in a very disordered state, one of high entropy. Energy must be put into the system, in the form of the student doing work and putting everything away, in order to bring the room back to a state of cleanliness and order. This state is one of low entropy. Similarly, a car or house must be constantly maintained with work in order to keep it in an ordered state. Left alone, the entropy of the house or car gradually increases through rust and degradation. Molecules and chemical reactions have varying amounts of entropy as well. For example, as chemical reactions reach a state of equilibrium, entropy increases, and as molecules at a high concentration in one place diffuse and spread out, entropy also increases.

Scientific Connection: Transfer of Energy and the Resulting Entropy

Set up a simple experiment to understand how energy is transferred and how a change in entropy results.

1. Take a block of ice. This is water in solid form, so it has a high structural order. This means that the molecules cannot move very much and are in a fixed position. The temperature of the ice is 0°C. As a result, the entropy of the system is low.
2. Allow the ice to melt at room temperature. What is the state of molecules in the liquid water now? How did the energy transfer take place? Is the entropy of the system higher or lower? Why?
3. Heat the water to its boiling point. What happens to the entropy of the system when the water is heated?

All physical systems can be thought of in this way: Living things are highly ordered, requiring constant energy input to be maintained in a state of low entropy. As living systems take in energy-storing molecules and transform them through chemical reactions, they lose some amount of usable energy in the process, because no reaction is completely efficient. They also produce waste and by-products that aren't useful energy sources. This process increases the entropy of the system's surroundings. Since all energy transfers result in the loss of some usable energy, the second law of thermodynamics states that every energy transfer or transformation increases the entropy of the universe. Even though living things are highly ordered and maintain a state of low entropy, the entropy of the universe in total is constantly increasing due to the loss of usable energy with each energy transfer that occurs. Essentially, living things are in a continuous uphill battle against this constant increase in universal entropy.

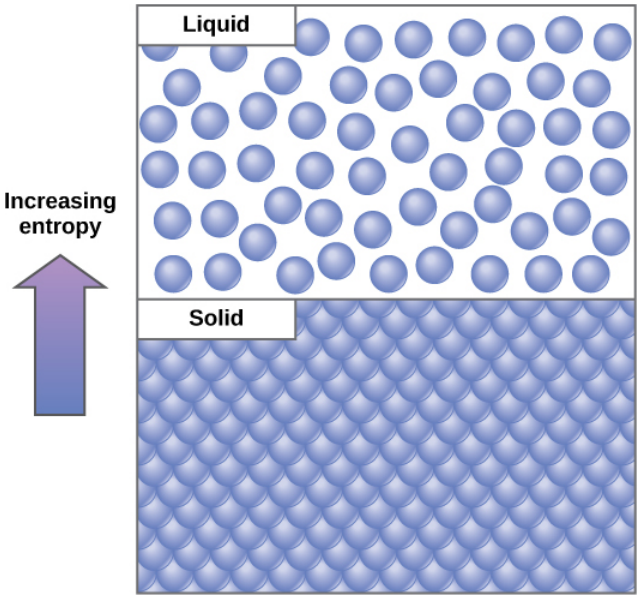


Figure 2.3.4.2: Entropy is a measure of randomness or disorder in a system. Gases have higher entropy than liquids, and liquids have higher entropy than solids.

Summary

In studying energy, scientists use the term "system" to refer to the matter and its environment involved in energy transfers. Everything outside of the system is called the surroundings. Single cells are biological systems. Systems can be thought of as having a certain amount of order. It takes energy to make a system more ordered. The more ordered a system is, the lower its entropy. Entropy is a measure of the disorder of a system. As a system becomes more disordered, the lower its energy and the higher its entropy become.

A series of laws, called the laws of thermodynamics, describe the properties and processes of energy transfer. The first law states that the total amount of energy in the universe is constant. This means that energy can't be created or destroyed, only transferred or transformed. The second law of thermodynamics states that every energy transfer involves some loss of energy in an unusable form, such as heat energy, resulting in a more disordered system. In other words, no energy transfer is completely efficient and tends toward disorder.

Glossary

entropy (S)

measure of randomness or disorder within a system

heat

energy energy transferred from one system to another that is not work (energy of the motion of molecules or particles)

thermodynamics

study of energy and energy transfer involving physical matter

---

This page titled 2.3.4: The Laws of Thermodynamics is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.3: The Laws of Thermodynamics** by OpenStax is licensed CC BY 4.0.

2.3.5: ATP- Adenosine Triphosphate

Skills to Develop

- Explain the role of ATP as the cellular energy currency
- Describe how energy is released through hydrolysis of ATP

Even exergonic, energy-releasing reactions require a small amount of activation energy in order to proceed. However, consider endergonic reactions, which require much more energy input, because their products have more free energy than their reactants. Within the cell, where does energy to power such reactions come from? The answer lies with an energy-supplying molecule called adenosine triphosphate, or ATP. ATP is a small, relatively simple molecule (Figure 2.3.5.1), but within some of its bonds, it contains the potential for a quick burst of energy that can be harnessed to perform cellular work. This molecule can be thought of as the primary energy currency of cells in much the same way that money is the currency that people exchange for things they need. ATP is used to power the majority of energy-requiring cellular reactions.

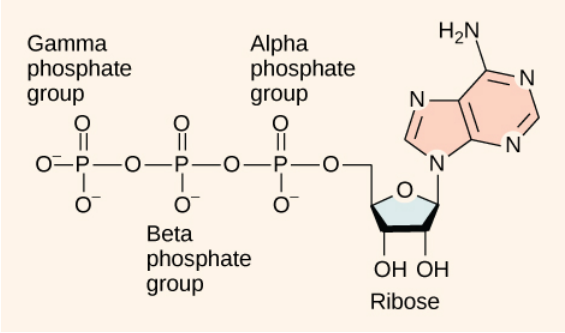


Figure 2.3.5.1: ATP is the primary energy currency of the cell. It has an adenosine backbone with three phosphate groups attached.

As its name suggests, adenosine triphosphate is comprised of adenosine bound to three phosphate groups (Figure 2.3.5.1). Adenosine is a nucleoside consisting of the nitrogenous base adenine and a five-carbon sugar, ribose. The three phosphate groups, in order of closest to furthest from the ribose sugar, are labeled alpha, beta, and gamma. Together, these chemical groups constitute an energy powerhouse. However, not all bonds within this molecule exist in a particularly high-energy state. Both bonds that link the phosphates are equally high-energy bonds (phosphoanhydride bonds) that, when broken, release sufficient energy to power a variety of cellular reactions and processes. These high-energy bonds are the bonds between the second and third (or beta and gamma) phosphate groups and between the first and second phosphate groups. The reason that these bonds are considered "high-energy" is because the products of such bond breaking—adenosine diphosphate (ADP) and one inorganic phosphate group (P_i)—have considerably lower free energy than the reactants: ATP and a water molecule. Because this reaction takes place with the use of a water molecule, it is considered a hydrolysis reaction. In other words, ATP is hydrolyzed into ADP in the following reaction:

$$\mathrm{ATP + H_2O \rightarrow ADP + P_i + free\ energy}$$

Like most chemical reactions, the hydrolysis of ATP to ADP is reversible. The reverse reaction regenerates ATP from ADP + P_i. Indeed, cells rely on the regeneration of ATP just as people rely on the regeneration of spent money through some sort of income. Since ATP hydrolysis releases energy, ATP regeneration must require an input of free energy. The formation of ATP is expressed in this equation:

$$\mathrm{ADP + P_i + free\ energy \rightarrow ATP + H_2O}$$

Two prominent questions remain with regard to the use of ATP as an energy source. Exactly how much free energy is released with the hydrolysis of ATP, and how is that free energy used to do cellular work? The calculated ΔG for the hydrolysis of one mole of ATP into ADP and P_i is −7.3 kcal/mole (−30.5 kJ/mol). Since this calculation is true under standard conditions, it would be expected that a different value exists under cellular conditions. In fact, the ΔG for the hydrolysis of one mole of ATP in a living cell is almost double the value at standard conditions: 14 kcal/mol (−57 kJ/mol).

ATP is a highly unstable molecule. Unless quickly used to perform work, ATP spontaneously dissociates into ADP + P_i, and the free energy released during this process is lost as heat. The second question posed above, that is, how the energy released by ATP

hydrolysis is used to perform work inside the cell, depends on a strategy called energy coupling. Cells couple the exergonic reaction of ATP hydrolysis with endergonic reactions, allowing them to proceed. One example of energy coupling using ATP involves a transmembrane ion pump that is extremely important for cellular function. This sodium-potassium pump (Na^+/K^+ pump) drives sodium out of the cell and potassium into the cell (Figure 2.3.5.2). A large percentage of a cell's ATP is spent powering this pump, because cellular processes bring a great deal of sodium into the cell and potassium out of the cell. The pump works constantly to stabilize cellular concentrations of sodium and potassium. In order for the pump to turn one cycle (exporting three Na^+ ions and importing two K^+ ions), one molecule of ATP must be hydrolyzed. When ATP is hydrolyzed, its gamma phosphate doesn't simply float away, but is actually transferred onto the pump protein. This process of a phosphate group binding to a molecule is called phosphorylation. As with most cases of ATP hydrolysis, a phosphate from ATP is transferred onto another molecule. In a phosphorylated state, the Na^+/K^+ pump has more free energy and is triggered to undergo a conformational change. This change allows it to release Na^+ to the outside of the cell. It then binds extracellular K^+, which, through another conformational change, causes the phosphate to detach from the pump. This release of phosphate triggers the K^+ to be released to the inside of the cell. Essentially, the energy released from the hydrolysis of ATP is coupled with the energy required to power the pump and transport Na^+ and K^+ ions. ATP performs cellular work using this basic form of energy coupling through phosphorylation.

Art Connection

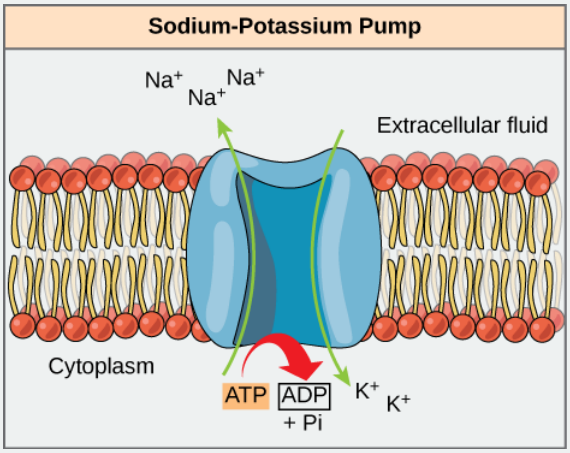
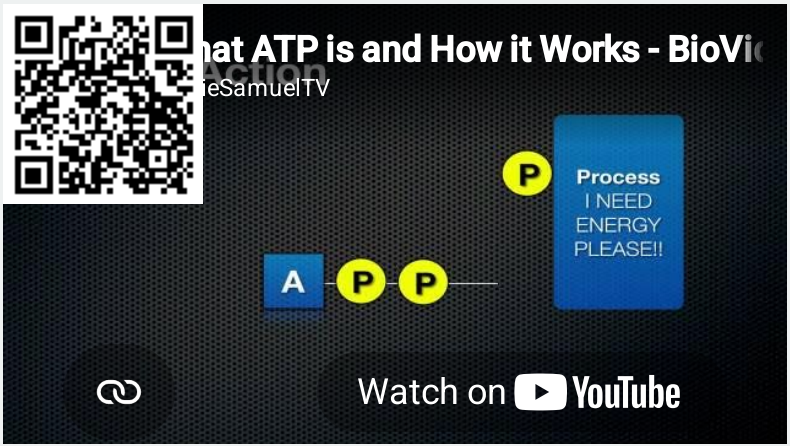


Figure 2.3.5.2: The sodium-potassium pump is an example of energy coupling. The energy derived from exergonic ATP hydrolysis is used to pump sodium and potassium ions across the cell membrane.

The hydrolysis of one ATP molecule releases 7.3 kcal/mol of energy ($\Delta G = -7.3$ kcal/mol of energy). If it takes 2.1 kcal/mol of energy to move one Na^+ across the membrane ($\Delta G = +2.1$ kcal/mol of energy), how many sodium ions could be moved by the hydrolysis of one ATP molecule?

Often during cellular metabolic reactions, such as the synthesis and breakdown of nutrients, certain molecules must be altered slightly in their conformation to become substrates for the next step in the reaction series. One example is during the very first steps of cellular respiration, when a molecule of the sugar glucose is broken down in the process of glycolysis. In the first step of this process, ATP is required for the phosphorylation of glucose, creating a high-energy but unstable intermediate. This phosphorylation reaction powers a conformational change that allows the phosphorylated glucose molecule to be converted to the phosphorylated sugar fructose. Fructose is a necessary intermediate for glycolysis to move forward. Here, the exergonic reaction of ATP hydrolysis is coupled with the endergonic reaction of converting glucose into a phosphorylated intermediate in the pathway. Once again, the energy released by breaking a phosphate bond within ATP was used for the phosphorylation of another molecule, creating an unstable intermediate and powering an important conformational change.

Video



Summary

ATP is the primary energy-supplying molecule for living cells. ATP is made up of a nucleotide, a five-carbon sugar, and three phosphate groups. The bonds that connect the phosphates (phosphoanhydride bonds) have high-energy content. The energy released from the hydrolysis of ATP into ADP + P_i is used to perform cellular work. Cells use ATP to perform work by coupling the exergonic reaction of ATP hydrolysis with endergonic reactions. ATP donates its phosphate group to another molecule via a process known as phosphorylation. The phosphorylated molecule is at a higher-energy state and is less stable than its unphosphorylated form, and this added energy from the addition of the phosphate allows the molecule to undergo its endergonic reaction.

Glossary

ATP
: adenosine triphosphate, the cell's energy currency

phosphoanhydride bond
: bond that connects phosphates in an ATP molecule

This page titled 2.3.5: ATP- Adenosine Triphosphate is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.4: ATP: Adenosine Triphosphate** by OpenStax is licensed CC BY 4.0.

2.3.6: Enzymes

Skills to Develop

- Describe the role of enzymes in metabolic pathways
- Explain how enzymes function as molecular catalysts
- Discuss enzyme regulation by various factors

A substance that helps a chemical reaction to occur is a catalyst, and the special molecules that catalyze biochemical reactions are called enzymes. Almost all enzymes are proteins, made up of chains of amino acids, and they perform the critical task of lowering the activation energies of chemical reactions inside the cell. Enzymes do this by binding to the reactant molecules, and holding them in such a way as to make the chemical bond-breaking and bond-forming processes take place more readily. It is important to remember that enzymes don't change the ΔG of a reaction. In other words, they don't change whether a reaction is exergonic (spontaneous) or endergonic. This is because they don't change the free energy of the reactants or products. They only reduce the activation energy required to reach the transition state (Figure 2.3.6.1).

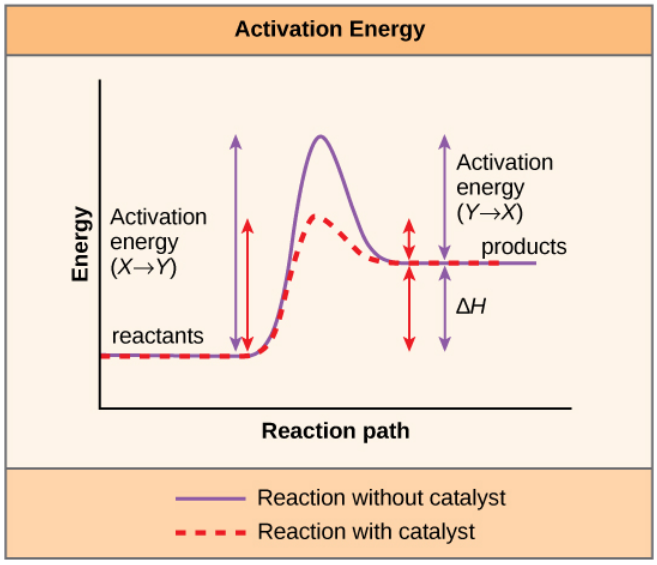


Figure 2.3.6.1: Enzymes lower the activation energy of the reaction but do not change the free energy of the reaction.

Enzyme Active Site and Substrate Specificity

The chemical reactants to which an enzyme binds are the enzyme's substrates. There may be one or more substrates, depending on the particular chemical reaction. In some reactions, a single-reactant substrate is broken down into multiple products. In others, two substrates may come together to create one larger molecule. Two reactants might also enter a reaction, both become modified, and leave the reaction as two products. The location within the enzyme where the substrate binds is called the enzyme's active site. The active site is where the "action" happens, so to speak. Since enzymes are proteins, there is a unique combination of amino acid residues (also called side chains, or R groups) within the active site. Each residue is characterized by different properties. Residues can be large or small, weakly acidic or basic, hydrophilic or hydrophobic, positively or negatively charged, or neutral. The unique combination of amino acid residues, their positions, sequences, structures, and properties, creates a very specific chemical environment within the active site. This specific environment is suited to bind, albeit briefly, to a specific chemical substrate (or substrates). Due to this jigsaw puzzle-like match between an enzyme and its substrates (which adapts to find the best fit between the transition state and the active site), enzymes are known for their specificity. The "best fit" results from the shape and the amino acid functional group's attraction to the substrate. There is a specifically matched enzyme for each substrate and, thus, for each chemical reaction; however, there is flexibility as well.

The fact that active sites are so perfectly suited to provide specific environmental conditions also means that they are subject to influences by the local environment. It is true that increasing the environmental temperature generally increases reaction rates,

enzyme-catalyzed or otherwise. However, increasing or decreasing the temperature outside of an optimal range can affect chemical bonds within the active site in such a way that they are less well suited to bind substrates. High temperatures will eventually cause enzymes, like other biological molecules, to denature, a process that changes the natural properties of a substance. Likewise, the pH of the local environment can also affect enzyme function. Active site amino acid residues have their own acidic or basic properties that are optimal for catalysis. These residues are sensitive to changes in pH that can impair the way substrate molecules bind. Enzymes are suited to function best within a certain pH range, and, as with temperature, extreme pH values (acidic or basic) of the environment can cause enzymes to denature.

Induced Fit and Enzyme Function

For many years, scientists thought that enzyme-substrate binding took place in a simple "lock-and-key" fashion. This model asserted that the enzyme and substrate fit together perfectly in one instantaneous step. However, current research supports a more refined view called induced fit (Figure 2.3.6.2). The induced-fit model expands upon the lock-and-key model by describing a more dynamic interaction between enzyme and substrate. As the enzyme and substrate come together, their interaction causes a mild shift in the enzyme's structure that confirms an ideal binding arrangement between the enzyme and the transition state of the substrate. This ideal binding maximizes the enzyme's ability to catalyze its reaction.

When an enzyme binds its substrate, an enzyme-substrate complex is formed. This complex lowers the activation energy of the reaction and promotes its rapid progression in one of many ways. On a basic level, enzymes promote chemical reactions that involve more than one substrate by bringing the substrates together in an optimal orientation. The appropriate region (atoms and bonds) of one molecule is juxtaposed to the appropriate region of the other molecule with which it must react. Another way in which enzymes promote the reaction of their substrates is by creating an optimal environment within the active site for the reaction to occur. Certain chemical reactions might proceed best in a slightly acidic or non-polar environment. The chemical properties that emerge from the particular arrangement of amino acid residues within an active site create the perfect environment for an enzyme's specific substrates to react.

You've learned that the activation energy required for many reactions includes the energy involved in manipulating or slightly contorting chemical bonds so that they can easily break and allow others to reform. Enzymatic action can aid this process. The enzyme-substrate complex can lower the activation energy by contorting substrate molecules in such a way as to facilitate bond-breaking, helping to reach the transition state. Finally, enzymes can also lower activation energies by taking part in the chemical reaction itself. The amino acid residues can provide certain ions or chemical groups that actually form covalent bonds with substrate molecules as a necessary step of the reaction process. In these cases, it is important to remember that the enzyme will always return to its original state at the completion of the reaction. One of the hallmark properties of enzymes is that they remain ultimately unchanged by the reactions they catalyze. After an enzyme is done catalyzing a reaction, it releases its product(s).

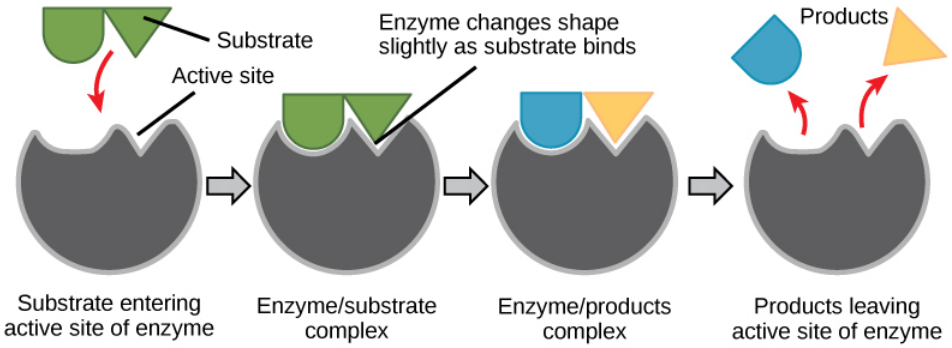
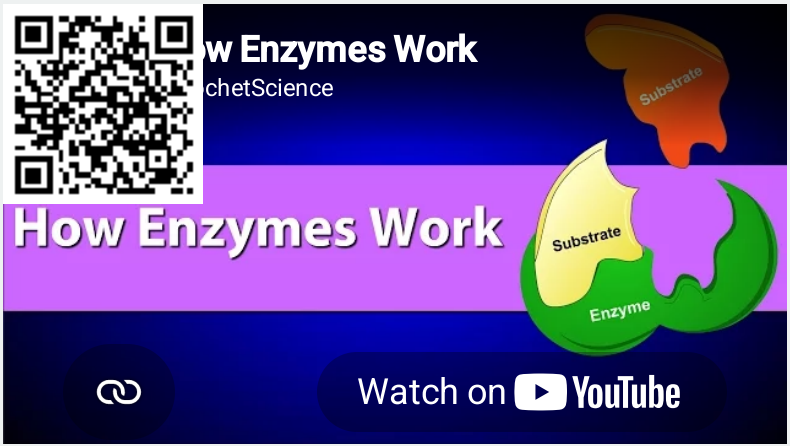


Figure 2.3.6.2: According to the induced-fit model, both enzyme and substrate undergo dynamic conformational changes upon binding. The enzyme contorts the substrate into its transition state, thereby increasing the rate of the reaction.

Video



Control of Metabolism Through Enzyme Regulation

It would seem ideal to have a scenario in which all of the enzymes encoded in an organism's genome existed in abundant supply and functioned optimally under all cellular conditions, in all cells, at all times. In reality, this is far from the case. A variety of mechanisms ensure that this does not happen. Cellular needs and conditions vary from cell to cell, and change within individual cells over time. The required enzymes and energetic demands of stomach cells are different from those of fat storage cells, skin cells, blood cells, and nerve cells. Furthermore, a digestive cell works much harder to process and break down nutrients during the time that closely follows a meal compared with many hours after a meal. As these cellular demands and conditions vary, so do the amounts and functionality of different enzymes.

Since the rates of biochemical reactions are controlled by activation energy, and enzymes lower and determine activation energies for chemical reactions, the relative amounts and functioning of the variety of enzymes within a cell ultimately determine which reactions will proceed and at which rates. This determination is tightly controlled. In certain cellular environments, enzyme activity is partly controlled by environmental factors, like pH and temperature. There are other mechanisms through which cells control the activity of enzymes and determine the rates at which various biochemical reactions will occur.

Regulation of Enzymes by Molecules

Enzymes can be regulated in ways that either promote or reduce their activity. There are many different kinds of molecules that inhibit or promote enzyme function, and various mechanisms exist for doing so. In some cases of enzyme inhibition, for example, an inhibitor molecule is similar enough to a substrate that it can bind to the active site and simply block the substrate from binding. When this happens, the enzyme is inhibited through competitive inhibition, because an inhibitor molecule competes with the substrate for active site binding (Figure 2.3.6.3). On the other hand, in noncompetitive inhibition, an inhibitor molecule binds to the enzyme in a location other than an allosteric site and still manages to block substrate binding to the active site.

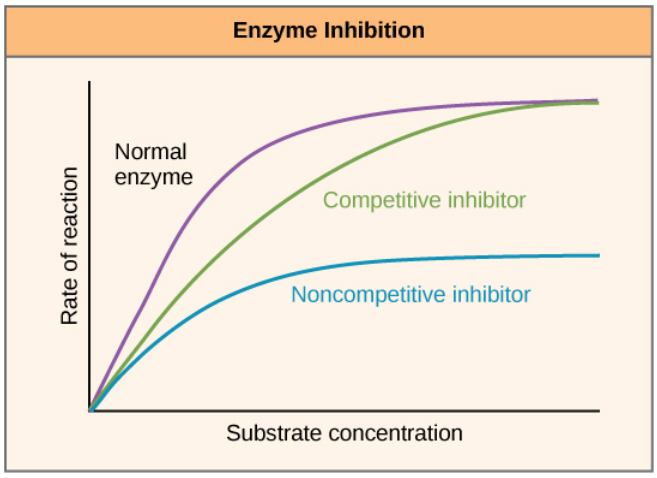


Figure 2.3.6.3: Competitive and noncompetitive inhibition affect the rate of reaction differently. Competitive inhibitors affect the initial rate but do not affect the maximal rate, whereas noncompetitive inhibitors affect the maximal rate.

Some inhibitor molecules bind to enzymes in a location where their binding induces a conformational change that reduces the affinity of the enzyme for its substrate. This type of inhibition is called allosteric inhibition (Figure 2.3.6.4). Most allosterically regulated enzymes are made up of more than one polypeptide, meaning that they have more than one protein subunit. When an allosteric inhibitor binds to an enzyme, all active sites on the protein subunits are changed slightly such that they bind their substrates with less efficiency. There are allosteric activators as well as inhibitors. Allosteric activators bind to locations on an enzyme away from the active site, inducing a conformational change that increases the affinity of the enzyme's active site(s) for its substrate(s).

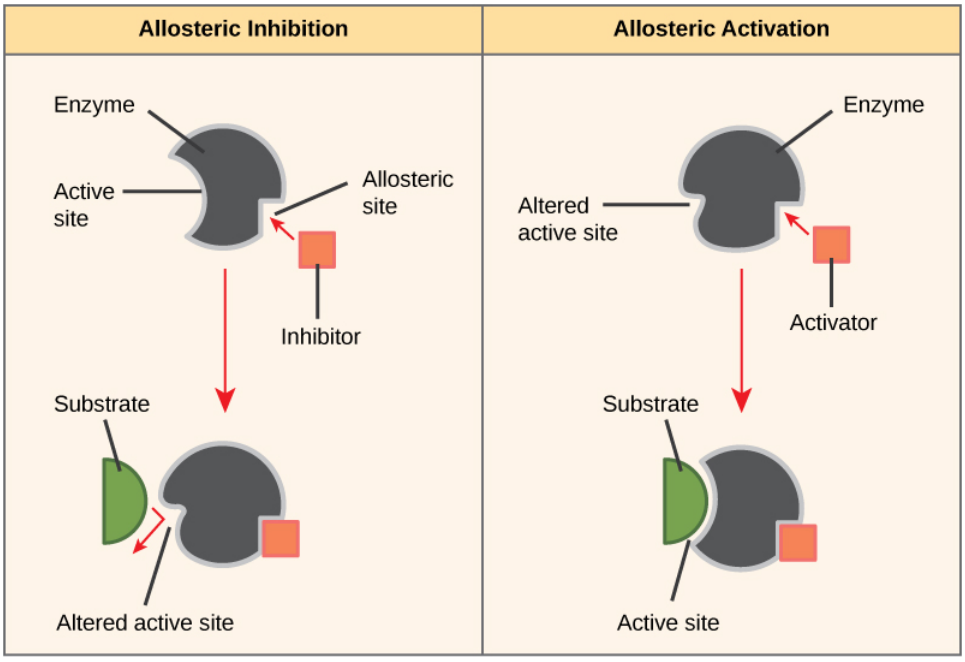


Figure 2.3.6.4: Allosteric inhibitors modify the active site of the enzyme so that substrate binding is reduced or prevented. In contrast, allosteric activators modify the active site of the enzyme so that the affinity for the substrate increases.

Everyday Connection: Drug Discovery by Looking for Inhibitors of Key Enzymes in Specific Pathways



Figure 2.3.6.5: Have you ever wondered how pharmaceutical drugs are developed? (credit: Deborah Austin)

Enzymes are key components of metabolic pathways. Understanding how enzymes work and how they can be regulated is a key principle behind the development of many of the pharmaceutical drugs (Figure 2.3.6.5) on the market today. Biologists working in this field collaborate with other scientists, usually chemists, to design drugs.

Consider statins for example—which is the name given to the class of drugs that reduces cholesterol levels. These compounds are essentially inhibitors of the enzyme HMG-CoA reductase. HMG-CoA reductase is the enzyme that synthesizes cholesterol from lipids in the body. By inhibiting this enzyme, the levels of cholesterol synthesized in the body can be reduced. Similarly, acetaminophen, popularly marketed under the brand name Tylenol, is an inhibitor of the enzyme cyclooxygenase. While it is effective in providing relief from fever and inflammation (pain), its mechanism of action is still not completely understood.

How are drugs developed? One of the first challenges in drug development is identifying the specific molecule that the drug is intended to target. In the case of statins, HMG-CoA reductase is the drug target. Drug targets are identified through painstaking research in the laboratory. Identifying the target alone is not sufficient; scientists also need to know how the target acts inside the cell and which reactions go awry in the case of disease. Once the target and the pathway are identified, then the actual process of drug design begins. During this stage, chemists and biologists work together to design and synthesize molecules that can either block or activate a particular reaction. However, this is only the beginning: both if and when a drug prototype is successful in performing its function, then it must undergo many tests from in vitro experiments to clinical trials before it can get FDA approval to be on the market.

Many enzymes don’t work optimally, or even at all, unless bound to other specific non-protein helper molecules, either temporarily through ionic or hydrogen bonds or permanently through stronger covalent bonds. Two types of helper molecules are cofactors and coenzymes. Binding to these molecules promotes optimal conformation and function for their respective enzymes. Cofactors are inorganic ions such as iron (Fe++) and magnesium (Mg++). One example of an enzyme that requires a metal ion as a cofactor is the enzyme that builds DNA molecules, DNA polymerase, which requires bound zinc ion (Zn++) to function. Coenzymes are organic helper molecules, with a basic atomic structure made up of carbon and hydrogen, which are required for enzyme action. The most common sources of coenzymes are dietary vitamins (Figure 2.3.6.6). Some vitamins are precursors to coenzymes and others act directly as coenzymes. Vitamin C is a coenzyme for multiple enzymes that take part in building the important connective tissue component, collagen. An important step in the breakdown of glucose to yield energy is catalysis by a multi-enzyme complex called pyruvate dehydrogenase. Pyruvate dehydrogenase is a complex of several enzymes that actually requires one cofactor (a magnesium ion) and five different organic coenzymes to catalyze its specific chemical reaction. Therefore, enzyme function is, in part, regulated by an abundance of various cofactors and coenzymes, which are supplied primarily by the diets of most organisms.

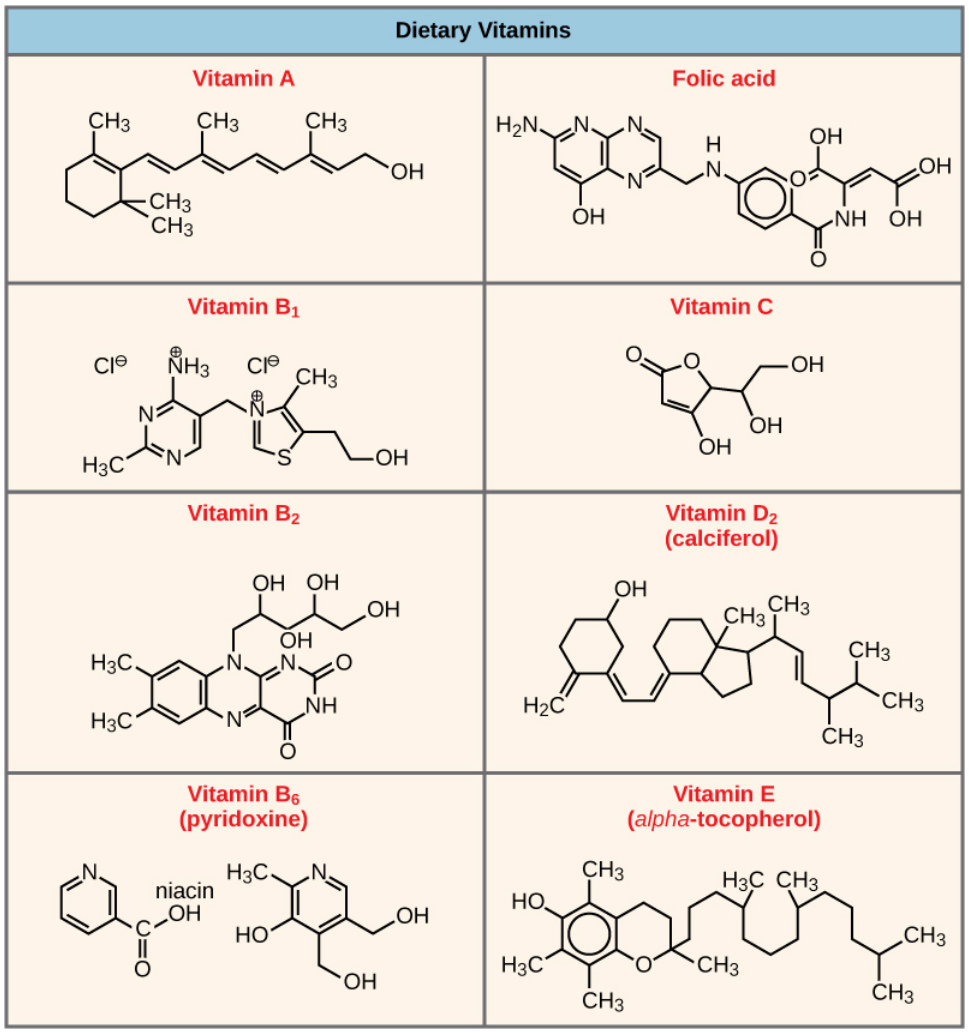


Figure 2.3.6.6: Vitamins are important coenzymes or precursors of coenzymes, and are required for enzymes to function properly. Multivitamin capsules usually contain mixtures of all the vitamins at different percentages.

Enzyme Compartmentalization

In eukaryotic cells, molecules such as enzymes are usually compartmentalized into different organelles. This allows for yet another level of regulation of enzyme activity. Enzymes required only for certain cellular processes can be housed separately along with their substrates, allowing for more efficient chemical reactions. Examples of this sort of enzyme regulation based on location and proximity include the enzymes involved in the latter stages of cellular respiration, which take place exclusively in the mitochondria, and the enzymes involved in the digestion of cellular debris and foreign materials, located within lysosomes.

Feedback Inhibition in Metabolic Pathways

Molecules can regulate enzyme function in many ways. A major question remains, however: What are these molecules and where do they come from? Some are cofactors and coenzymes, ions, and organic molecules, as you've learned. What other molecules in the cell provide enzymatic regulation, such as allosteric modulation, and competitive and noncompetitive inhibition? The answer is that a wide variety of molecules can perform these roles. Some of these molecules include pharmaceutical and non-pharmaceutical drugs, toxins, and poisons from the environment. Perhaps the most relevant sources of enzyme regulatory molecules, with respect to cellular metabolism, are the products of the cellular metabolic reactions themselves. In a most efficient and elegant way, cells have evolved to use the products of their own reactions for feedback inhibition of enzyme activity. Feedback inhibition involves the use of a reaction product to regulate its own further production (Figure 2.3.6.7). The cell responds to the abundance of specific products by slowing down production during anabolic or catabolic reactions. Such reaction products may inhibit the enzymes that catalyzed their production through the mechanisms described above.

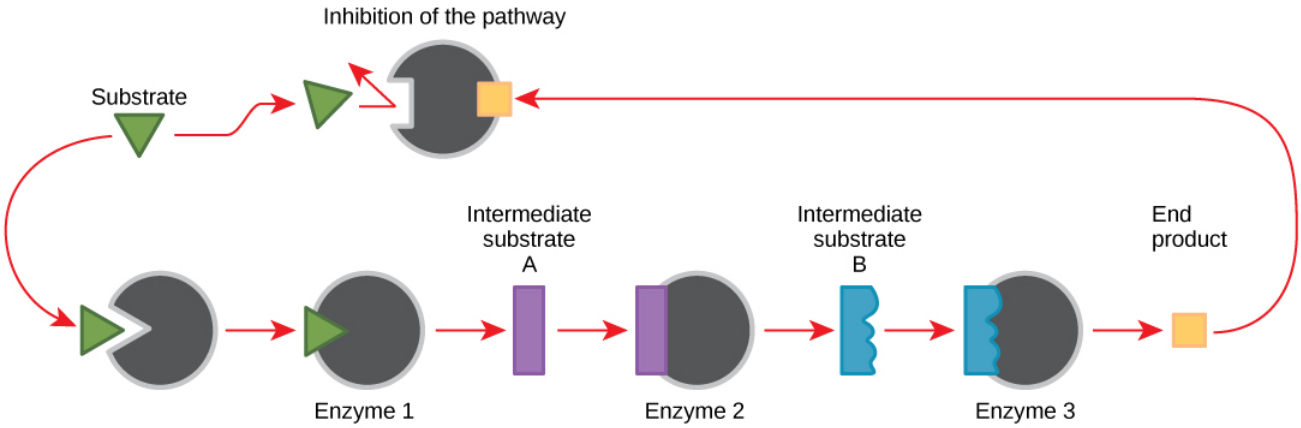
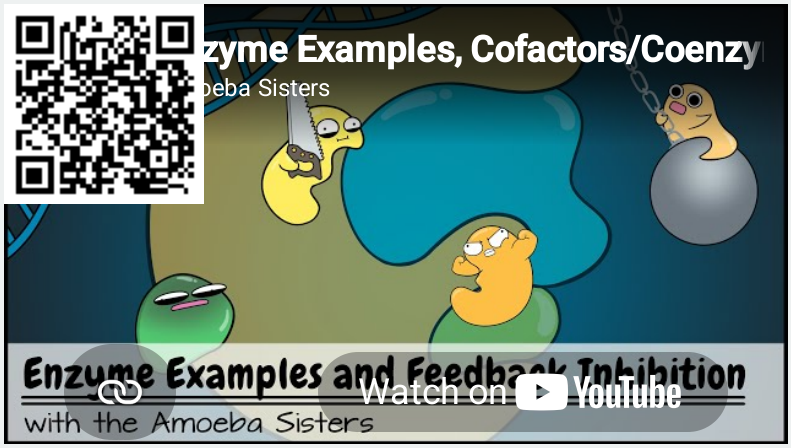


Figure 2.3.6.7: Metabolic pathways are a series of reactions catalyzed by multiple enzymes. Feedback inhibition, where the end product of the pathway inhibits an upstream step, is an important regulatory mechanism in cells.

The production of both amino acids and nucleotides is controlled through feedback inhibition. Additionally, ATP is an allosteric regulator of some of the enzymes involved in the catabolic breakdown of sugar, the process that produces ATP. In this way, when ATP is abundant, the cell can prevent its further production. Remember that ATP is an unstable molecule that can spontaneously dissociate into ADP. If too much ATP were present in a cell, much of it would go to waste. On the other hand, ADP serves as a positive allosteric regulator (an allosteric activator) for some of the same enzymes that are inhibited by ATP. Thus, when relative levels of ADP are high compared to ATP, the cell is triggered to produce more ATP through the catabolism of sugar.

Video



Video



Summary

Enzymes are chemical catalysts that accelerate chemical reactions at physiological temperatures by lowering their activation energy. Enzymes are usually proteins consisting of one or more polypeptide chains. Enzymes have an active site that provides a unique chemical environment, made up of certain amino acid R groups (residues). This unique environment is perfectly suited to convert particular chemical reactants for that enzyme, called substrates, into unstable intermediates called transition states. Enzymes and substrates are thought to bind with an induced fit, which means that enzymes undergo slight conformational adjustments upon substrate contact, leading to full, optimal binding. Enzymes bind to substrates and catalyze reactions in four different ways: bringing substrates together in an optimal orientation, compromising the bond structures of substrates so that bonds can be more easily broken, providing optimal environmental conditions for a reaction to occur, or participating directly in their chemical reaction by forming transient covalent bonds with the substrates.

Enzyme action must be regulated so that in a given cell at a given time, the desired reactions are being catalyzed and the undesired reactions are not. Enzymes are regulated by cellular conditions, such as temperature and pH. They are also regulated through their location within a cell, sometimes being compartmentalized so that they can only catalyze reactions under certain circumstances. Inhibition and activation of enzymes via other molecules are other important ways that enzymes are regulated. Inhibitors can act competitively, noncompetitively, or allosterically; noncompetitive inhibitors are usually allosteric. Activators can also enhance the function of enzymes allosterically. The most common method by which cells regulate the enzymes in metabolic pathways is through feedback inhibition. During feedback inhibition, the products of a metabolic pathway serve as inhibitors (usually allosteric) of one or more of the enzymes (usually the first committed enzyme of the pathway) involved in the pathway that produces them.

Glossary

active site

specific region of the enzyme to which the substrate binds

allosteric inhibition

inhibition by a binding event at a site different from the active site, which induces a conformational change and reduces the affinity of the enzyme for its substrate

coenzyme

small organic molecule, such as a vitamin or its derivative, which is required to enhance the activity of an enzyme

cofactor

inorganic ion, such as iron and magnesium ions, required for optimal regulation of enzyme activity

competitive inhibition

type of inhibition in which the inhibitor competes with the substrate molecule by binding to the active site of the enzyme

denature

process that changes the natural properties of a substance

feedback inhibition

effect of a product of a reaction sequence to decrease its further production by inhibiting the activity of the first enzyme in the pathway that produces it

induced fit

dynamic fit between the enzyme and its substrate, in which both components modify their structures to allow for ideal binding

substrate

molecule on which the enzyme acts

This page titled 2.3.6: Enzymes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.5: Enzymes** by OpenStax is licensed CC BY 4.0.

2.3.E: Metabolism (Exercises)

6.1: Energy and Metabolism

Multiple Choice

Energy is stored long-term in the bonds of _____ and used short-term to perform work from a(n) _____ molecule.

A. ATP : glucose
B. an anabolic molecule : catabolic molecule
C. glucose : ATP
D. a catabolic molecule : anabolic molecule

Answer

C

DNA replication involves unwinding two strands of parent DNA, copying each strand to synthesize complementary strands, and releasing the parent and daughter DNA. Which of the following accurately describes this process?

A. This is an anabolic process
B. This is a catabolic process
C. This is both anabolic and catabolic
D. This is a metabolic process but is neither anabolic nor catabolic

Answer

A

Free Response

Does physical exercise involve anabolic and/or catabolic processes? Give evidence for your answer.

Answer

Physical exercise involves both anabolic and catabolic processes. Body cells break down sugars to provide ATP to do the work necessary for exercise, such as muscle contractions. This is catabolism. Muscle cells also must repair muscle tissue damaged by exercise by building new muscle. This is anabolism.

Name two different cellular functions that require energy that parallel human energy-requiring functions.

Answer

Energy is required for cellular motion, through beating of cilia or flagella, as well as human motion, produced by muscle contraction. Cells also need energy to perform digestion, as humans require energy to digest food.

6.2: Potential, Kinetic, Free, and Activation Energy

Review Questions

Consider a pendulum swinging. Which type(s) of energy is/are associated with the pendulum in the following instances: i. the moment at which it completes one cycle, just before it begins to fall back towards the other end, ii. the moment that it is in the middle between the two ends, iii. just before it reaches the end of one cycle (just before instant i.).

A. i. potential and kinetic, ii. potential and kinetic, iii. kinetic
B. i. potential, ii. potential and kinetic, iii. potential and kinetic

C. i. potential, ii. kinetic, iii. potential and kinetic
D. i. potential and kinetic, ii. kinetic iii. kinetic

Answer

C

Which of the following comparisons or contrasts between endergonic and exergonic reactions is false?

A. Endergonic reactions have a positive ΔG and exergonic reactions have a negative ΔG
B. Endergonic reactions consume energy and exergonic reactions release energy
C. Both endergonic and exergonic reactions require a small amount of energy to overcome an activation barrier
D. Endergonic reactions take place slowly and exergonic reactions take place quickly

Answer

D

Which of the following is the best way to judge the relative activation energies between two given chemical reactions?

A. Compare the ΔG values between the two reactions
B. Compare their reaction rates
C. Compare their ideal environmental conditions
D. Compare the spontaneity between the two reactions

Answer

B

Free Response

Explain in your own words the difference between a spontaneous reaction and one that occurs instantaneously, and what causes this difference.

Answer

A spontaneous reaction is one that has a negative ΔG and thus releases energy. However, a spontaneous reaction need not occur quickly or suddenly like an instantaneous reaction. It may occur over long periods due to a large energy of activation, which prevents the reaction from occurring quickly.

Describe the position of the transition state on a vertical energy scale, from low to high, relative to the position of the reactants and products, for both endergonic and exergonic reactions.

Answer

The transition state is always higher in energy than the reactants and the products of a reaction (therefore, above), regardless of whether the reaction is endergonic or exergonic.

6.3: The Laws of Thermodynamics

Review Questions

Which of the following is not an example of an energy transformation?

A. Turning on a light switch
B. Solar panels at work
C. Formation of static electricity

D. None of the above

Answer

A

Label each of the following systems as high or low entropy: i. the instant that a perfume bottle is sprayed compared with 30 seconds later, ii. an old 1950s car compared with a brand new car, and iii. a living cell compared with a dead cell.

A. i. low, ii. high, iii. low
B. i. low, ii. high, iii. high
C. i. high, ii. low, iii. high
D. i. high, ii. low, iii. Low

Answer

A

Free Response

Imagine an elaborate ant farm with tunnels and passageways through the sand where ants live in a large community. Now imagine that an earthquake shook the ground and demolished the ant farm. In which of these two scenarios, before or after the earthquake, was the ant farm system in a state of higher or lower entropy?

Answer

The ant farm had lower entropy before the earthquake because it was a highly ordered system. After the earthquake, the system became much more disordered and had higher entropy.

Energy transfers take place constantly in everyday activities. Think of two scenarios: cooking on a stove and driving. Explain how the second law of thermodynamics applies to these two scenarios.

Answer

While cooking, food is heating up on the stove, but not all of the heat goes to cooking the food, some of it is lost as heat energy to the surrounding air, increasing entropy. While driving, cars burn gasoline to run the engine and move the car. This reaction is not completely efficient, as some energy during this process is lost as heat energy, which is why the hood and the components underneath it heat up while the engine is turned on. The tires also heat up because of friction with the pavement, which is additional energy loss. This energy transfer, like all others, also increases entropy.

6.4: ATP: Adenosine Triphosphate

Review Questions

The energy released by the hydrolysis of ATP is

A. primarily stored between the alpha and beta phosphates
B. equal to −57 kcal/mol
C. harnessed as heat energy by the cell to perform work
D. providing energy to coupled reactions

Answer

D

Which of the following molecules is likely to have the most potential energy?

A. sucrose
B. ATP
C. glucose
D. ADP

Answer

A

Free Response

Do you think that the E_A for ATP hydrolysis is relatively low or high? Explain your reasoning.

Answer

The activation energy for hydrolysis is very low. Not only is ATP hydrolysis an exergonic process with a large $-\Delta G$, but ATP is also a very unstable molecule that rapidly breaks down into ADP + P_i if not utilized quickly. This suggests a very low E_A since it hydrolyzes so quickly.

6.5: Enzymes

Review Questions

Which of the following is not true about enzymes:

A. They increase ΔG of reactions
B. They are usually made of amino acids
C. They lower the activation energy of chemical reactions
D. Each one is specific to the particular substrate(s) to which it binds

Answer

A

An allosteric inhibitor does which of the following?

A. Binds to an enzyme away from the active site and changes the conformation of the active site, increasing its affinity for substrate binding
B. Binds to the active site and blocks it from binding substrate
C. Binds to an enzyme away from the active site and changes the conformation of the active site, decreasing its affinity for the substrate
D. Binds directly to the active site and mimics the substrate

Answer

C

Which of the following analogies best describe the induced-fit model of enzyme-substrate binding?

A. A hug between two people
B. A key fitting into a lock
C. A square peg fitting through the square hole and a round peg fitting through the round hole of a children's toy
D. The fitting together of two jigsaw puzzle pieces.

Answer

A

Free Response

With regard to enzymes, why are vitamins necessary for good health? Give examples.

Answer

Most vitamins and minerals act as coenzymes and cofactors for enzyme action. Many enzymes require the binding of certain cofactors or coenzymes to be able to catalyze their reactions. Since enzymes catalyze many important reactions, it is critical to obtain sufficient vitamins and minerals from the diet and from supplements. Vitamin C (ascorbic acid) is a coenzyme necessary for the action of enzymes that build collagen, an important protein component of connective tissue throughout the body. Magnesium ion (Mg^{++}) is an important cofactor that is necessary for the enzyme pyruvate dehydrogenase to catalyze part of the pathway that breaks down sugar to produce energy. Vitamins cannot be produced in the human body and therefore must be obtained in the diet.

Explain in your own words how enzyme feedback inhibition benefits a cell.

Answer

Feedback inhibition allows cells to control the amounts of metabolic products produced. If there is too much of a particular product relative to what the cell's needs, feedback inhibition effectively causes the cell to decrease production of that particular product. In general, this reduces the production of superfluous products and conserves energy, maximizing energy efficiency.

This page titled 2.3.E: Metabolism (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.E: Metabolism (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

2.4: Cellular Respiration

Like a generating plant, plants and animals also must take in energy from the environment and convert it into a form that their cells can use. Energy enters an organism's body in one form and is converted into another form that can fuel the organism's life functions. In the process of photosynthesis, plants and other photosynthetic producers take in energy in the form of light (solar energy) and convert it into chemical energy, glucose, which stores this energy in its chemical bonds. Then, a series of metabolic pathways, collectively called cellular respiration, extracts the energy from the bonds in glucose and converts it into a form that all living things can use—both producers, such as plants, and consumers, such as animals.

2.4.1: Prelude to Cellular Respiration
2.4.2: Energy in Living Systems
2.4.3: Glycolysis
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
2.4.5: Oxidative Phosphorylation
2.4.6: Metabolism without Oxygen
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
2.4.E: Cellular Respiration (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.4: Cellular Respiration is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

2.4.1: Prelude to Cellular Respiration



Figure 2.4.1.1: This geothermal energy plant transforms thermal energy from deep in the ground into electrical energy, which can be easily used. (credit: modification of work by the U.S. Department of Defense)

The electrical energy plant in Figure 2.4.1.1 converts energy from one form to another form that can be more easily used. This type of generating plant starts with underground thermal energy (heat) and transforms it into electrical energy that will be transported to homes and factories. Like a generating plant, plants and animals also must take in energy from the environment and convert it into a form that their cells can use. Energy enters an organism's body in one form and is converted into another form that can fuel the organism's life functions. In the process of photosynthesis, plants and other photosynthetic producers take in energy in the form of light (solar energy) and convert it into chemical energy, glucose, which stores this energy in its chemical bonds. Then, a series of metabolic pathways, collectively called cellular respiration, extracts the energy from the bonds in glucose and converts it into a form that all living things can use—both producers, such as plants, and consumers, such as animals.

Video



This page titled 2.4.1: Prelude to Cellular Respiration is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.0: Prelude to Cellular Respiration** by OpenStax is licensed CC BY 4.0.

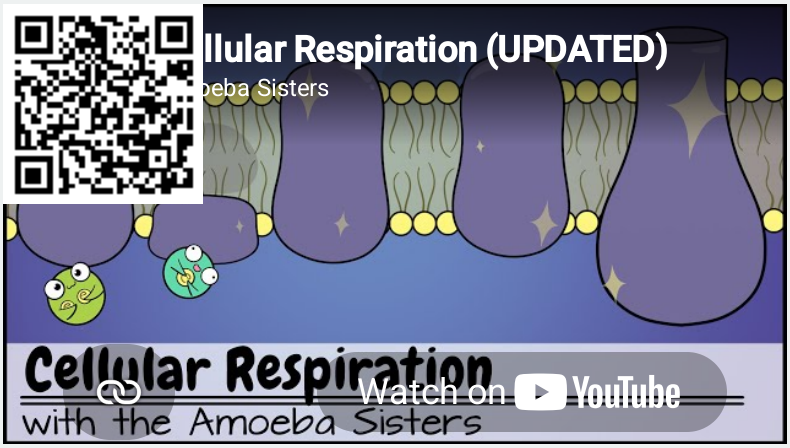
2.4.2: Energy in Living Systems

Skills to Develop

- Discuss the importance of electrons in the transfer of energy in living systems
- Explain how ATP is used by the cell as an energy source

Energy production within a cell involves many coordinated chemical pathways. Most of these pathways are combinations of oxidation and reduction reactions. Oxidation and reduction occur in tandem. An oxidation reaction strips an electron from an atom in a compound, and the addition of this electron to another compound is a reduction reaction. Because oxidation and reduction usually occur together, these pairs of reactions are called oxidation reduction reactions, or redox reactions.

Video



Electrons and Energy

The removal of an electron from a molecule, oxidizing it, results in a decrease in potential energy in the oxidized compound. The electron (sometimes as part of a hydrogen atom), does not remain unbonded, however, in the cytoplasm of a cell. Rather, the electron is shifted to a second compound, reducing the second compound. The shift of an electron from one compound to another removes some potential energy from the first compound (the oxidized compound) and increases the potential energy of the second compound (the reduced compound). The transfer of electrons between molecules is important because most of the energy stored in atoms and used to fuel cell functions is in the form of high-energy electrons. The transfer of energy in the form of electrons allows the cell to transfer and use energy in an incremental fashion—in small packages rather than in a single, destructive burst. This chapter focuses on the extraction of energy from food; you will see that as you track the path of the transfers, you are tracking the path of electrons moving through metabolic pathways.

Electron Carriers

In living systems, a small class of compounds functions as electron shuttles: They bind and carry high-energy electrons between compounds in pathways. The principal electron carriers we will consider are derived from the B vitamin group and are derivatives of nucleotides. These compounds can be easily reduced (that is, they accept electrons) or oxidized (they lose electrons). Nicotinamide adenine dinucleotide (NAD) (Figure 2.4.2.1) is derived from vitamin B_3, niacin. NAD^+ is the oxidized form of the molecule; NADH is the reduced form of the molecule after it has accepted two electrons and a proton (which together are the equivalent of a hydrogen atom with an extra electron).

NAD^+ can accept electrons from an organic molecule according to the general equation:

$$\underset{\text{reducing agent}}{\text{RH}} + \underset{\text{oxidizing agent}}{\text{NAD}^+} \rightarrow \underset{\text{reduced}}{\text{NADH}} + \underset{\text{oxidized}}{\text{R}^+}$$

When electrons are added to a compound, they are reduced. A compound that reduces another is called a reducing agent. In the above equation, RH is a reducing agent, and NAD^+ is reduced to NADH. When electrons are removed from compound, it oxidized.

A compound that oxidizes another is called an oxidizing agent. In the above equation, NAD^+ is an oxidizing agent, and RH is oxidized to R.

Similarly, flavin adenine dinucleotide (FAD^+) is derived from vitamin B_2, also called riboflavin. Its reduced form is $FADH_2$. A second variation of NAD, NADP, contains an extra phosphate group. Both NAD^+ and FAD^+ are extensively used in energy extraction from sugars, and NADP plays an important role in anabolic reactions and photosynthesis.

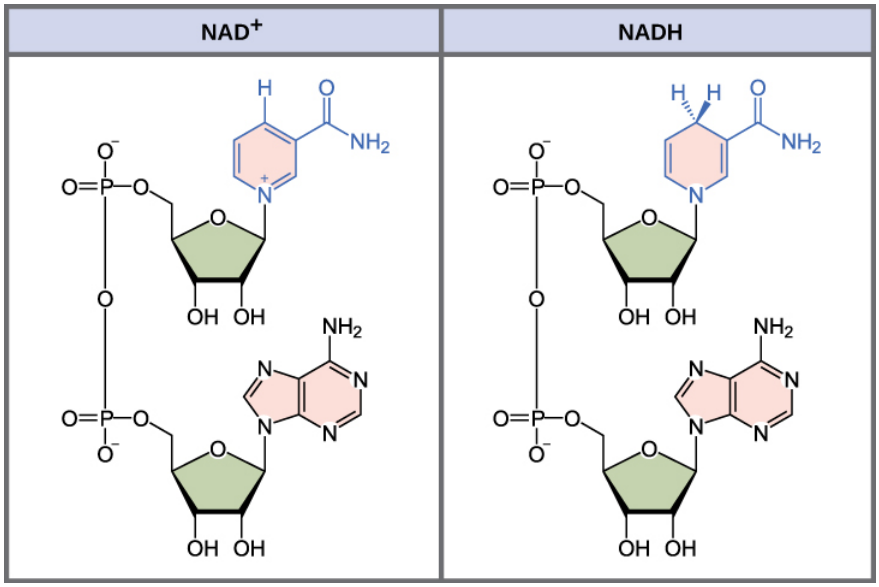


Figure 2.4.2.1: The oxidized form of the electron carrier (NAD^+) is shown on the left and the reduced form (NADH) is shown on the right. The nitrogenous base in NADH has one more hydrogen ion and two more electrons than in NAD^+.

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 to a single phosphate group (Figure 2.4.2.2). 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).

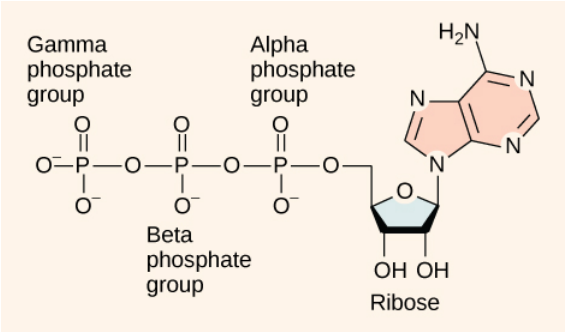


Figure 2.4.2.2: ATP (adenosine triphosphate) has three phosphate groups that can be removed by hydrolysis to form ADP (adenosine diphosphate) or AMP (adenosine monophosphate).The negative charges on the phosphate group naturally repel each other, requiring energy to bond them together and releasing energy when these bonds are broken.

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 more readily react with each other; 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 is illustrated by the following generic reaction:

$$\mathrm{A + enzyme + ATP \rightarrow [A - enzyme - {\sim}P] \rightarrow B + enzyme + ADP + phosphate\ ion}$$

When the intermediate complex breaks apart, the energy is used to modify the substrate and convert it into a product of the reaction. 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 2.4.2.3). This very direct method of phosphorylation is called substrate-level phosphorylation.

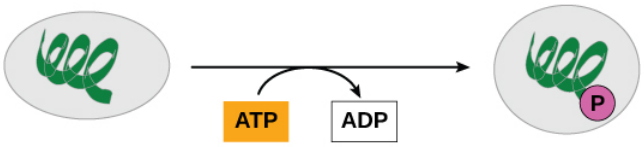


Figure 2.4.2.3: In phosphorylation reactions, the gamma phosphate of ATP is attached to a protein.

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 2.4.2.4) within a eukaryotic cell or the plasma membrane of a prokaryotic cell. Chemiosmosis, a process of ATP production in cellular metabolism, is used to generate 90 percent of the ATP made during glucose catabolism and 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 of the involvement of oxygen in the process.

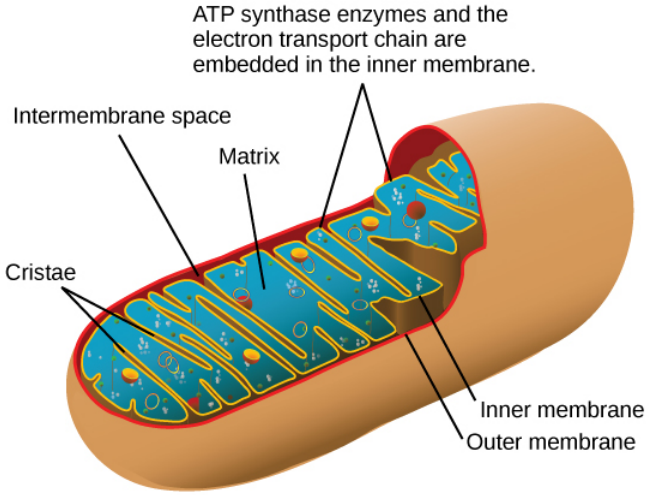


Figure 2.4.2.4: In eukaryotes, oxidative phosphorylation takes place in mitochondria. In prokaryotes, this process takes place in the plasma membrane. (Credit: modification of work by Mariana Ruiz Villareal)

Career Connections: 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

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 are 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.

chemiosmosis
process in which there is a production of adenosine triphosphate (ATP) in cellular metabolism by the involvement of a proton gradient across a membrane

dephosphorylation
removal of a phosphate group from a molecule

oxidative phosphorylation
production of ATP using the process of chemiosmosis and oxygen

phosphorylation
addition of a high-energy phosphate to a compound, usually a metabolic intermediate, a protein, or ADP

redox reaction
chemical reaction that consists of the coupling of an oxidation reaction and a reduction reaction

substrate-level phosphorylation
production of ATP from ADP using the excess energy from a chemical reaction and a phosphate group from a reactant

---

This page titled 2.4.2: Energy in Living Systems is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.1: Energy in Living Systems** by OpenStax is licensed CC BY 4.0.

2.4.3: Glycolysis

Skills to Develop

- Describe the overall result in terms of molecules produced in the breakdown of glucose by glycolysis
- Compare the output of glycolysis in terms of ATP molecules and NADH molecules produced

You have read that nearly all of the energy used by living cells comes to them in the bonds of the sugar, glucose. Glycolysis is the first step in the breakdown of glucose to extract energy for cellular metabolism. Nearly all living organisms carry out glycolysis as part of their metabolism. The process does not use oxygen and is therefore anaerobic. Glycolysis takes place in the cytoplasm of both prokaryotic and eukaryotic cells. Glucose enters heterotrophic cells in two ways. One method is through secondary active transport in which the transport takes place against the glucose concentration gradient. The other mechanism uses a group of integral proteins called GLUT proteins, also known as glucose transporter proteins. These transporters assist in the facilitated diffusion of glucose.

Glycolysis begins with the six carbon ring-shaped structure of a single glucose molecule and ends with two molecules of a three-carbon sugar called pyruvate. Glycolysis consists of two distinct phases. The first part of the glycolysis pathway traps the glucose molecule in the cell and uses energy to modify it so that the six-carbon sugar molecule can be split evenly into the two three-carbon molecules. The second part of glycolysis extracts energy from the molecules and stores it in the form of ATP and NADH, the reduced form of NAD.

First Half of Glycolysis (Energy-Requiring Steps)

Step 1. The first step in glycolysis (Figure 2.4.3.1) is catalyzed by hexokinase, an enzyme with broad specificity that catalyzes the phosphorylation of six-carbon sugars. Hexokinase phosphorylates glucose using ATP as the source of the phosphate, producing glucose-6-phosphate, a more reactive form of glucose. This reaction prevents the phosphorylated glucose molecule from continuing to interact with the GLUT proteins, and it can no longer leave the cell because the negatively charged phosphate will not allow it to cross the hydrophobic interior of the plasma membrane.

Step 2. In the second step of glycolysis, an isomerase converts glucose-6-phosphate into one of its isomers, fructose-6-phosphate. An isomerase is an enzyme that catalyzes the conversion of a molecule into one of its isomers. (This change from phosphoglucose to phosphofructose allows the eventual split of the sugar into two three-carbon molecules.).

Step 3. The third step is the phosphorylation of fructose-6-phosphate, catalyzed by the enzyme phosphofructokinase. A second ATP molecule donates a high-energy phosphate to fructose-6-phosphate, producing fructose-1,6-bisphosphate. In this pathway, phosphofructokinase is a rate-limiting enzyme. It is active when the concentration of ADP is high; it is less active when ADP levels are low and the concentration of ATP is high. Thus, if there is “sufficient” ATP in the system, the pathway slows down. This is a type of end product inhibition, since ATP is the end product of glucose catabolism.

Step 4. The newly added high-energy phosphates further destabilize fructose-1,6-bisphosphate. The fourth step in glycolysis employs an enzyme, aldolase, to cleave 1,6-bisphosphate into two three-carbon isomers: dihydroxyacetone-phosphate and glyceraldehyde-3-phosphate.

Step 5. In the fifth step, an isomerase transforms the dihydroxyacetone-phosphate into its isomer, glyceraldehyde-3-phosphate. Thus, the pathway will continue with two molecules of a single isomer. At this point in the pathway, there is a net investment of energy from two ATP molecules in the breakdown of one glucose molecule.

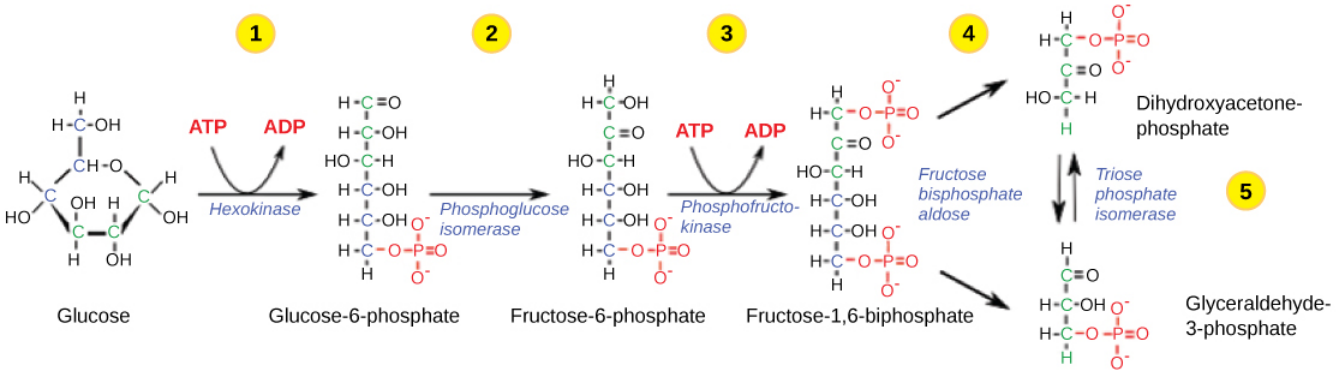


Figure 2.4.3.1: The first half of glycolysis uses two ATP molecules in the phosphorylation of glucose, which is then split into two three-carbon molecules.

Second Half of Glycolysis (Energy-Releasing Steps)

So far, glycolysis has cost the cell two ATP molecules and produced two small, three-carbon sugar molecules. Both of these molecules will proceed through the second half of the pathway, and sufficient energy will be extracted to pay back the two ATP molecules used as an initial investment and produce a profit for the cell of two additional ATP molecules and two even higher-energy NADH molecules.

Step 6. The sixth step in glycolysis (Figure 2.4.3.2) oxidizes the sugar (glyceraldehyde-3-phosphate), extracting high-energy electrons, which are picked up by the electron carrier NAD^+, producing NADH. The sugar is then phosphorylated by the addition of a second phosphate group, producing 1,3-bisphosphoglycerate. Note that the second phosphate group does not require another ATP molecule.

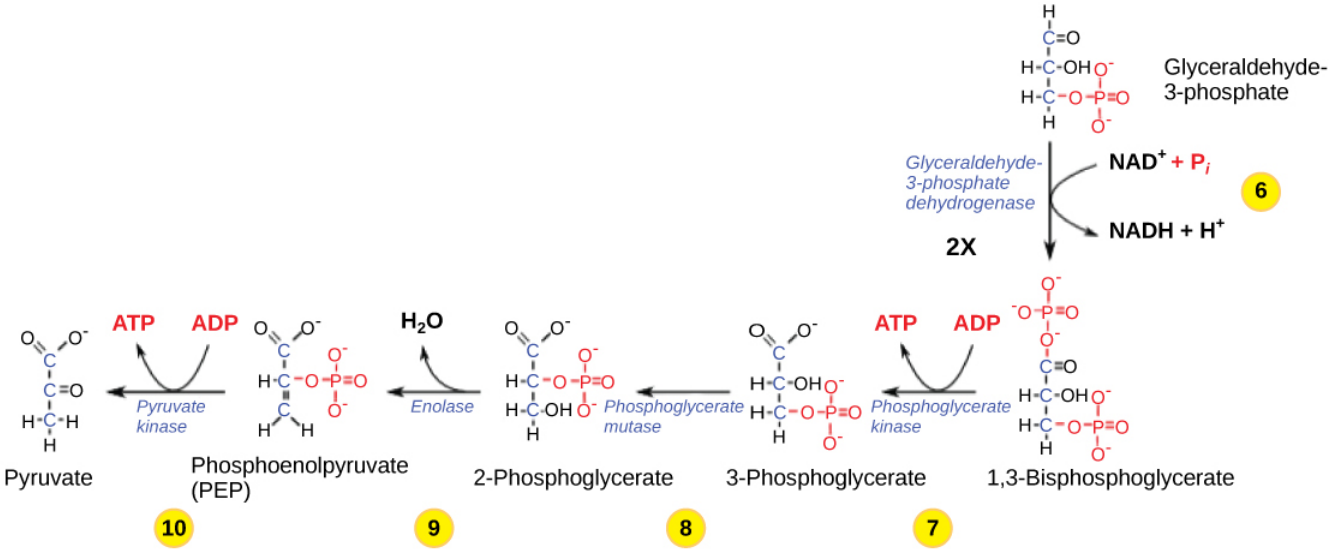


Figure 2.4.3.2: The second half of glycolysis involves phosphorylation without ATP investment (step 6) and produces two NADH and four ATP molecules per glucose.

Here again is a potential limiting factor for this pathway. The continuation of the reaction depends upon the availability of the oxidized form of the electron carrier, NAD^+. Thus, NADH must be continuously oxidized back into NAD^+ in order to keep this step going. If NAD^+ is not available, the second half of glycolysis slows down or stops. If oxygen is available in the system, the NADH will be oxidized readily, though indirectly, and the high-energy electrons from the hydrogen released in this process will be used to produce ATP. In an environment without oxygen, an alternate pathway (fermentation) can provide the oxidation of NADH to NAD^+.

Step 7. In the seventh step, catalyzed by phosphoglycerate kinase (an enzyme named for the reverse reaction), 1,3-bisphosphoglycerate donates a high-energy phosphate to ADP, forming one molecule of ATP. (This is an example of substrate-level

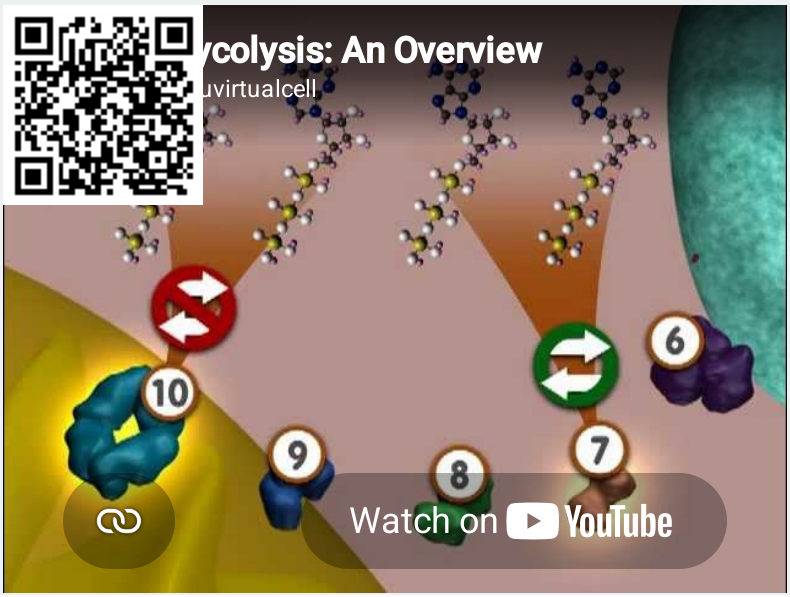
phosphorylation.) A carbonyl group on the 1,3-bisphosphoglycerate is oxidized to a carboxyl group, and 3-phosphoglycerate is formed.

Step 8. In the eighth step, the remaining phosphate group in 3-phosphoglycerate moves from the third carbon to the second carbon, producing 2-phosphoglycerate (an isomer of 3-phosphoglycerate). The enzyme catalyzing this step is a mutase (isomerase).

Step 9. Enolase catalyzes the ninth step. This enzyme causes 2-phosphoglycerate to lose water from its structure; this is a dehydration reaction, resulting in the formation of a double bond that increases the potential energy in the remaining phosphate bond and produces phosphoenolpyruvate (PEP).

Step 10. The last step in glycolysis is catalyzed by the enzyme pyruvate kinase (the enzyme in this case is named for the reverse reaction of pyruvate's conversion into PEP) and results in the production of a second ATP molecule by substrate-level phosphorylation and the compound pyruvic acid (or its salt form, pyruvate). Many enzymes in enzymatic pathways are named for the reverse reactions, since the enzyme can catalyze both forward and reverse reactions (these may have been described initially by the reverse reaction that takes place in vitro, under non-physiological conditions).

Video



Outcomes of Glycolysis

Glycolysis starts with glucose and ends with two pyruvate molecules, a total of four ATP molecules and two molecules of NADH. Two ATP molecules were used in the first half of the pathway to prepare the six-carbon ring for cleavage, so the cell has a net gain of two ATP molecules and 2 NADH molecules for its use. If the cell cannot catabolize the pyruvate molecules further, it will harvest only two ATP molecules from one molecule of glucose. Mature mammalian red blood cells are not capable of aerobic respiration—the process in which organisms convert energy in the presence of oxygen—and glycolysis is their sole source of ATP. If glycolysis is interrupted, these cells lose their ability to maintain their sodium-potassium pumps, and eventually, they die.

The last step in glycolysis will not occur if pyruvate kinase, the enzyme that catalyzes the formation of pyruvate, is not available in sufficient quantities. In this situation, the entire glycolysis pathway will proceed, but only two ATP molecules will be made in the second half. Thus, pyruvate kinase is a rate-limiting enzyme for glycolysis.

Summary

Glycolysis is the first pathway used in the breakdown of glucose to extract energy. It was probably one of the earliest metabolic pathways to evolve and is used by nearly all of the organisms on earth. Glycolysis consists of two parts: The first part prepares the six-carbon ring of glucose for cleavage into two three-carbon sugars. ATP is invested in the process during this half to energize the separation. The second half of glycolysis extracts ATP and high-energy electrons from hydrogen atoms and attaches them to NAD^+.

Two ATP molecules are invested in the first half and four ATP molecules are formed by substrate phosphorylation during the second half. This produces a net gain of two ATP and two NADH molecules for the cell.

Glossary

aerobic respiration
process in which organisms convert energy in the presence of oxygen

anaerobic
process that does not use oxygen

glycolysis
process of breaking glucose into two three-carbon molecules with the production of ATP and NADH

isomerase
enzyme that converts a molecule into its isomer

pyruvate
three-carbon sugar that can be decarboxylated and oxidized to make acetyl CoA, which enters the citric acid cycle under aerobic conditions; the end product of glycolysis

---

This page titled 2.4.3: Glycolysis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.2: Glycolysis** by OpenStax is licensed CC BY 4.0.

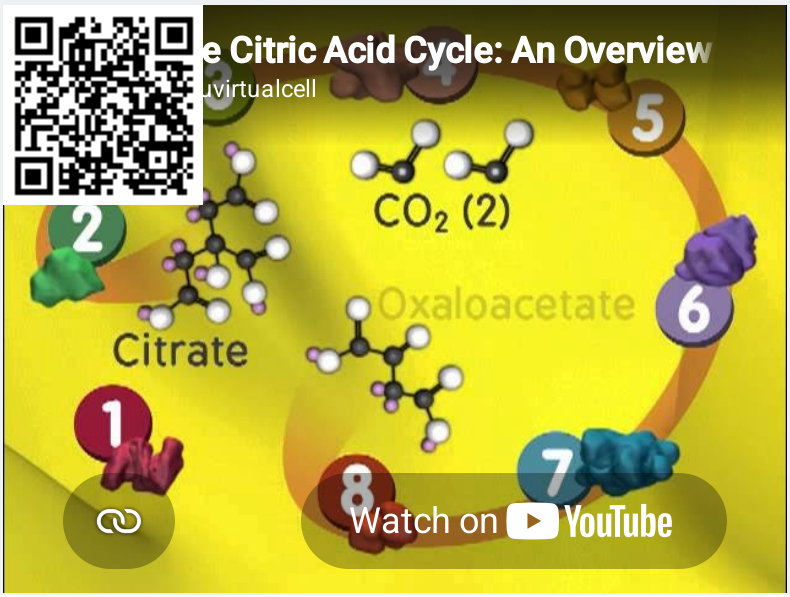
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle

Skills to Develop

- Explain how a circular pathway, such as the citric acid cycle, fundamentally differs from a linear pathway, such as glycolysis
- Describe how pyruvate, the product of glycolysis, is prepared for entry into the citric acid cycle

If oxygen is available, aerobic respiration will go forward. In eukaryotic cells, the pyruvate molecules produced at the end of glycolysis are transported into mitochondria, which are the sites of cellular respiration. There, pyruvate will be transformed into an acetyl group that will be picked up and activated by a carrier compound called coenzyme A (CoA). The resulting compound is called acetyl CoA. CoA is made from vitamin B5, pantothenic acid. Acetyl CoA can be used in a variety of ways by the cell, but its major function is to deliver the acetyl group derived from pyruvate to the next stage of the pathway in glucose catabolism.

Video



Breakdown of Pyruvate

In order for pyruvate, the product of glycolysis, to enter the next pathway, it must undergo several changes. The conversion is a three-step process (Figure 2.4.4.1).

Step 1. A carboxyl group is removed from pyruvate, releasing a molecule of carbon dioxide into the surrounding medium. The result of this step is a two-carbon hydroxyethyl group bound to the enzyme (pyruvate dehydrogenase). This is the first of the six carbons from the original glucose molecule to be removed. This step proceeds twice (remember: there are *two* pyruvate molecules produced at the end of glycolsis) for every molecule of glucose metabolized; thus, two of the six carbons will have been removed at the end of both steps.

Step 2. The hydroxyethyl group is oxidized to an acetyl group, and the electrons are picked up by NAD^+, forming NADH. The high-energy electrons from NADH will be used later to generate ATP.

Step 3. The enzyme-bound acetyl group is transferred to CoA, producing a molecule of acetyl CoA.

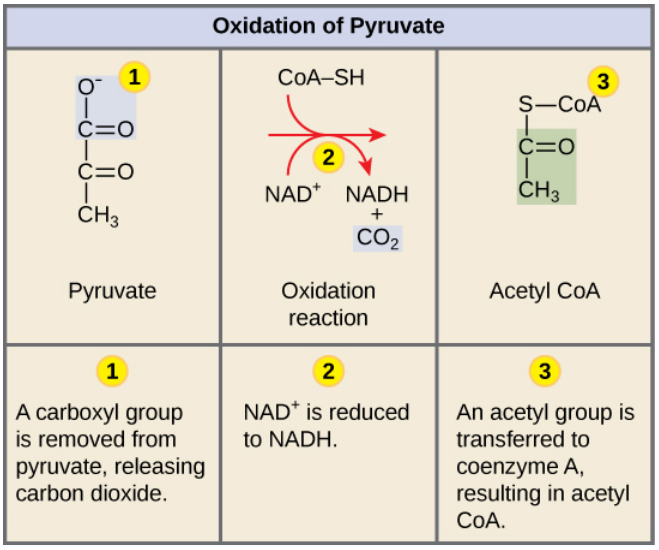


Figure 2.4.4.1: Upon entering the mitochondrial matrix, a multi-enzyme complex converts pyruvate into acetyl CoA. In the process, carbon dioxide is released and one molecule of NADH is formed.

Note that during the second stage of glucose metabolism, whenever a carbon atom is removed, it is bound to two oxygen atoms, producing carbon dioxide, one of the major end products of cellular respiration.

Acetyl CoA to CO_2

In the presence of oxygen, acetyl CoA delivers its acetyl group to a four-carbon molecule, oxaloacetate, to form citrate, a six-carbon molecule with three carboxyl groups; this pathway will harvest the remainder of the extractable energy from what began as a glucose molecule. This single pathway is called by different names: the citric acid cycle (for the first intermediate formed—citric acid, or citrate—when acetate joins to the oxaloacetate), the TCA cycle (since citric acid or citrate and isocitrate are tricarboxylic acids), and the Krebs cycle, after Hans Krebs, who first identified the steps in the pathway in the 1930s in pigeon flight muscles.

Citric Acid Cycle

Like the conversion of pyruvate to acetyl CoA, the citric acid cycle takes place in the matrix of mitochondria. Almost all of the enzymes of the citric acid cycle are soluble, with the single exception of the enzyme succinate dehydrogenase, which is embedded in the inner membrane of the mitochondrion. Unlike glycolysis, the citric acid cycle is a closed loop: The last part of the pathway regenerates the compound used in the first step. The eight steps of the cycle are a series of redox, dehydration, hydration, and decarboxylation reactions that produce two carbon dioxide molecules, one GTP/ATP, and reduced forms of NADH and $FADH_2$ (Figure 2.4.4.2). This is considered an aerobic pathway because the NADH and $FADH_2$ produced must transfer their electrons to the next pathway in the system, which will use oxygen. If this transfer does not occur, the oxidation steps of the citric acid cycle also do not occur. Note that the citric acid cycle produces very little ATP directly and does not directly consume oxygen.

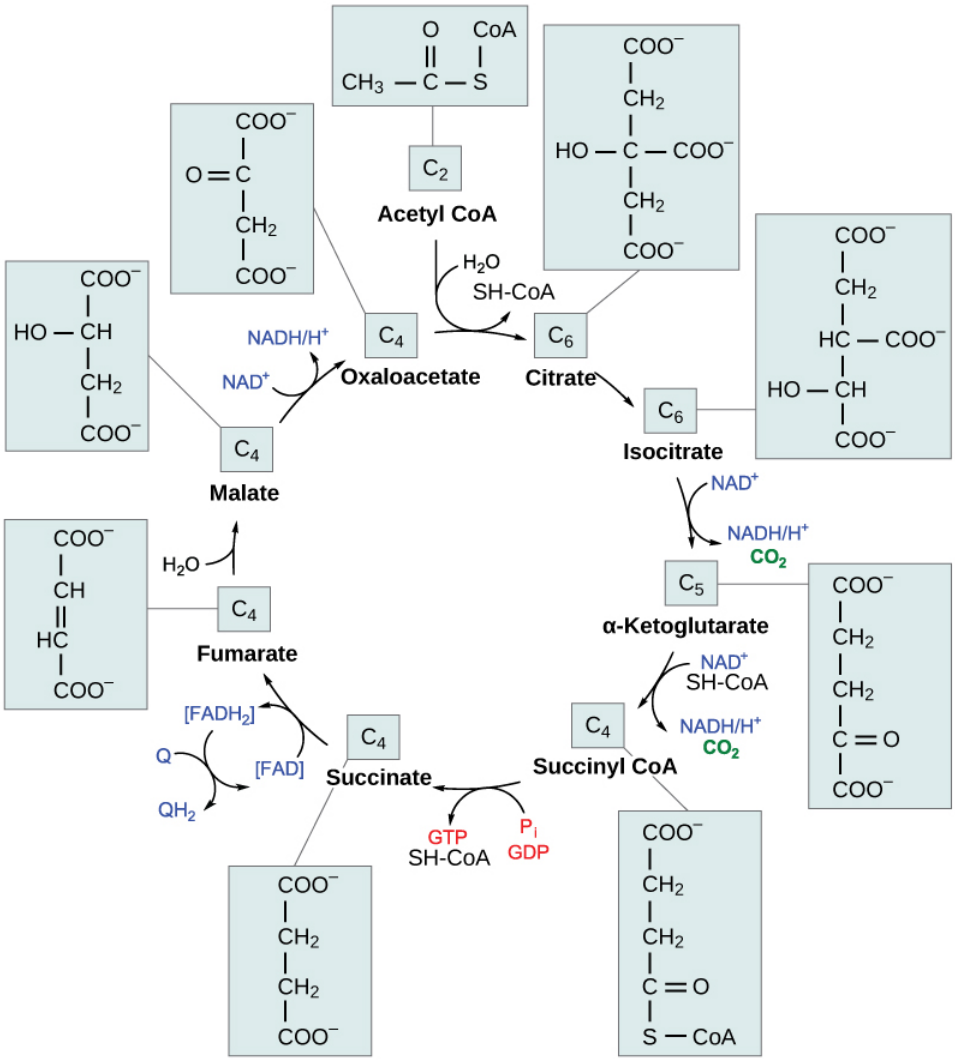


Figure 2.4.4.2: In the citric acid cycle, the acetyl group from acetyl CoA is attached to a four-carbon oxaloacetate molecule to form a six-carbon citrate molecule. Through a series of steps, citrate is oxidized, releasing two carbon dioxide molecules for each acetyl group fed into the cycle. In the process, three NAD^+ molecules are reduced to NADH, one FAD molecule is reduced to $FADH_2$, and one ATP or GTP (depending on the cell type) is produced (by substrate-level phosphorylation). Because the final product of the citric acid cycle is also the first reactant, the cycle runs continuously in the presence of sufficient reactants. (credit: modification of work by "Yikrazuul"/Wikimedia Commons)

Steps in the Citric Acid Cycle

Step 1. Prior to the start of the first step, a transitional phase occurs during which pyruvic acid is converted to acetyl CoA. Then, the first step of the cycle begins: This is a condensation step, combining the two-carbon acetyl group with a four-carbon oxaloacetate molecule to form a six-carbon molecule of citrate. CoA is bound to a sulfhydryl group (-SH) and diffuses away to eventually combine with another acetyl group. This step is irreversible because it is highly exergonic. The rate of this reaction is controlled by negative feedback and the amount of ATP available. If ATP levels increase, the rate of this reaction decreases. If ATP is in short supply, the rate increases.

Step 2. In step two, citrate loses one water molecule and gains another as citrate is converted into its isomer, isocitrate.

Step 3. In step three, isocitrate is oxidized, producing a five-carbon molecule, α-ketoglutarate, together with a molecule of CO_2 and two electrons, which reduce NAD^+ to NADH. This step is also regulated by negative feedback from ATP and NADH, and a positive effect of ADP.

Steps 3 and 4. Steps three and four are both oxidation and decarboxylation steps, which release electrons that reduce NAD^+ to NADH and release carboxyl groups that form CO_2 molecules. α-Ketoglutarate is the product of step three, and a succinyl group is

the product of step four. CoA binds the succinyl group to form succinyl CoA. The enzyme that catalyzes step four is regulated by feedback inhibition of ATP, succinyl CoA, and NADH.

Step 5. In step five, a phosphate group is substituted for coenzyme A, and a high-energy bond is formed. This energy is used in substrate-level phosphorylation (during the conversion of the succinyl group to succinate) to form either guanine triphosphate (GTP) or ATP. There are two forms of the enzyme, called isoenzymes, for this step, depending upon the type of animal tissue in which they are found. One form is found in tissues that use large amounts of ATP, such as heart and skeletal muscle. This form produces ATP. The second form of the enzyme is found in tissues that have a high number of anabolic pathways, such as liver. This form produces GTP. GTP is energetically equivalent to ATP; however, its use is more restricted. In particular, protein synthesis primarily uses GTP.

Step 6. Step six is a dehydration process that converts succinate into fumarate. Two hydrogen atoms are transferred to FAD, producing $FADH_2$. The energy contained in the electrons of these atoms is insufficient to reduce NAD^+ but adequate to reduce FAD. Unlike NADH, this carrier remains attached to the enzyme and transfers the electrons to the electron transport chain directly. This process is made possible by the localization of the enzyme catalyzing this step inside the inner membrane of the mitochondrion.

Step 7. Water is added to fumarate during step seven, and malate is produced. The last step in the citric acid cycle regenerates oxaloacetate by oxidizing malate. Another molecule of NADH is produced in the process.

Link to Learning

Click through each step of the citric acid cycle here.

Products of the Citric Acid Cycle

Two carbon atoms come into the citric acid cycle from each acetyl group, representing four out of the six carbons of one glucose molecule. Two carbon dioxide molecules are released on each turn of the cycle; however, these do not necessarily contain the most recently added carbon atoms. The two acetyl carbon atoms will eventually be released on later turns of the cycle; thus, all six carbon atoms from the original glucose molecule are eventually incorporated into carbon dioxide. Each turn of the cycle forms three NADH molecules and one $FADH_2$ molecule. These carriers will connect with the last portion of aerobic respiration to produce ATP molecules. One GTP or ATP is also made in each cycle. Several of the intermediate compounds in the citric acid cycle can be used in synthesizing non-essential amino acids; therefore, the cycle is amphibolic (both catabolic and anabolic).

Summary

In the presence of oxygen, pyruvate is transformed into an acetyl group attached to a carrier molecule of coenzyme A. The resulting acetyl CoA can enter several pathways, but most often, the acetyl group is delivered to the citric acid cycle for further catabolism. During the conversion of pyruvate into the acetyl group, a molecule of carbon dioxide and two high-energy electrons are removed. The carbon dioxide accounts for two (conversion of two pyruvate molecules) of the six carbons of the original glucose molecule. The electrons are picked up by NAD^+, and the NADH carries the electrons to a later pathway for ATP production. At this point, the glucose molecule that originally entered cellular respiration has been completely oxidized. Chemical potential energy stored within the glucose molecule has been transferred to electron carriers or has been used to synthesize a few ATPs.

The citric acid cycle is a series of redox and decarboxylation reactions that remove high-energy electrons and carbon dioxide. The electrons temporarily stored in molecules of NADH and $FADH_2$ are used to generate ATP in a subsequent pathway. One molecule of either GTP or ATP is produced by substrate-level phosphorylation on each turn of the cycle. There is no comparison of the cyclic pathway with a linear one.

Glossary

acetyl CoA
: combination of an acetyl group derived from pyruvic acid and coenzyme A, which is made from pantothenic acid (a B-group vitamin)

citric acid cycle
: (also, Krebs cycle) series of enzyme-catalyzed chemical reactions of central importance in all living cells

Krebs cycle
: (also, citric acid cycle) alternate name for the citric acid cycle, named after Hans Krebs who first identified the steps in the pathway in the 1930s in pigeon flight muscles; see citric acid cycle

TCA cycle
: (also, citric acid cycle) alternate name for the citric acid cycle, named after the group name for citric acid, tricarboxylic acid (TCA); see citric acid cycle

---

This page titled 2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.3: Oxidation of Pyruvate and the Citric Acid Cycle** by OpenStax is licensed CC BY 4.0.

2.4.5: Oxidative Phosphorylation

Skills to Develop

- Describe how electrons move through the electron transport chain and what happens to their energy levels
- Explain how a proton (H^+) gradient is established and maintained by the electron transport chain

You have just read about two pathways in glucose catabolism—glycolysis and the citric acid cycle—that generate ATP. Most of the ATP generated during the aerobic catabolism of glucose, however, is not generated directly from these pathways. Rather, it is derived from a process that begins with moving electrons through a series of electron transporters that undergo redox reactions. This causes hydrogen ions to accumulate within the matrix space. Therefore, a concentration gradient forms in which hydrogen ions diffuse out of the matrix space by passing through ATP synthase. The current of hydrogen ions powers the catalytic action of ATP synthase, which phosphorylates ADP, producing ATP.

Electron Transport Chain

The electron transport chain (Figure 2.4.5.1) is the last component of aerobic respiration and is the only part of glucose metabolism that uses atmospheric oxygen. Oxygen continuously diffuses into plants; in animals, it enters the body through the respiratory system. Electron transport is a series of redox reactions that resemble a relay race or bucket brigade in that electrons are passed rapidly from one component to the next, to the endpoint of the chain where the electrons reduce molecular oxygen, producing water. There are four complexes composed of proteins, labeled I through IV in Figure 2.4.5.1, and the aggregation of these four complexes, together with associated mobile, accessory electron carriers, is called the electron transport chain. The electron transport chain is present in multiple copies in the inner mitochondrial membrane of eukaryotes and the plasma membrane of prokaryotes.

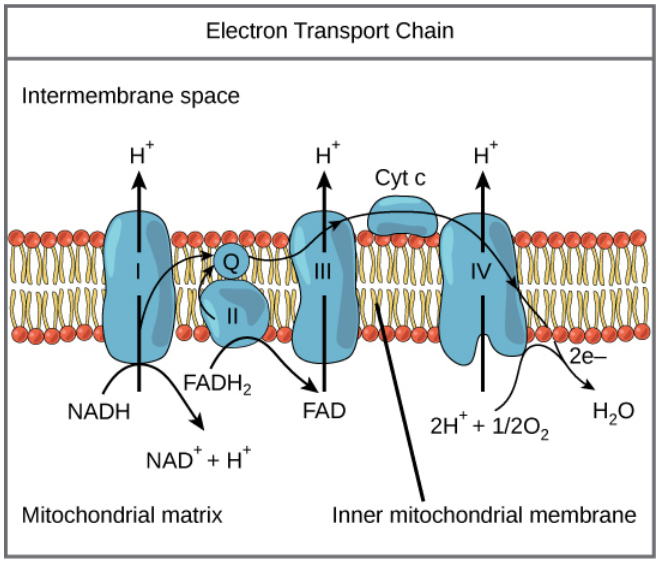


Figure 2.4.5.1: The electron transport chain is a series of electron transporters embedded in the inner mitochondrial membrane that shuttles electrons from NADH and $FADH_2$ to molecular oxygen. In the process, protons are pumped from the mitochondrial matrix to the intermembrane space, and oxygen is reduced to form water.

Complex I

To start, two electrons are carried to the first complex aboard NADH. This complex, labeled I, is composed of flavin mononucleotide (FMN) and an iron-sulfur (Fe-S)-containing protein. FMN, which is derived from vitamin B_2, also called riboflavin, is one of several prosthetic groups or co-factors in the electron transport chain. A prosthetic group is a non-protein molecule required for the activity of a protein. Prosthetic groups are organic or inorganic, non-peptide molecules bound to a protein that facilitate its function; prosthetic groups include co-enzymes, which are the prosthetic groups of enzymes. The enzyme in complex I is NADH dehydrogenase and is a very large protein, containing 45 amino acid chains. Complex I can pump four

hydrogen ions across the membrane from the matrix into the intermembrane space, and it is in this way that the hydrogen ion gradient is established and maintained between the two compartments separated by the inner mitochondrial membrane.

Q and Complex II

Complex II directly receives $FADH_2$, which does not pass through complex I. The compound connecting the first and second complexes to the third is ubiquinone (Q). The Q molecule is lipid soluble and freely moves through the hydrophobic core of the membrane. Once it is reduced, (QH_2), ubiquinone delivers its electrons to the next complex in the electron transport chain. Q receives the electrons derived from NADH from complex I and the electrons derived from $FADH_2$ from complex II, including succinate dehydrogenase. This enzyme and $FADH_2$ form a small complex that delivers electrons directly to the electron transport chain, bypassing the first complex. Since these electrons bypass and thus do not energize the proton pump in the first complex, fewer ATP molecules are made from the $FADH_2$ electrons. The number of ATP molecules ultimately obtained is directly proportional to the number of protons pumped across the inner mitochondrial membrane.

Complex III

The third complex is composed of cytochrome b, another Fe-S protein, Rieske center (2Fe-2S center), and cytochrome c proteins; this complex is also called cytochrome oxidoreductase. Cytochrome proteins have a prosthetic group of heme. The heme molecule is similar to the heme in hemoglobin, but it carries electrons, not oxygen. As a result, the iron ion at its core is reduced and oxidized as it passes the electrons, fluctuating between different oxidation states: Fe^{++} (reduced) and Fe^{+++} (oxidized). The heme molecules in the cytochromes have slightly different characteristics due to the effects of the different proteins binding them, giving slightly different characteristics to each complex. Complex III pumps protons through the membrane and passes its electrons to cytochrome c for transport to the fourth complex of proteins and enzymes (cytochrome c is the acceptor of electrons from Q; however, whereas Q carries pairs of electrons, cytochrome c can accept only one at a time).

Complex IV

The fourth complex is composed of cytochrome proteins c, a, and a_3. This complex contains two heme groups (one in each of the two cytochromes, a, and a_3) and three copper ions (a pair of Cu_A and one Cu_B in cytochrome a_3). The cytochromes hold an oxygen molecule very tightly between the iron and copper ions until the oxygen is completely reduced. The reduced oxygen then picks up two hydrogen ions from the surrounding medium to make water (H_2O). The removal of the hydrogen ions from the system contributes to the ion gradient used in the process of chemiosmosis.

Chemiosmosis

In chemiosmosis, the free energy from the series of redox reactions just described is used to pump hydrogen ions (protons) across the membrane. The uneven distribution of H^+ ions across the membrane establishes both concentration and electrical gradients (thus, an electrochemical gradient), owing to the hydrogen ions' positive charge and their aggregation on one side of the membrane.

If the membrane were open to diffusion by the hydrogen ions, the ions would tend to diffuse back across into the matrix, driven by their electrochemical gradient. Recall that many ions cannot diffuse through the nonpolar regions of phospholipid membranes without the aid of ion channels. Similarly, hydrogen ions in the matrix space can only pass through the inner mitochondrial membrane through an integral membrane protein called ATP synthase (Figure 2.4.5.2). This complex protein acts as a tiny generator, turned by the force of the hydrogen ions diffusing through it, down their electrochemical gradient. The turning of parts of this molecular machine facilitates the addition of a phosphate to ADP, forming ATP, using the potential energy of the hydrogen ion gradient.

Art Connection

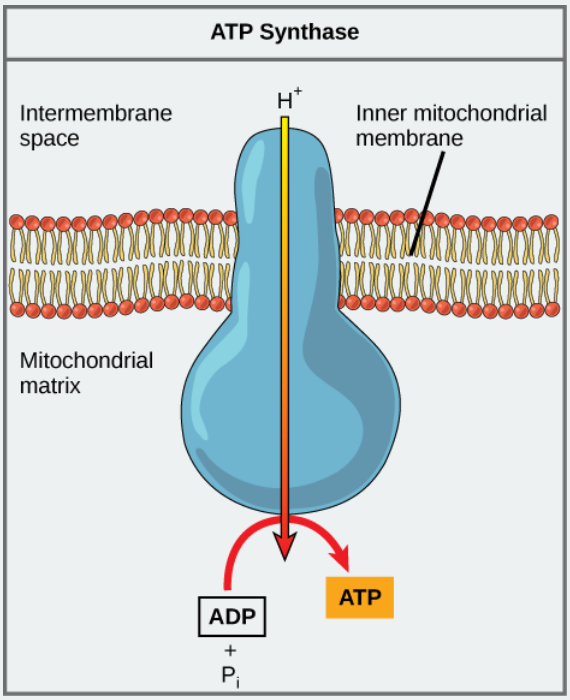
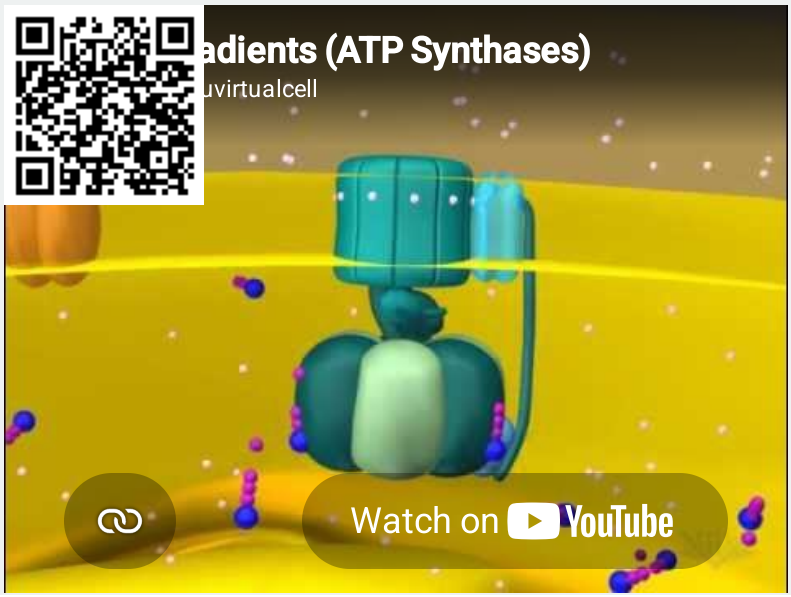


Figure 2.4.5.2: ATP synthase is a complex, molecular machine that uses a proton (H^+) gradient to form ATP from ADP and inorganic phosphate (Pi). (Credit: modification of work by Klaus Hoffmeier)

Note



Chemiosmosis (Figure 2.4.5.3) is used to generate 90 percent of the ATP made during aerobic glucose catabolism; it is also the method used in the light reactions of photosynthesis to harness the energy of sunlight in the process of photophosphorylation. Recall that the production of ATP using the process of chemiosmosis in mitochondria is called oxidative phosphorylation. The overall result of these reactions is the production of ATP from the energy of the electrons removed from hydrogen atoms. These atoms were originally part of a glucose molecule. At the end of the pathway, the electrons are used to reduce an oxygen molecule to oxygen ions. The extra electrons on the oxygen attract hydrogen ions (protons) from the surrounding medium, and water is formed.

Art Connection

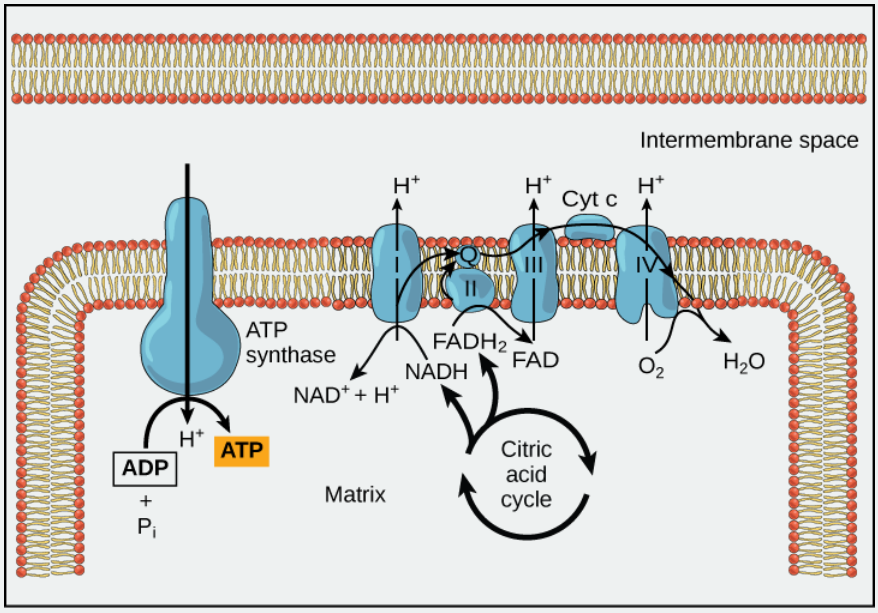


Figure 2.4.5.3: In oxidative phosphorylation, the pH gradient formed by the electron transport chain is used by ATP synthase to form ATP.

Video



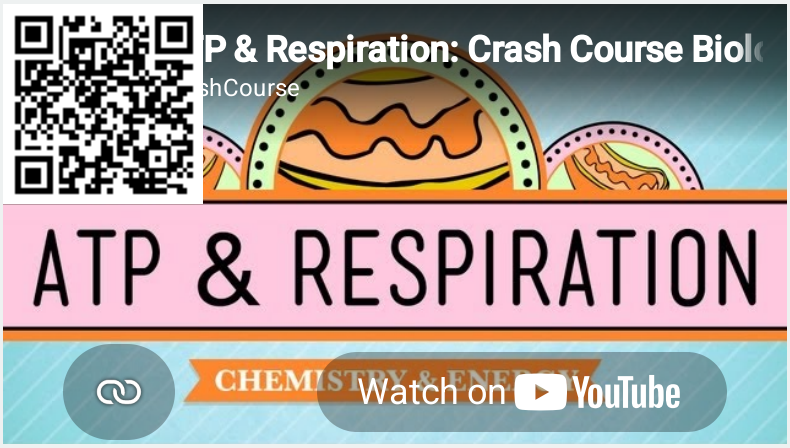
ATP Yield

The number of ATP molecules generated from the catabolism of glucose varies. For example, the number of hydrogen ions that the electron transport chain complexes can pump through the membrane varies between species. Another source of variance stems from the shuttle of electrons across the membranes of the mitochondria. (The NADH generated from glycolysis cannot easily enter mitochondria.) Thus, electrons are picked up on the inside of mitochondria by either NAD^+ or FAD^+. As you have learned earlier, these FAD^+ molecules can transport fewer ions; consequently, fewer ATP molecules are generated when FAD^+ acts as a carrier. NAD^+ is used as the electron transporter in the liver and FAD^+ acts in the brain.

Another factor that affects the yield of ATP molecules generated from glucose is the fact that intermediate compounds in these pathways are used for other purposes. Glucose catabolism connects with the pathways that build or break down all other biochemical compounds in cells, and the result is somewhat messier than the ideal situations described thus far. For example,

sugars other than glucose are fed into the glycolytic pathway for energy extraction. Moreover, the five-carbon sugars that form nucleic acids are made from intermediates in glycolysis. Certain nonessential amino acids can be made from intermediates of both glycolysis and the citric acid cycle. Lipids, such as cholesterol and triglycerides, are also made from intermediates in these pathways, and both amino acids and triglycerides are broken down for energy through these pathways. Overall, in living systems, these pathways of glucose catabolism extract about 34 percent of the energy contained in glucose.

Video



Summary

The electron transport chain is the portion of aerobic respiration that uses free oxygen as the final electron acceptor of the electrons removed from the intermediate compounds in glucose catabolism. The electron transport chain is composed of four large, multiprotein complexes embedded in the inner mitochondrial membrane and two small diffusible electron carriers shuttling electrons between them. The electrons are passed through a series of redox reactions, with a small amount of free energy used at three points to transport hydrogen ions across a membrane. This process contributes to the gradient used in chemiosmosis. The electrons passing through the electron transport chain gradually lose energy, High-energy electrons donated to the chain by either NADH or $FADH_2$ complete the chain, as low-energy electrons reduce oxygen molecules and form water. The level of free energy of the electrons drops from about 60 kcal/mol in NADH or 45 kcal/mol in $FADH_2$ to about 0 kcal/mol in water. The end products of the electron transport chain are water and ATP. A number of intermediate compounds of the citric acid cycle can be diverted into the anabolism of other biochemical molecules, such as nonessential amino acids, sugars, and lipids. These same molecules can serve as energy sources for the glucose pathways.

Art Connections

Figure 2.4.5.2: Dinitrophenol (DNP) is an uncoupler that makes the inner mitochondrial membrane leaky to protons. It was used until 1938 as a weight-loss drug. What effect would you expect DNP to have on the change in pH across the inner mitochondrial membrane? Why do you think this might be an effective weight-loss drug?

Answer

After DNP poisoning, the electron transport chain can no longer form a proton gradient, and ATP synthase can no longer make ATP. DNP is an effective diet drug because it uncouples ATP synthesis; in other words, after taking it, a person obtains less energy out of the food he or she eats. Interestingly, one of the worst side effects of this drug is hyperthermia, or overheating of the body. Since ATP cannot be formed, the energy from electron transport is lost as heat.

Figure 2.4.5.3: Cyanide inhibits cytochrome c oxidase, a component of the electron transport chain. If cyanide poisoning occurs, would you expect the pH of the intermembrane space to increase or decrease? What effect would cyanide have on ATP synthesis?

Answer

> After cyanide poisoning, the electron transport chain can no longer pump electrons into the intermembrane space. The pH of the intermembrane space would increase, the pH gradient would decrease, and ATP synthesis would stop.

Glossary

ATP synthase
(also, F1F0 ATP synthase) membrane-embedded protein complex that adds a phosphate to ADP with energy from protons diffusing through it

prosthetic group
(also, prosthetic cofactor) molecule bound to a protein that facilitates the function of the protein

ubiquinone
soluble electron transporter in the electron transport chain that connects the first or second complex to the third

---

This page titled 2.4.5: Oxidative Phosphorylation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.4: Oxidative Phosphorylation** by OpenStax is licensed CC BY 4.0.

2.4.6: Metabolism without Oxygen

Skills to Develop

- Discuss the fundamental difference between anaerobic cellular respiration and fermentation
- Describe the type of fermentation that readily occurs in animal cells and the conditions that initiate that fermentation

In aerobic respiration, the final electron acceptor is an oxygen molecule, O_2. If aerobic respiration occurs, then ATP will be produced using the energy of high-energy electrons carried by NADH or $FADH_2$ to the electron transport chain. If aerobic respiration does not occur, NADH must be reoxidized to NAD^+ for reuse as an electron carrier for the glycolytic pathway to continue. How is this done? Some living systems use an organic molecule as the final electron acceptor. Processes that use an organic molecule to regenerate NAD^+ from NADH are collectively referred to as fermentation. In contrast, some living systems use an inorganic molecule as a final electron acceptor. Both methods are called anaerobic cellular respiration in which organisms convert energy for their use in the absence of oxygen.

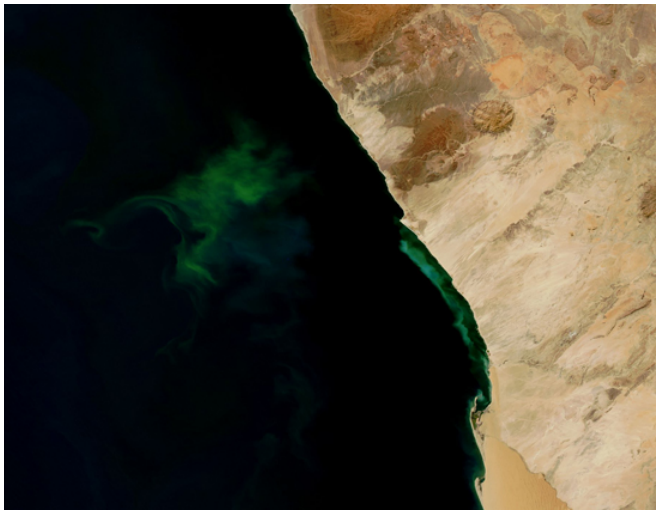
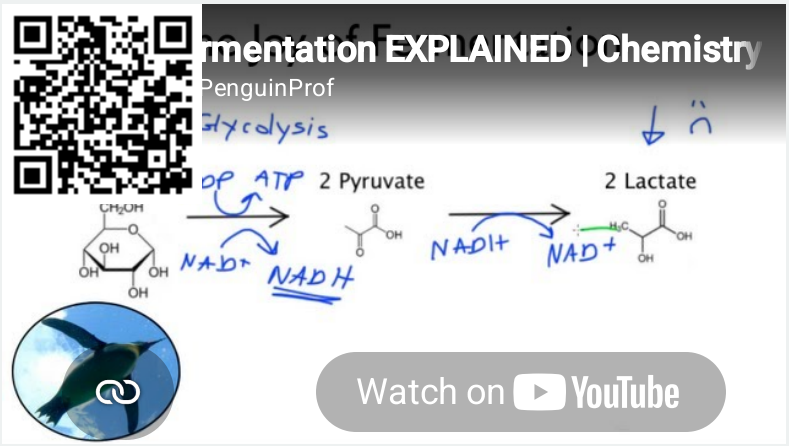


Figure 2.4.6.1: The green color seen in these coastal waters is from an eruption of hydrogen sulfide-producing bacteria. These anaerobic, sulfate-reducing bacteria release hydrogen sulfide gas as they decompose algae in the water. (credit: modification of work by NASA/Jeff Schmaltz, MODIS Land Rapid Response Team at NASA GSFC, Visible Earth Catalog of NASA images)

Anaerobic Cellular Respiration

Certain prokaryotes, including some species of bacteria and Archaea, use anaerobic respiration. For example, the group of Archaea called methanogens reduces carbon dioxide to methane to oxidize NADH. These microorganisms are found in soil and in the digestive tracts of ruminants, such as cows and sheep. Similarly, sulfate-reducing bacteria and Archaea, most of which are anaerobic (Figure 2.4.6.1), reduce sulfate to hydrogen sulfide to regenerate NAD^+ from NADH.

Video



Lactic Acid Fermentation

The fermentation method used by animals and certain bacteria, like those in yogurt, is lactic acid fermentation (Figure 2.4.6.2). This type of fermentation is used routinely in mammalian red blood cells and in skeletal muscle that has an insufficient oxygen supply to allow aerobic respiration to continue (that is, in muscles used to the point of fatigue). In muscles, lactic acid accumulation must be removed by the blood circulation and the lactate brought to the liver for further metabolism. The chemical reactions of lactic acid fermentation are the following:

$$\text{Pyruvic acid} + \text{NADH} \leftrightarrow \text{lactic acid} + \text{NAD}^+$$

The enzyme used in this reaction is lactate dehydrogenase (LDH). The reaction can proceed in either direction, but the reaction from left to right is inhibited by acidic conditions. Such lactic acid accumulation was once believed to cause muscle stiffness, fatigue, and soreness, although more recent research disputes this hypothesis. Once the lactic acid has been removed from the muscle and circulated to the liver, it can be reconverted into pyruvic acid and further catabolized for energy.

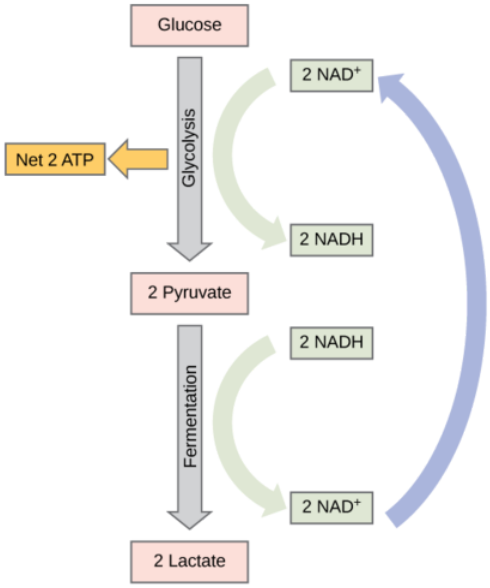


Figure 2.4.6.2: Lactic acid fermentation is common in muscle cells that have run out of oxygen.

? Exercise 2.4.6.1

Tremetol, a metabolic poison found in the white snake root plant, prevents the metabolism of lactate. When cows eat this plant, it is concentrated in the milk they produce. Humans who consume the milk become ill. Symptoms of this disease, which include vomiting, abdominal pain, and tremors, become worse after exercise. Why do you think this is the case?

Answer

The illness is caused by lactate accumulation. Lactate levels rise after exercise, making the symptoms worse. Milk sickness is rare today, but was common in the Midwestern United States in the early 1800s.

Alcohol Fermentation

Another familiar fermentation process is alcohol fermentation (Figure 2.4.6.3) that produces ethanol, an alcohol. The first chemical reaction of alcohol fermentation is the following (CO_2 does not participate in the second reaction):

$$\text{Pyruvic acid} \rightarrow CO_2 + \text{acetaldehyde} + \text{NADH} \rightarrow \text{ethanol} + NAD^+$$

The first reaction is catalyzed by pyruvate decarboxylase, a cytoplasmic enzyme, with a coenzyme of thiamine pyrophosphate (TPP, derived from vitamin B_1 and also called thiamine). A carboxyl group is removed from pyruvic acid, releasing carbon dioxide as a gas. The loss of carbon dioxide reduces the size of the molecule by one carbon, making acetaldehyde. The second reaction is catalyzed by alcohol dehydrogenase to oxidize NADH to NAD^+ and reduce acetaldehyde to ethanol. The fermentation of pyruvic acid by yeast produces the ethanol found in alcoholic beverages. Ethanol tolerance of yeast is variable, ranging from about 5 percent to 21 percent, depending on the yeast strain and environmental conditions.



Figure 2.4.6.3: Fermentation of grape juice into wine produces CO_2 as a byproduct. Fermentation tanks have valves so that the pressure inside the tanks created by the carbon dioxide produced can be released.

Other Types of Fermentation

Other fermentation methods occur in bacteria. Many prokaryotes are facultatively anaerobic. This means that they can switch between aerobic respiration and fermentation, depending on the availability of oxygen. Certain prokaryotes, like *Clostridia*, are obligate anaerobes. Obligate anaerobes live and grow in the absence of molecular oxygen. Oxygen is a poison to these microorganisms and kills them on exposure. It should be noted that all forms of fermentation, except lactic acid fermentation, produce gas. The production of particular types of gas is used as an indicator of the fermentation of specific carbohydrates, which plays a role in the laboratory identification of the bacteria. Various methods of fermentation are used by assorted organisms to ensure an adequate supply of NAD^+ for the sixth step in glycolysis. Without these pathways, that step would not occur and no ATP would be harvested from the breakdown of glucose.

Summary

If NADH cannot be oxidized through aerobic respiration, another electron acceptor is used. Most organisms will use some form of fermentation to accomplish the regeneration of NAD^+, ensuring the continuation of glycolysis. The regeneration of NAD^+ in fermentation is not accompanied by ATP production; therefore, the potential of NADH to produce ATP using an electron transport chain is not utilized.

anaerobic cellular respiration

process in which organisms convert energy for their use in the absence of oxygen

fermentation

process of regenerating NAD^+ with either an inorganic or organic compound serving as the final electron acceptor, occurs in the absence; occurs in the absence of oxygen

---

This page titled 2.4.6: Metabolism without Oxygen is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.5: Metabolism without Oxygen** by OpenStax is licensed CC BY 4.0.

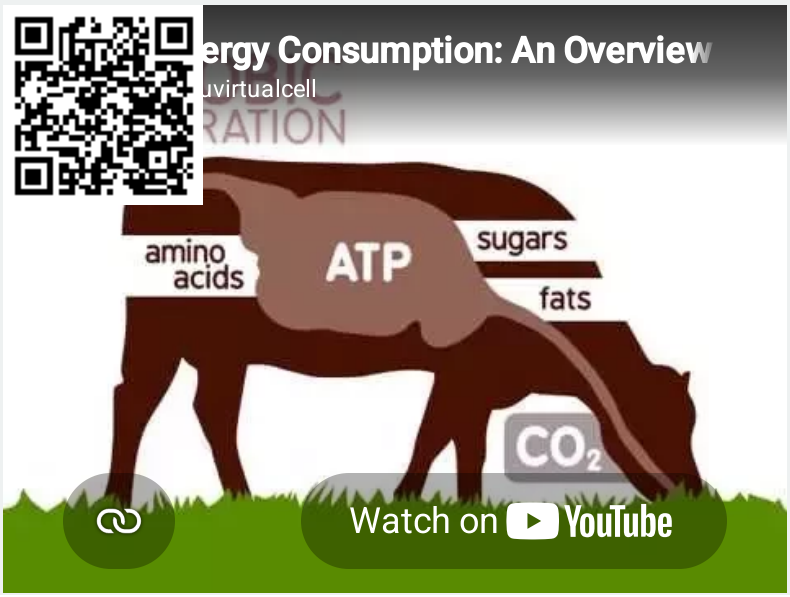
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways

Skills to Develop

- Discuss the ways in which carbohydrate metabolic pathways, glycolysis, and the citric acid cycle interrelate with protein and lipid metabolic pathways
- Explain why metabolic pathways are not considered closed systems

You have learned about the catabolism of glucose, which provides energy to living cells. But living things consume more than glucose for food. How does a turkey sandwich end up as ATP in your cells? This happens because all of the catabolic pathways for carbohydrates, proteins, and lipids eventually connect into glycolysis and the citric acid cycle pathways (see Figure 2.4.7.2). Metabolic pathways should be thought of as porous—that is, substances enter from other pathways, and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways.

Video



Connections of Other Sugars to Glucose Metabolism

Glycogen, a polymer of glucose, is an energy storage molecule in animals. When there is adequate ATP present, excess glucose is shunted into glycogen for storage. Glycogen is made and stored in both liver and muscle. The glycogen will be hydrolyzed into glucose monomers (G-1-P) if blood sugar levels drop. The presence of glycogen as a source of glucose allows ATP to be produced for a longer period of time during exercise. Glycogen is broken down into G-1-P and converted into G-6-P in both muscle and liver cells, and this product enters the glycolytic pathway.

Sucrose is a disaccharide with a molecule of glucose and a molecule of fructose bonded together with a glycosidic linkage. Fructose is one of the three dietary monosaccharides, along with glucose and galactose (which is part of the milk sugar, the disaccharide lactose), which are absorbed directly into the bloodstream during digestion. The catabolism of both fructose and galactose produces the same number of ATP molecules as glucose.

Connections of Proteins to Glucose Metabolism

Proteins are hydrolyzed by a variety of enzymes in cells. Most of the time, the amino acids are recycled into the synthesis of new proteins. If there are excess amino acids, however, or if the body is in a state of starvation, some amino acids will be shunted into the pathways of glucose catabolism (Figure 2.4.7.1). Each amino acid must have its amino group removed prior to entry into these pathways. The amino group is converted into ammonia. In mammals, the liver synthesizes urea from two ammonia molecules and a

carbon dioxide molecule. Thus, urea is the principal waste product in mammals produced from the nitrogen originating in amino acids, and it leaves the body in urine.

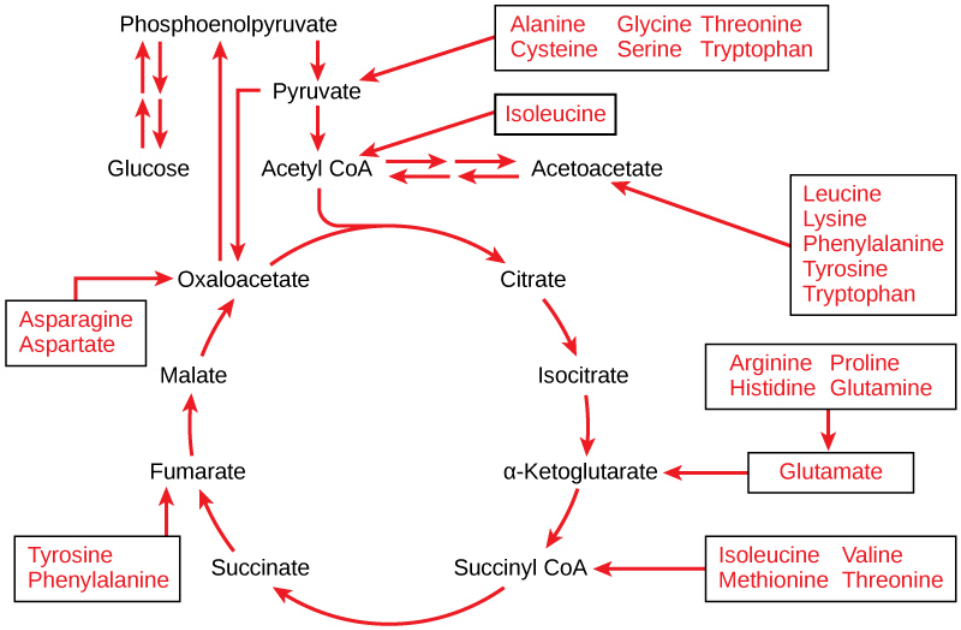


Figure 2.4.7.1: The carbon skeletons of certain amino acids (indicated in boxes) derived from proteins can feed into the citric acid cycle. (credit: modification of work by Mikael Häggström)

Connections of Lipid and Glucose Metabolisms

The lipids that are connected to the glucose pathways are cholesterol and triglycerides. Cholesterol is a lipid that contributes to cell membrane flexibility and is a precursor of steroid hormones. The synthesis of cholesterol starts with acetyl groups and proceeds in only one direction. The process cannot be reversed.

Triglycerides are a form of long-term energy storage in animals. Triglycerides are made of glycerol and three fatty acids. Animals can make most of the fatty acids they need. Triglycerides can be both made and broken down through parts of the glucose catabolism pathways. Glycerol can be phosphorylated to glycerol-3-phosphate, which continues through glycolysis. Fatty acids are catabolized in a process called beta-oxidation that takes place in the matrix of the mitochondria and converts their fatty acid chains into two carbon units of acetyl groups. The acetyl groups are picked up by CoA to form acetyl CoA that proceeds into the citric acid cycle.

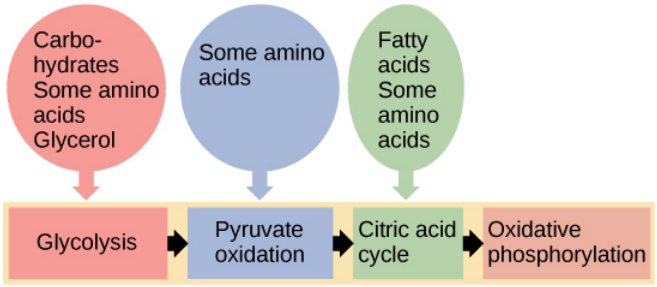


Figure 2.4.7.2: Glycogen from the liver and muscles, hydrolyzed into glucose-1-phosphate, together with fats and proteins, can feed into the catabolic pathways for carbohydrates.

Evolution Connection: Pathways of Photosynthesis and Cellular Metabolism

The processes of photosynthesis and cellular metabolism consist of several very complex pathways. It is generally thought that the first cells arose in an aqueous environment—a “soup” of nutrients—probably on the surface of some porous clays. If these cells reproduced successfully and their numbers climbed steadily, it follows that the cells would begin to deplete the nutrients from the medium in which they lived as they shifted the nutrients into the components of their own bodies. This hypothetical

situation would have resulted in natural selection favoring those organisms that could exist by using the nutrients that remained in their environment and by manipulating these nutrients into materials upon which they could survive. Selection would favor those organisms that could extract maximal value from the nutrients to which they had access.

An early form of photosynthesis developed that harnessed the sun's energy using water as a source of hydrogen atoms, but this pathway did not produce free oxygen (anoxygenic photosynthesis). (Early photosynthesis did not produce free oxygen because it did not use water as the source of hydrogen ions; instead, it used materials like hydrogen sulfide and consequently produced sulfur). It is thought that glycolysis developed at this time and could take advantage of the simple sugars being produced, but these reactions were unable to fully extract the energy stored in the carbohydrates. The development of glycolysis probably predated the evolution of photosynthesis, as it was well suited to extract energy from materials spontaneously accumulating in the "primeval soup." A later form of photosynthesis used water as a source of electrons and hydrogen, and generated free oxygen. Over time, the atmosphere became oxygenated, but not before the oxygen released oxidized metals in the ocean and created a "rust" layer in the sediment, permitting the dating of the rise of the first oxygenic photosynthesizers. Living things adapted to exploit this new atmosphere that allowed aerobic respiration as we know it to evolve. When the full process of oxygenic photosynthesis developed and the atmosphere became oxygenated, cells were finally able to use the oxygen expelled by photosynthesis to extract considerably more energy from the sugar molecules using the citric acid cycle and oxidative phosphorylation.

Summary

The breakdown and synthesis of carbohydrates, proteins, and lipids connect with the pathways of glucose catabolism. The simple sugars are galactose, fructose, glycogen, and pentose. These are catabolized during glycolysis. The amino acids from proteins connect with glucose catabolism through pyruvate, acetyl CoA, and components of the citric acid cycle. Cholesterol synthesis starts with acetyl groups, and the components of triglycerides come from glycerol-3-phosphate from glycolysis and acetyl groups produced in the mitochondria from pyruvate.

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.6: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways** by OpenStax is licensed CC BY 4.0.

2.4.E: Cellular Respiration (Exercises)

7.1: Energy in Living Systems

Energy production within a cell involves many coordinated chemical pathways. Most of these pathways are combinations of oxidation and reduction reactions. Oxidation and reduction occur in tandem. An oxidation reaction strips an electron from an atom in a compound, and the addition of this electron to another compound is a reduction reaction. Because oxidation and reduction usually occur together, these pairs of reactions are called oxidation reduction reactions, or redox reactions.

Review Questions

The energy currency used by cells is _____.

A. ATP
B. ADP
C. AMP
D. adenosine

Answer

A

A reducing chemical reaction _____.

A. reduces the compound to a simpler form
B. adds an electron to the substrate
C. removes a hydrogen atom from the substrate
D. is a catabolic reaction

Answer

B

Free Response

Why is it beneficial for cells to use ATP rather than energy directly from the bonds of carbohydrates? What are the greatest drawbacks to harnessing energy directly from the bonds of several different compounds?

Answer

ATP provides the cell with a way to handle energy in an efficient manner. The molecule can be charged, stored, and used as needed. Moreover, the energy from hydrolyzing ATP is delivered as a consistent amount. Harvesting energy from the bonds of several different compounds would result in energy deliveries of different quantities.

7.2: Glycolysis

Glycolysis is the first step in the breakdown of glucose to extract energy for cellular metabolism. Nearly all living organisms carry out glycolysis as part of their metabolism. The process does not use oxygen and is therefore anaerobic. Glycolysis takes place in the cytoplasm of both prokaryotic and eukaryotic cells.

Review Questions

During the second half of glycolysis, what occurs?

A. ATP is used up.
B. Fructose is split in two.
C. ATP is made.

D. Glucose becomes fructose.

Answer

C

Free Response

Nearly all organisms on earth carry out some form of glycolysis. How does that fact support or not support the assertion that glycolysis is one of the oldest metabolic pathways?

Answer

If glycolysis evolved relatively late, it likely would not be as universal in organisms as it is. It probably evolved in very primitive organisms and persisted, with the addition of other pathways of carbohydrate metabolism that evolved later.

Red blood cells do not perform aerobic respiration, but they do perform glycolysis. Why do all cells need an energy source, and what would happen if glycolysis were blocked in a red blood cell?

Answer

All cells must consume energy to carry out basic functions, such as pumping ions across membranes. A red blood cell would lose its membrane potential if glycolysis were blocked, and it would eventually die.

7.3: Oxidation of Pyruvate and the Citric Acid Cycle

If oxygen is available, aerobic respiration will go forward. In eukaryotic cells, the pyruvate molecules produced at the end of glycolysis are transported into mitochondria, which are the sites of cellular respiration. There, pyruvate will be transformed into an acetyl group that will be picked up and activated by a carrier compound called coenzyme A (CoA). The resulting compound is called acetyl CoA. CoA is made from vitamin B5, pantothenic acid.

Review Questions

What is removed from pyruvate during its conversion into an acetyl group?

A. oxygen
B. ATP
C. B vitamin
D. carbon dioxide

Answer

D

What do the electrons added to NAD^+ do?

A. They become part of a fermentation pathway.
B. They go to another pathway for ATP production.
C. They energize the entry of the acetyl group into the citric acid cycle.
D. They are converted to NADP.

Answer

B

GTP or ATP is produced during the conversion of _____.

A. isocitrate into α-ketoglutarate
B. succinyl CoA into succinate
C. fumarate into malate
D. malate into oxaloacetate

Answer

B

How many NADH molecules are produced on each turn of the citric acid cycle?

A. one
B. two
C. three
D. four

Answer

C

Free Response

What is the primary difference between a circular pathway and a linear pathway?

Answer

In a circular pathway, the final product of the reaction is also the initial reactant. The pathway is self-perpetuating, as long as any of the intermediates of the pathway are supplied. Circular pathways are able to accommodate multiple entry and exit points, thus being particularly well suited for amphibolic pathways. In a linear pathway, one trip through the pathway completes the pathway, and a second trip would be an independent event.

7.4: Oxidative Phosphorylation

You have just read about two pathways in glucose catabolism—glycolysis and the citric acid cycle—that generate ATP. Most of the ATP generated during the aerobic catabolism of glucose, however, is not generated directly from these pathways. Rather, it is derived from a process that begins with moving electrons through a series of electron transporters that undergo redox reactions. This causes hydrogen ions to accumulate within the matrix space.

Review Questions

What compound receives electrons from NADH?

A. FMN
B. ubiquinone
C. cytochrome c_1
D. oxygen

Answer

A

Chemiosmosis involves _____.

A. the movement of electrons across the cell membrane
B. the movement of hydrogen atoms across a mitochondrial membrane
C. the movement of hydrogen ions across a mitochondrial membrane
D. the movement of glucose through the cell membrane

Answer

C

Free Response

How do the roles of ubiquinone and cytochrome c differ from the other components of the electron transport chain?

Answer

Q and cytochrome c are transport molecules. Their function does not result directly in ATP synthesis in that they are not pumps. Moreover, Q is the only component of the electron transport chain that is not a protein. Ubiquinone and cytochrome c are small, mobile, electron carriers, whereas the other components of the electron transport chain are large complexes anchored in the inner mitochondrial membrane.

What accounts for the different number of ATP molecules that are formed through cellular respiration?

Answer

Few tissues except muscle produce the maximum possible amount of ATP from nutrients. The intermediates are used to produce needed amino acids, fatty acids, cholesterol, and sugars for nucleic acids. When NADH is transported from the cytoplasm to the mitochondria, an active transport mechanism is used, which decreases the amount of ATP that can be made. The electron transport chain differs in composition between species, so different organisms will make different amounts of ATP using their electron transport chains.

7.5: Metabolism without Oxygen

In aerobic respiration, the final electron acceptor is an oxygen molecule, O2. If aerobic respiration occurs, then ATP will be produced using the energy of high-energy electrons carried by NADH or FADH2 to the electron transport chain. If aerobic respiration does not occur, NADH must be reoxidized to NAD+ for reuse as an electron carrier for the glycolytic pathway to continue.

Review Questions

Which of the following fermentation methods can occur in animal skeletal muscles?

A. lactic acid fermentation
B. alcohol fermentation
C. mixed acid fermentation
D. propionic fermentation

Answer

A

Free Response

What is the primary difference between fermentation and anaerobic respiration?

Answer

Fermentation uses glycolysis only. Anaerobic respiration uses all three parts of cellular respiration, including the parts in the mitochondria like the citric acid cycle and electron transport; it also uses a different final electron acceptor instead of oxygen gas.

7.6: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways

All of the catabolic pathways for carbohydrates, proteins, and lipids eventually connect into glycolysis and the citric acid cycle pathways. Metabolic pathways should be thought of as porous—that is, substances enter from other pathways, and intermediates leave for other pathways. These pathways are not closed systems. Many of the substrates, intermediates, and products in a particular pathway are reactants in other pathways.

Review Questions

A major connection for sugars in glycolysis is _____.

A. glucose-6-phosphate
B. fructose-1,6-bisphosphate
C. dihydroxyacetone phosphate
D. phosphoenolpyruvate

Answer

A

Beta-oxidation is _____.

A. the breakdown of sugars
B. the assembly of sugars
C. the breakdown of fatty acids
D. the removal of amino groups from amino acids

Answer

C

Free Response

Would you describe metabolic pathways as inherently wasteful or inherently economical, and why?

Answer

They are very economical. The substrates, intermediates, and products move between pathways and do so in response to finely tuned feedback inhibition loops that keep metabolism balanced overall. Intermediates in one pathway may occur in another, and they can move from one pathway to another fluidly in response to the needs of the cell.

7.7: Regulation of Cellular Respiration

Cellular respiration must be regulated in order to provide balanced amounts of energy in the form of ATP. The cell also must generate a number of intermediate compounds that are used in the anabolism and catabolism of macromolecules. Without controls, metabolic reactions would quickly come to a stand still as the forward and backward reactions reached a state of equilibrium. Resources would be used inappropriately.

Review Questions

The effect of high levels of ADP is to _____.

A. increase the activity of the enzyme
B. decrease the activity of the enzyme
C. have no effect on the activity of the enzyme
D. slow down the pathway

Answer

A

The control of which enzyme exerts the most control on glycolysis?

A. hexokinase
B. phosphofructokinase
C. glucose-6-phosphatase
D. aldolase

Answer

B

Free Response

How does citrate from the citric acid cycle affect glycolysis?

Answer

Citrate can inhibit phosphofructokinase by feedback regulation.

Why might negative feedback mechanisms be more common than positive feedback mechanisms in living cells?

Answer

Negative feedback mechanisms actually control a process; it can turn it off, whereas positive feedback accelerates the process, allowing the cell no control over it. Negative feedback naturally maintains homeostasis, whereas positive feedback drives the system away from equilibrium.

This page titled 2.4.E: Cellular Respiration (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **7.E: Cellular Respiration (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

2.5: Photosynthesis

The processes in all organisms—from bacteria to humans—require energy. To get this energy, many organisms access stored energy by eating, that is, by ingesting other organisms. But where does the stored energy in food originate? All of this energy can be traced back to photosynthesis.

2.5.1: Prelude to Photosynthesis
2.5.2: Overview of Photosynthesis
2.5.3: The Light-Dependent Reactions of Photosynthesis
2.5.4: Using Light Energy to Make Organic Molecules
2.5.E: Photosynthesis (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.5: Photosynthesis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

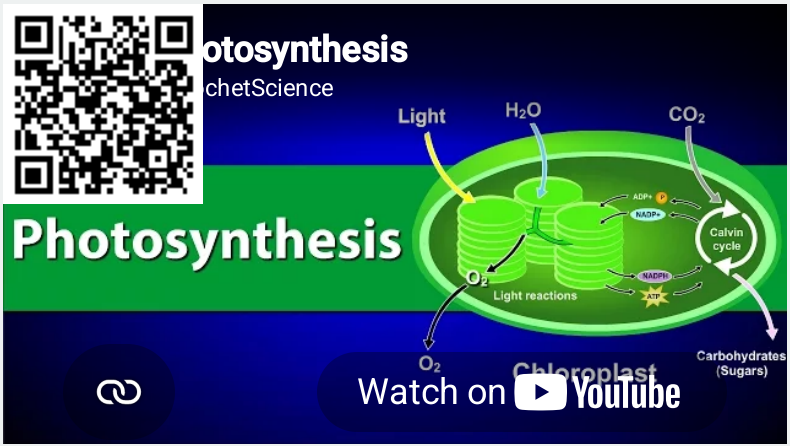
2.5.1: Prelude to Photosynthesis

> **Note**
>
> The ideal gas law is easy to remember and apply in solving problems, as long as you get the **proper values a**

Figure 2.5.1.1: This world map shows Earth's distribution of photosynthesis as seen via chlorophyll a concentrations. On land, this is evident via terrestrial plants, and in oceanic zones, via phytoplankton. (credit: modification of work by SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE)

The processes in all organisms—from bacteria to humans—require energy. To get this energy, many organisms access stored energy by eating, that is, by ingesting other organisms. But where does the stored energy in food originate? All of this energy can be traced back to photosynthesis.

> **Video**



This page titled 2.5.1: Prelude to Photosynthesis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **8.0: Prelude to Photosynthesis** by OpenStax is licensed CC BY 4.0.

2.5.2: Overview of Photosynthesis

Skills to Develop

- Explain the relevance of photosynthesis to other living things
- Describe the main structures involved in photosynthesis
- Identify the substrates and products of photosynthesis
- Summarize the process of photosynthesis

Photosynthesis is essential to all life on earth; both plants and animals depend on it. It is the only biological process that can capture energy that originates in outer space (sunlight) and convert it into chemical compounds (carbohydrates) that every organism uses to power its metabolism. In brief, the energy of sunlight is captured and used to energize electrons, which are 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 sunlight energy captured and stored by photosynthesis almost 200 million years ago.

Plants, algae, and a group of bacteria called cyanobacteria are the only organisms capable of performing photosynthesis (Figure 2.5.2.1). Because they use light to manufacture their own 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; hence, they are referred to as chemoautotrophs.

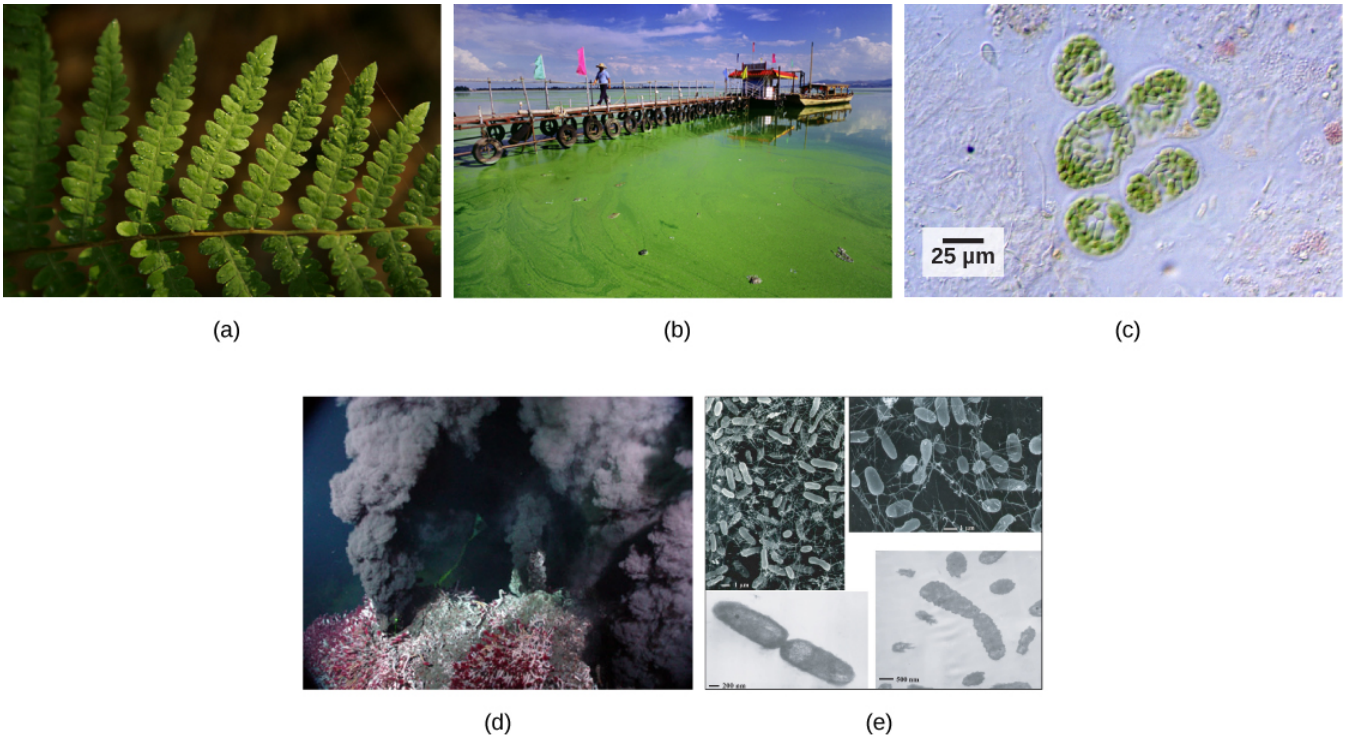


Figure 2.5.2.1: Photoautotrophs including (a) plants, (b) algae, and (c) cyanobacteria synthesize their organic compounds via photosynthesis using sunlight as an energy source. Cyanobacteria and planktonic algae can grow over enormous areas in water, at times completely covering the surface. In a (d) deep sea vent, chemoautotrophs, such as these (e) thermophilic bacteria, capture energy from inorganic compounds to produce organic compounds. The ecosystem surrounding the vents has a diverse array of animals, such as tubeworms, crustaceans, and octopuses that derive energy from the bacteria. (credit a: modification of work by Steve Hillebrand, U.S. Fish and Wildlife Service; credit b: modification of work by "eutrophication&hypoxia"/Flickr; credit c: modification of work by NASA; credit d: University of Washington, NOAA; credit e: modification of work by Mark Amend, West Coast and Polar Regions Undersea Research Center, UAF, NOAA)

The importance of photosynthesis is not just that it can capture sunlight's energy. A lizard sunning itself on a cold day can use the sun's energy to warm up. Photosynthesis is vital because it evolved as a way to store the energy in solar radiation (the "photo-" part) as high-energy electrons 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 2.5.2.2), the wolf is at the end of an energy path that went from nuclear reactions on the surface of the sun, to light, to photosynthesis, to vegetation, to deer, and finally to wolf.



Figure 2.5.2.2: 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. (credit: modification of work by Steve VanRiper, U.S. Fish and Wildlife Service)

Main Structures and Summary of Photosynthesis

Photosynthesis is a multi-step process that requires sunlight, carbon dioxide (which is low in energy), and water as substrates (Figure 2.5.2.3). After the process is complete, it releases oxygen and produces glyceraldehyde-3-phosphate (GA3P), simple carbohydrate molecules (which are high in energy) that can subsequently 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.

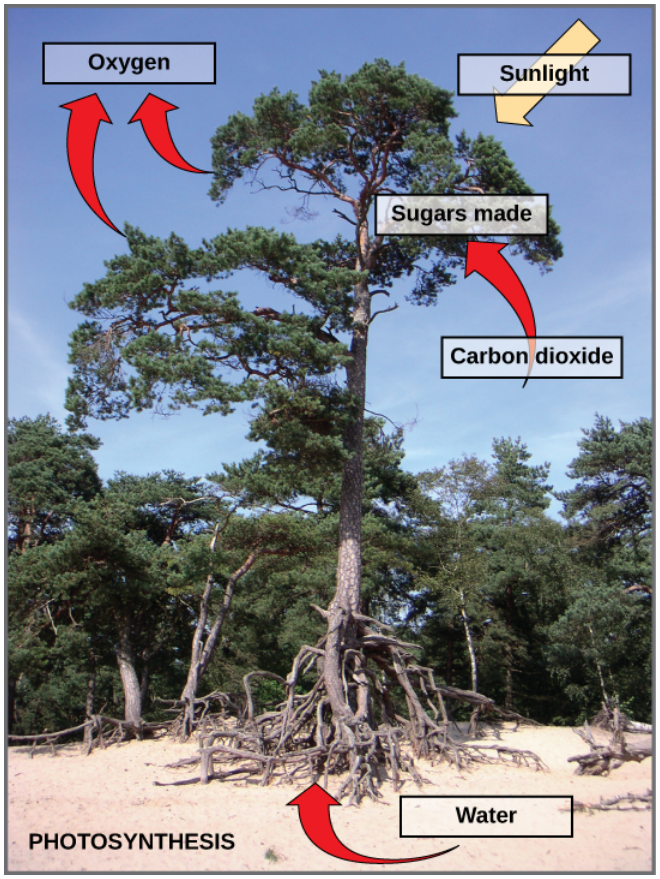


Figure 2.5.2.3: Photosynthesis uses solar energy, carbon dioxide, and water to produce energy-storing carbohydrates. Oxygen is generated as a waste product of photosynthesis.

The following is the chemical equation for photosynthesis (Figure 2.5.2.4):

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

Figure 2.5.2.4: 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 GA3Ps.

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.

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. 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. For plants, chloroplast-containing cells exist in the mesophyll. Chloroplasts have a double membrane envelope (composed of an outer membrane and an inner membrane). 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. As shown in Figure 2.5.2.5, 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).

Art Connection

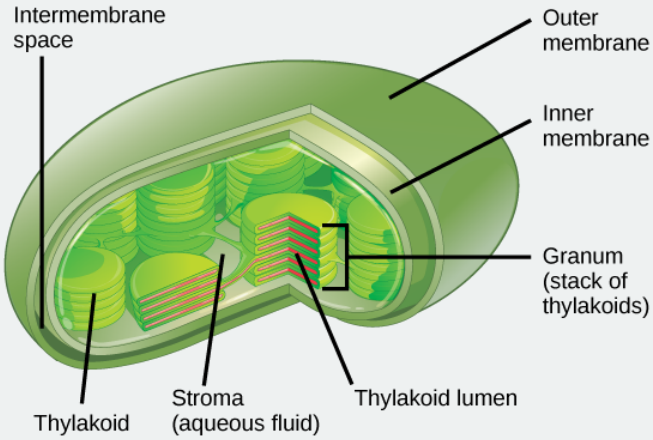


Figure 2.5.2.5: Photosynthesis takes place in chloroplasts, which have an outer membrane and an inner membrane. Stacks of thylakoids called grana form a third membrane layer.

On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?

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 drive 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, 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. Figure2.5.2.6 illustrates the components inside the chloroplast where the light-dependent and light-independent reactions take place.

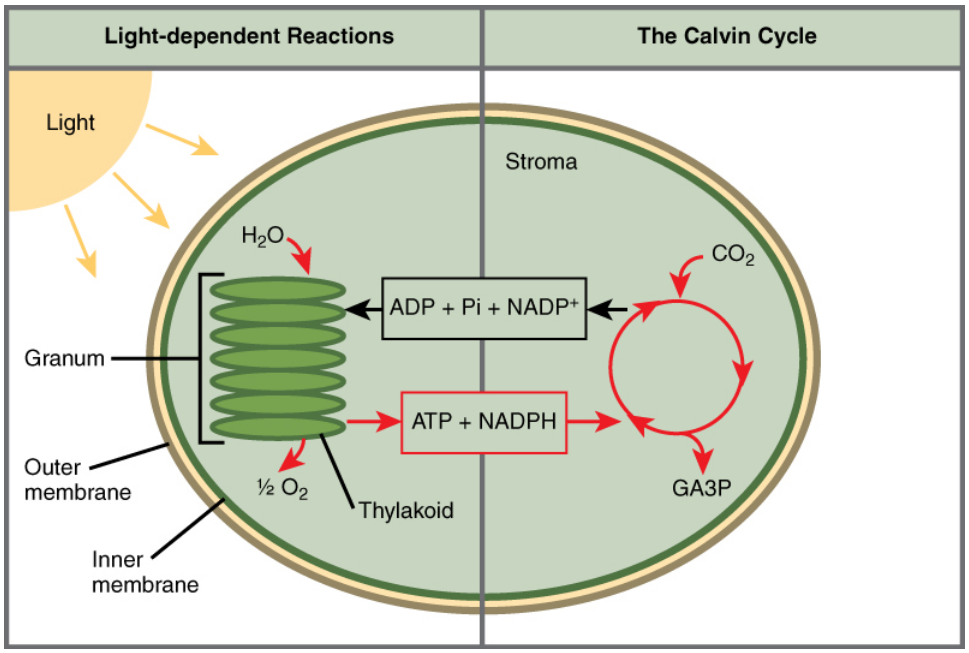


Figure 2.5.2.6: Photosynthesis takes place in two stages: light dependent reactions and the Calvin cycle. Light-dependent reactions, which take place in the thylakoid membrane, use light energy to make ATP and NADPH. The Calvin cycle, which takes place in the stroma, uses energy derived from these compounds to make GA3P from CO_2.

Everyday Connection: Photosynthesis at the Grocery Store



Figure 2.5.2.7: Foods that humans consume originate from photosynthesis. (credit: Associação Brasileira de Supermercados)

Major grocery stores in the United States are organized into departments, such as dairy, meats, produce, bread, cereals, and so forth. Each aisle (Figure 2.5.2.7) contains hundreds, if not thousands, of different products for customers to buy and consume.

Although there is a large variety, each item links back to photosynthesis. Meats and dairy link, because the animals were fed plant-based foods. The breads, cereals, and pastas come largely from starchy grains, which are the seeds of photosynthesis-dependent plants. What about desserts and drinks? All of these products contain sugar—sucrose is a plant product, a disaccharide, a carbohydrate molecule, which is built directly from photosynthesis. Moreover, many items are less obviously derived from plants: For instance, paper goods are generally plant products, and many plastics (abundant as products and packaging) are derived from algae. Virtually every spice and flavoring in the spice aisle was produced by a plant as a leaf, root, bark, flower, fruit, or stem. Ultimately, photosynthesis connects to every meal and every food a person consumes.

Video



Summary

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. 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.

Art Connections

Figure 2.5.2.5: On a hot, dry day, plants close their stomata to conserve water. What impact will this have on photosynthesis?

Answer

Levels of carbon dioxide (a necessary photosynthetic substrate) will immediately fall. As a result, the rate of photosynthesis will be inhibited.

Glossary

chemoautotroph
organism that can build organic molecules using energy derived from inorganic chemicals instead of sunlight

chloroplast
organelle in which photosynthesis takes place

granum
stack of thylakoids located inside a chloroplast

heterotroph
organism that consumes organic substances or other organisms for food

light-dependent reaction
first stage of photosynthesis where certain wavelengths of the visible light are absorbed to form two energy-carrying molecules (ATP and NADPH)

light-independent reaction

second stage of photosynthesis, though which carbon dioxide is used to build carbohydrate molecules using energy from ATP and NADPH

mesophyll

middle layer of chlorophyll-rich cells in a leaf

photoautotroph

organism capable of producing its own organic compounds from sunlight

pigment

molecule that is capable of absorbing certain wavelengths of light and reflecting others (which accounts for its color)

stoma

opening that regulates gas exchange and water evaporation between leaves and the environment, typically situated on the underside of leaves

stroma

fluid-filled space surrounding the grana inside a chloroplast where the light-independent reactions of photosynthesis take place

thylakoid

disc-shaped, membrane-bound structure inside a chloroplast where the light-dependent reactions of photosynthesis take place; stacks of thylakoids are called grana

thylakoid lumen

aqueous space bound by a thylakoid membrane where protons accumulate during light-driven electron transport

---

This page titled 2.5.2: Overview of Photosynthesis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **8.1: Overview of Photosynthesis** by OpenStax is licensed CC BY 4.0.

2.5.3: The Light-Dependent Reactions of Photosynthesis

Skills to Develop

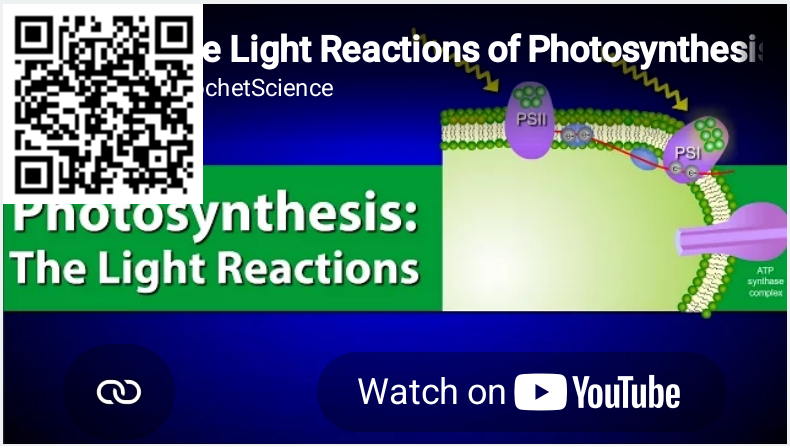
- Explain how plants absorb energy from sunlight
- Describe short and long wavelengths of light
- Describe how and where photosynthesis takes place within a plant

How can light be used to make food? When a person turns on a lamp, electrical energy becomes light energy. Like all other forms of kinetic energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is converted into chemical energy, which photoautotrophs use to build carbohydrate molecules (Figure 2.5.3.1). However, autotrophs only use a few specific components of sunlight.



Figure 2.5.3.1: Photoautotrophs can capture light energy from the sun, converting it into the chemical energy used to build food molecules. (credit: Gerry Atwell)

Video



What Is Light Energy?

The sun emits an enormous amount of electromagnetic radiation (solar energy). Humans can see only a fraction of this energy, which portion is therefore referred to as “visible light.” The manner in which solar energy travels is described as waves. Scientists can determine the amount of energy of a wave by measuring its wavelength, the distance between consecutive points of a wave. A single wave is measured from two consecutive points, such as from crest to crest or from trough to trough (Figure 2.5.3.2).

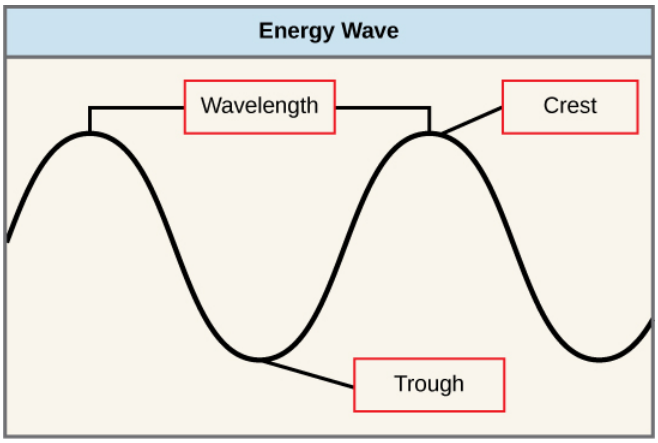


Figure 2.5.3.2: The wavelength of a single wave is the distance between two consecutive points of similar position (two crests or two troughs) along the wave.

Visible light constitutes only one of many types of electromagnetic radiation emitted from the sun and other stars. Scientists differentiate the various types of radiant energy from the sun within the electromagnetic spectrum. The electromagnetic spectrum is the range of all possible frequencies of radiation (Figure 2.5.3.3). The difference between wavelengths relates to the amount of energy carried by them.

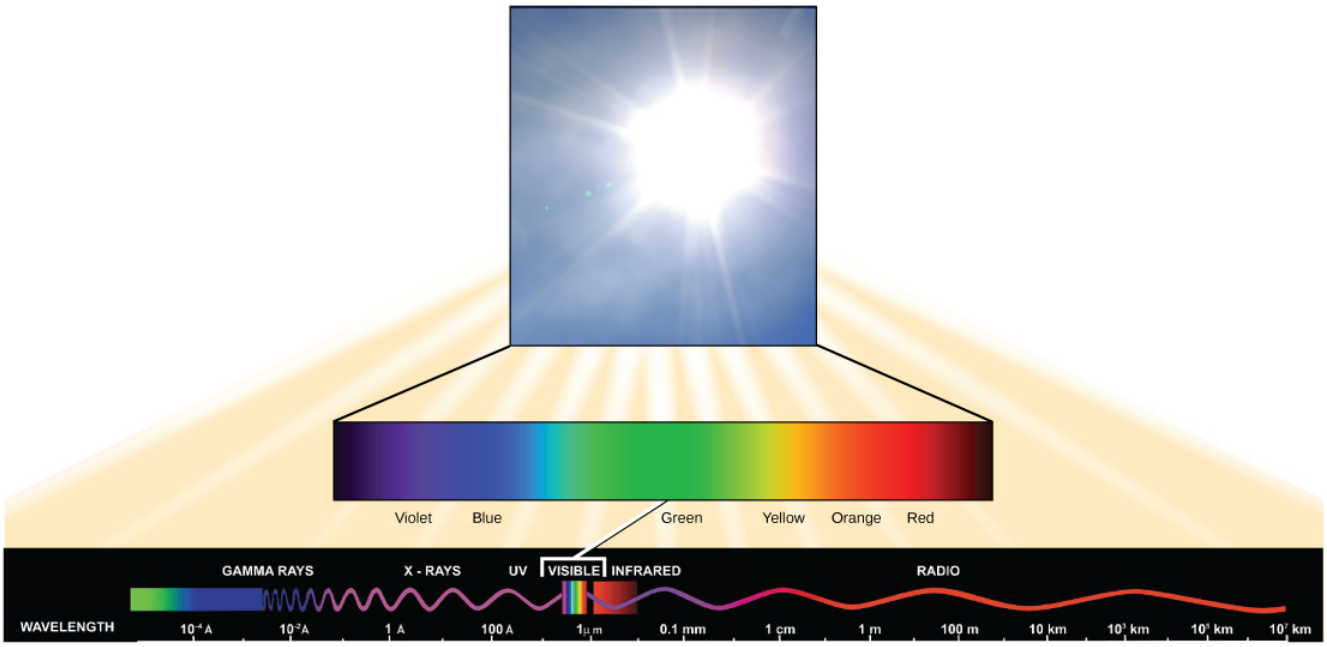


Figure 2.5.3.3: The sun emits energy in the form of electromagnetic radiation. This radiation exists at different wavelengths, each of which has its own characteristic energy. All electromagnetic radiation, including visible light, is characterized by its wavelength.

Each type of electromagnetic radiation travels at a particular wavelength. The longer the wavelength (or the more stretched out it appears in the diagram), the less energy is carried. Short, tight waves carry the most energy. This may seem illogical, but think of it in terms of a piece of moving a heavy rope. It takes little effort by a person to move a rope in long, wide waves. To make a rope move in short, tight waves, a person would need to apply significantly more energy.

The electromagnetic spectrum (Figure 2.5.3.3) shows several types of electromagnetic radiation originating from the sun, including X-rays and ultraviolet (UV) rays. The higher-energy waves can penetrate tissues and damage cells and DNA, explaining why both X-rays and UV rays can be harmful to living organisms.

Absorption of Light

Light energy initiates the process of photosynthesis when pigments absorb the light. Organic pigments, whether in the human retina or the chloroplast thylakoid, have a narrow range of energy levels that they can absorb. Energy levels lower than those represented by red light are insufficient to raise an orbital electron to a populatable, excited (quantum) state. Energy levels higher than those in blue light will physically tear the molecules apart, called bleaching. So retinal pigments can only “see” (absorb) 700 nm to 400 nm light, which is therefore called visible light. For the same reasons, plants pigment molecules absorb only light in the wavelength range of 700 nm to 400 nm; plant physiologists refer to this range for plants as photosynthetically active radiation.

The visible light seen by humans as white light actually exists in a rainbow of colors. Certain objects, such as a prism or a drop of water, disperse white light to reveal the colors to the human eye. The visible light portion of the electromagnetic spectrum shows the rainbow of colors, with violet and blue having shorter wavelengths, and therefore higher energy. At the other end of the spectrum toward red, the wavelengths are longer and have lower energy (Figure 2.5.3.4).

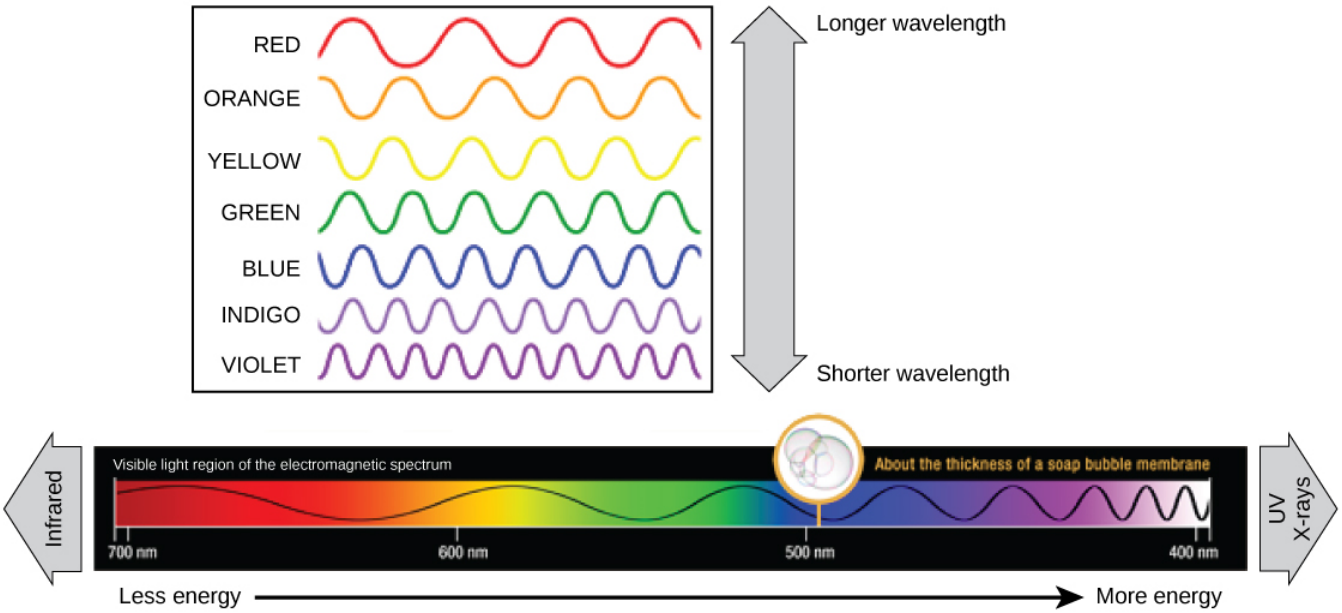


Figure 2.5.3.4: The colors of visible light do not carry the same amount of energy. Violet has the shortest wavelength and therefore carries the most energy, whereas red has the longest wavelength and carries the least amount of energy. (credit: modification of work by NASA)

Understanding Pigments

Different kinds of pigments exist, and each has evolved to absorb only certain wavelengths (colors) of visible light. Pigments reflect or transmit the wavelengths they cannot absorb, making them appear in the corresponding color.

Chlorophylls and carotenoids are the two major classes of photosynthetic pigments found in plants and algae; each class has multiple types of pigment molecules. There are five major chlorophylls: *a*, *b*, *c* and *d* and a related molecule found in prokaryotes called bacteriochlorophyll. Chlorophyll *a* and chlorophyll *b* are found in higher plant chloroplasts and will be the focus of the following discussion.

With dozens of different forms, carotenoids are a much larger group of pigments. The carotenoids found in fruit—such as the red of tomato (lycopene), the yellow of corn seeds (zeaxanthin), or the orange of an orange peel (β-carotene)—are used as advertisements to attract seed dispersers. In photosynthesis, carotenoids function as photosynthetic pigments that are very efficient molecules for the disposal of excess energy. When a leaf is exposed to full sun, the light-dependent reactions are required to process an enormous amount of energy; if that energy is not handled properly, it can do significant damage. Therefore, many carotenoids reside in the thylakoid membrane, absorb excess energy, and safely dissipate that energy as heat.

Each type of pigment can be identified by the specific pattern of wavelengths it absorbs from visible light, which is the absorption spectrum. The graph in Figure 2.5.3.5 shows the absorption spectra for chlorophyll *a*, chlorophyll *b*, and a type of carotenoid pigment called β-carotene (which absorbs blue and green light). Notice how each pigment has a distinct set of peaks and troughs, revealing a highly specific pattern of absorption. Chlorophyll *a* absorbs wavelengths from either end of the visible spectrum (blue and red), but not green. Because green is reflected or transmitted, chlorophyll appears green. Carotenoids absorb in the short-wavelength blue region, and reflect the longer yellow, red, and orange wavelengths.

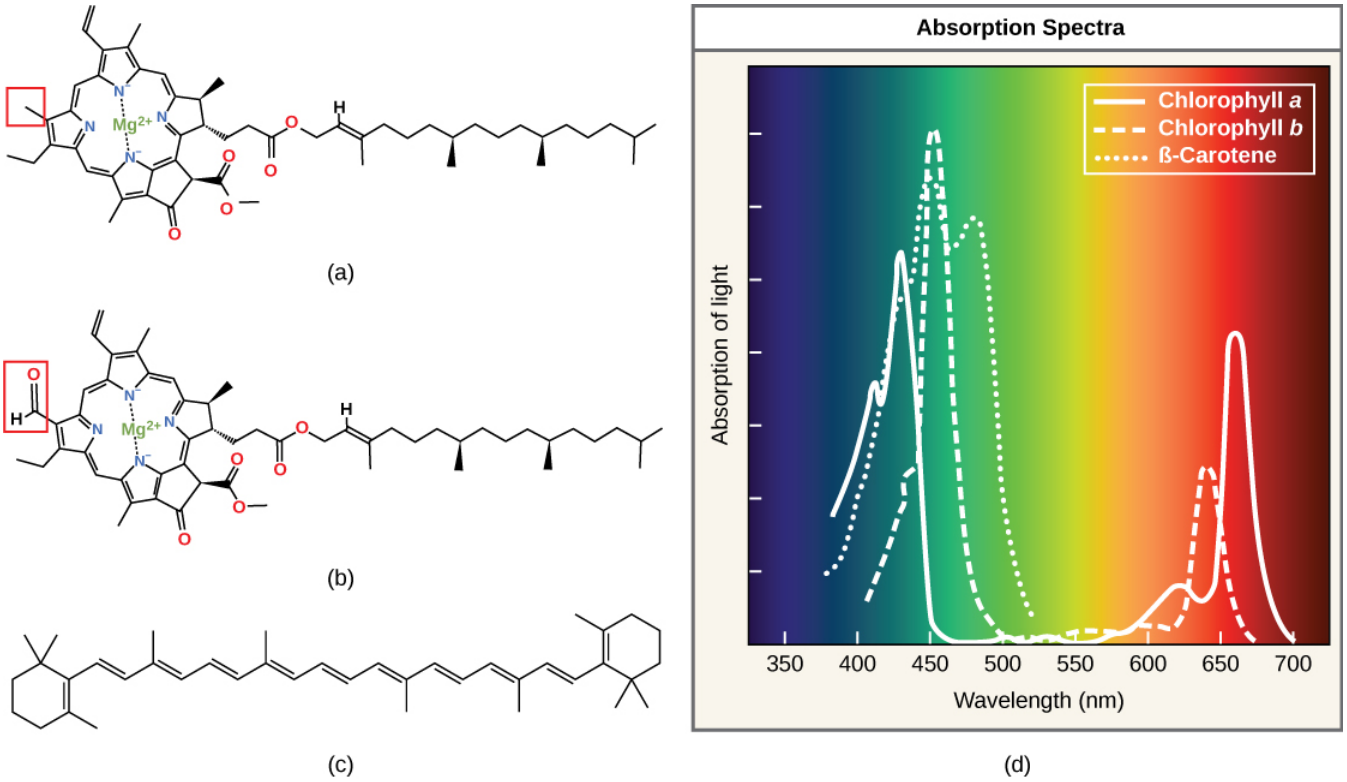


Figure 2.5.3.5: (a) Chlorophyll *a*, (b) chlorophyll *b*, and (c) *β*-carotene are hydrophobic organic pigments found in the thylakoid membrane. Chlorophyll *a* and *b*, which are identical except for the part indicated in the red box, are responsible for the green color of leaves. *β*-carotene is responsible for the orange color in carrots. Each pigment has (d) a unique absorbance spectrum.

Many photosynthetic organisms have a mixture of pigments; using them, the organism can absorb energy from a wider range of wavelengths. Not all photosynthetic organisms have full access to sunlight. Some organisms grow underwater where light intensity and quality decrease and change with depth. Other organisms grow in competition for light. Plants on the rainforest floor must be able to absorb any bit of light that comes through, because the taller trees absorb most of the sunlight and scatter the remaining solar radiation (Figure 2.5.3.6).

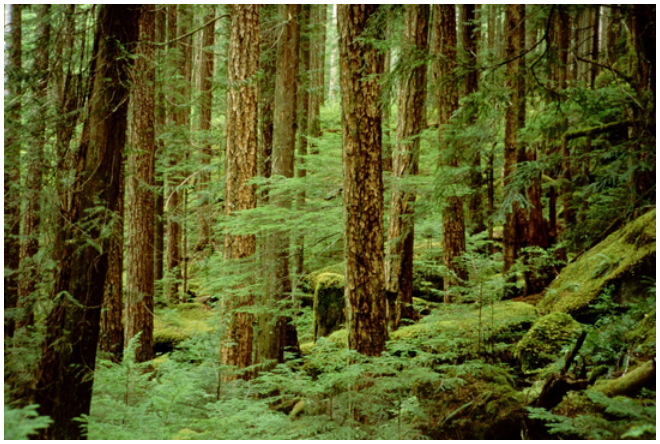


Figure 2.5.3.6: Plants that commonly grow in the shade have adapted to low levels of light by changing the relative concentrations of their chlorophyll pigments. (credit: Jason Hollinger)

When studying a photosynthetic organism, scientists can determine the types of pigments present by generating absorption spectra. An instrument called a spectrophotometer can differentiate which wavelengths of light a substance can absorb. Spectrophotometers measure transmitted light and compute from it the absorption. By extracting pigments from leaves and placing these samples into a spectrophotometer, scientists can identify which wavelengths of light an organism can absorb. Additional methods for the identification of plant pigments include various types of chromatography that separate the pigments by their relative affinities to solid and mobile phases.

How Light-Dependent Reactions Work

The overall function of light-dependent reactions is to convert solar energy into chemical energy in the form of NADPH and ATP. This chemical energy supports the light-independent reactions and fuels the assembly of sugar molecules. The light-dependent reactions are depicted in Figure 2.5.3.7. Protein complexes and pigment molecules work together to produce NADPH and ATP.

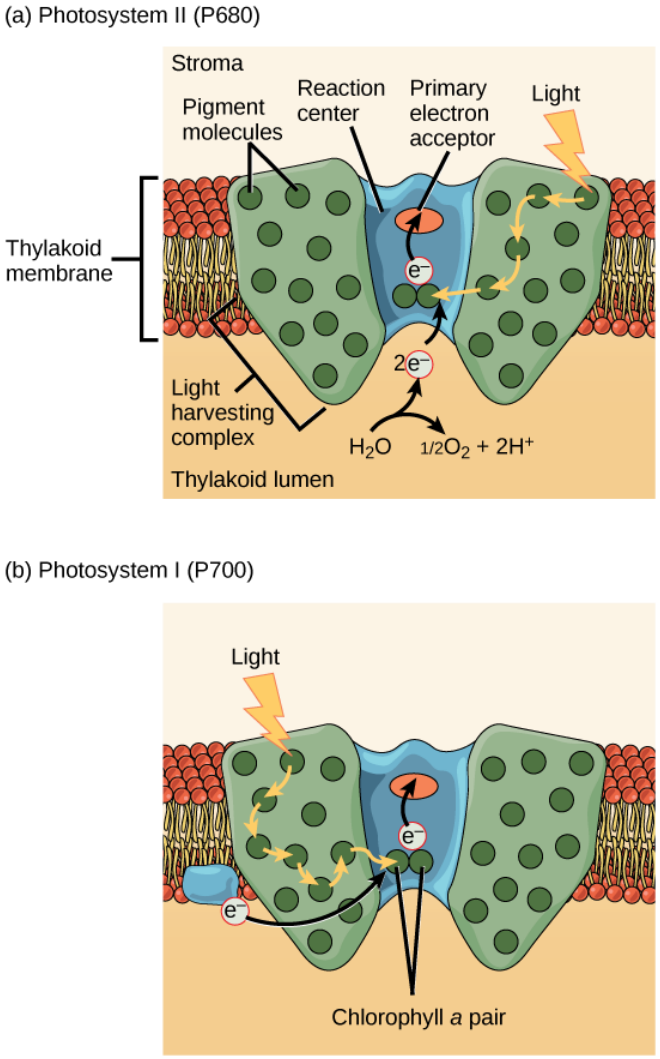


Figure 2.5.3.7: A photosystem consists of a light-harvesting complex and a reaction center. Pigments in the light-harvesting complex pass light energy to two special chlorophyll a molecules in the reaction center. The light excites an electron from the chlorophyll a pair, which passes to the primary electron acceptor. The excited electron must then be replaced. In (a) photosystem II, the electron comes from the splitting of water, which releases oxygen as a waste product. In (b) photosystem I, the electron comes from the chloroplast electron transport chain discussed below.

The actual step that converts light energy into chemical energy takes place in a multiprotein complex called a photosystem, two types of which are found embedded in the thylakoid membrane, photosystem II (PSII) and photosystem I (PSI) (Figure 2.5.3.7). The two complexes differ on the basis of what they oxidize (that is, the source of the low-energy electron supply) and what they reduce (the place to which they deliver their energized electrons).

Both photosystems have the same basic structure; a number of antenna proteins to which the chlorophyll molecules are bound surround the reaction center where the photochemistry takes place. Each photosystem is serviced by the light-harvesting complex, which passes energy from sunlight to the reaction center; it consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules as well as other pigments like carotenoids. The absorption of a single photon or distinct quantity or "packet" of light by any of the chlorophylls pushes that molecule into an excited state. In short, the light energy has now been captured by biological molecules but is not stored in any useful form yet. The energy is transferred from chlorophyll to chlorophyll

until eventually (after about a millionth of a second), it is delivered to the reaction center. Up to this point, only energy has been transferred between molecules, not electrons.

Art Connection

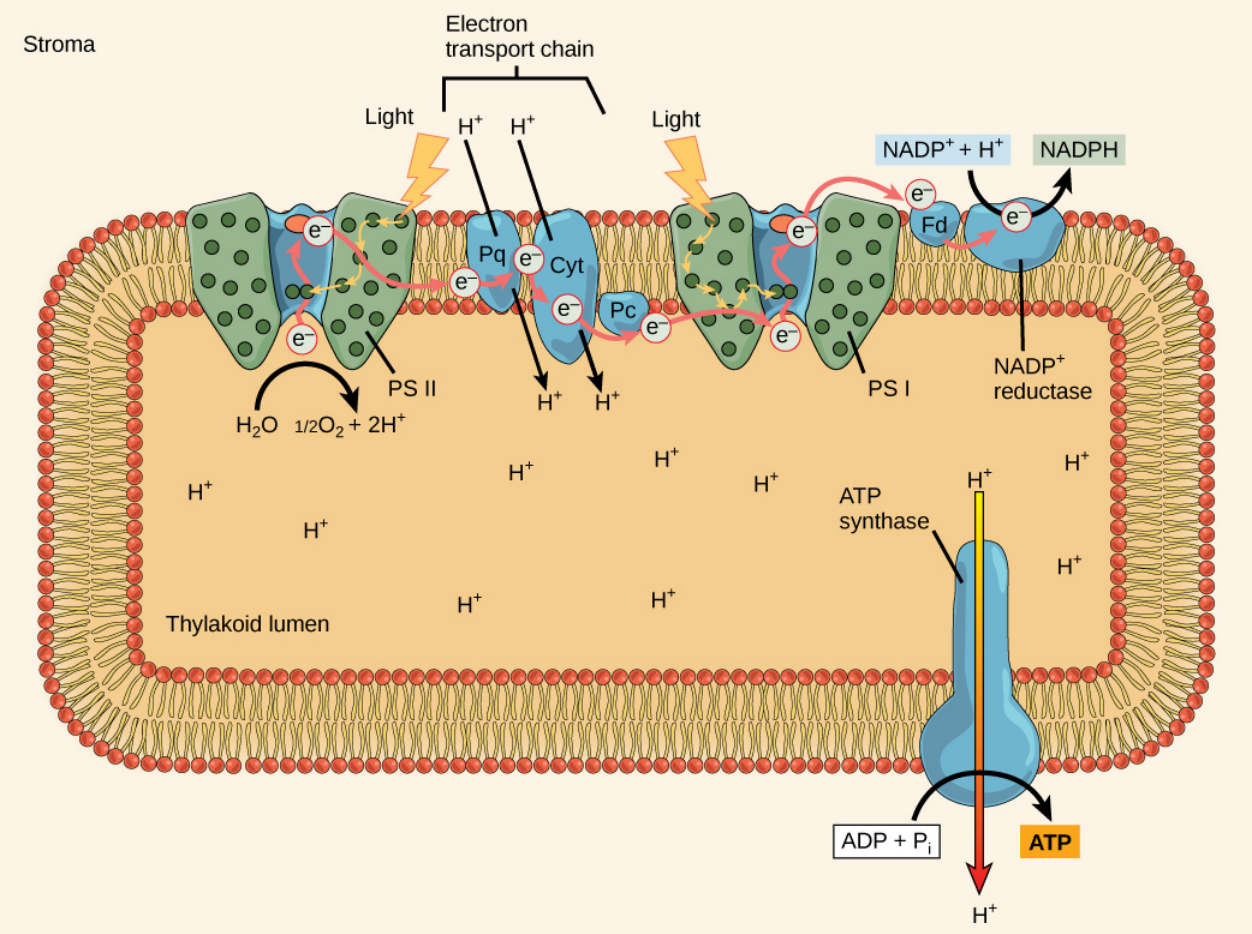


Figure 2.5.3.8: In the photosystem II (PSII) reaction center, energy from sunlight is used to extract electrons from water. The electrons travel through the chloroplast electron transport chain to photosystem I (PSI), which reduces $NADP^+$ to NADPH. The electron transport chain moves protons across the thylakoid membrane into the lumen. At the same time, splitting of water adds protons to the lumen, and reduction of NADPH removes protons from the stroma. The net result is a low pH in the thylakoid lumen, and a high pH in the stroma. ATP synthase uses this electrochemical gradient to make ATP.

What is the initial source of electrons for the chloroplast electron transport chain?

A. water
B. oxygen
C. carbon dioxide
D. NADPH

The reaction center contains a pair of chlorophyll *a* molecules with a special property. Those two chlorophylls can undergo oxidation upon excitation; they can actually give up an electron in a process called a photoact. It is at this step in the reaction center, this step in photosynthesis, that light energy is converted into an excited electron. All of the subsequent steps involve getting that electron onto the energy carrier NADPH for delivery to the Calvin cycle where the electron is deposited onto carbon for long-term storage in the form of a carbohydrate.PSII and PSI are two major components of the photosynthetic electron transport chain, which also includes the cytochrome complex. The cytochrome complex, an enzyme composed of two protein complexes, transfers the electrons from the carrier molecule plastoquinone (Pq) to the protein plastocyanin (Pc), thus enabling both the transfer of protons across the thylakoid membrane and the transfer of electrons from PSII to PSI.

The reaction center of PSII (called P680) delivers its high-energy electrons, one at the time, to the primary electron acceptor, and through the electron transport chain (Pq to cytochrome complex to plastocyanine) to PSI. P680's missing electron is replaced by extracting a low-energy electron from water; thus, water is split and PSII is re-reduced after every photoact. Splitting one H_2O molecule releases two electrons, two hydrogen atoms, and one atom of oxygen. Splitting two molecules is required to form one molecule of diatomic O_2 gas. About 10 percent of the oxygen is used by mitochondria in the leaf to support oxidative phosphorylation. The remainder escapes to the atmosphere where it is used by aerobic organisms to support respiration.

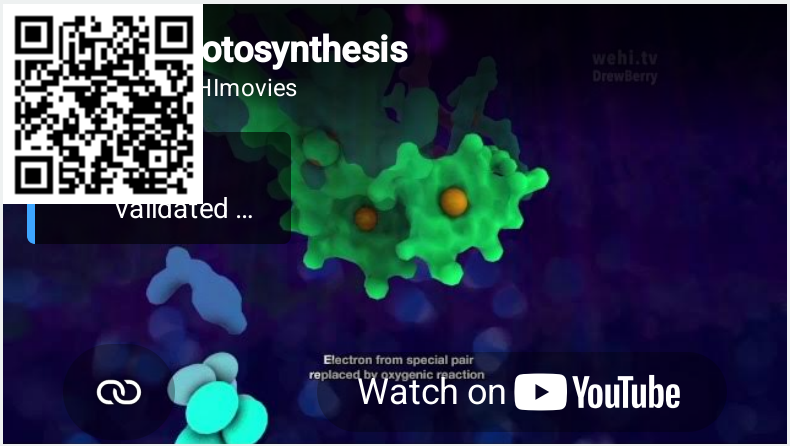
As electrons move through the proteins that reside between PSII and PSI, they lose energy. That energy is used to move hydrogen atoms from the stromal side of the membrane to the thylakoid lumen. Those hydrogen atoms, plus the ones produced by splitting water, accumulate in the thylakoid lumen and will be used synthesize ATP in a later step. Because the electrons have lost energy prior to their arrival at PSI, they must be re-energized by PSI, hence, another photon is absorbed by the PSI antenna. That energy is relayed to the PSI reaction center (called P700). P700 is oxidized and sends a high-energy electron to $NADP^+$ to form NADPH. Thus, PSII captures the energy to create proton gradients to make ATP, and PSI captures the energy to reduce $NADP^+$ into NADPH. The two photosystems work in concert, in part, to guarantee that the production of NADPH will roughly equal the production of ATP. Other mechanisms exist to fine tune that ratio to exactly match the chloroplast's constantly changing energy needs.

Generating an Energy Carrier: ATP

As in the intermembrane space of the mitochondria during cellular respiration, the buildup of hydrogen ions inside the thylakoid lumen creates a concentration gradient. The passive diffusion of hydrogen ions from high concentration (in the thylakoid lumen) to low concentration (in the stroma) is harnessed to create ATP, just as in the electron transport chain of cellular respiration. The ions build up energy because of diffusion and because they all have the same electrical charge, repelling each other.

To release this energy, hydrogen ions will rush through any opening, similar to water jetting through a hole in a dam. In the thylakoid, that opening is a passage through a specialized protein channel called the ATP synthase. The energy released by the hydrogen ion stream allows ATP synthase to attach a third phosphate group to ADP, which forms a molecule of ATP (Figure 2.5.3.8). The flow of hydrogen ions through ATP synthase is called chemiosmosis because the ions move from an area of high to an area of low concentration through a semi-permeable structure.

Video



Summary

The pigments of the first part of photosynthesis, the light-dependent reactions, absorb energy from sunlight. A photon strikes the antenna pigments of photosystem II to initiate photosynthesis. The energy travels to the reaction center that contains chlorophyll *a* to the electron transport chain, which pumps hydrogen ions into the thylakoid interior. This action builds up a high concentration of ions. The ions flow through ATP synthase via chemiosmosis to form molecules of ATP, which are used for the formation of sugar molecules in the second stage of photosynthesis. Photosystem I absorbs a second photon, which results in the formation of an NADPH molecule, another energy and reducing power carrier for the light-independent reactions.

Art Connections

Figure 2.5.3.8: What is the source of electrons for the chloroplast electron transport chain?

A. Water
B. Oxygen
C. Carbon dioxide
D. NADPH

Answer

A.

Glossary

absorption spectrum
range of wavelengths of electromagnetic radiation absorbed by a given substance

antenna protein
pigment molecule that directly absorbs light and transfers the energy absorbed to other pigment molecules

carotenoid
photosynthetic pigment that functions to dispose of excess energy

chlorophyll *a*
form of chlorophyll that absorbs violet-blue and red light and consequently has a bluish-green color; the only pigment molecule that performs the photochemistry by getting excited and losing an electron to the electron transport chain

chlorophyll *b*
accessory pigment that absorbs blue and red-orange light and consequently has a yellowish-green tint

cytochrome complex
group of reversibly oxidizable and reducible proteins that forms part of the electron transport chain between photosystem II and photosystem I

electromagnetic spectrum
range of all possible frequencies of radiation

electron transport chain
group of proteins between PSII and PSI that pass energized electrons and use the energy released by the electrons to move hydrogen ions against their concentration gradient into the thylakoid lumen

light harvesting complex
complex that passes energy from sunlight to the reaction center in each photosystem; it consists of multiple antenna proteins that contain a mixture of 300–400 chlorophyll *a* and *b* molecules as well as other pigments like carotenoids

P680
reaction center of photosystem II

P700
reaction center of photosystem I

photoact
ejection of an electron from a reaction center using the energy of an absorbed photon

photon

distinct quantity or “packet” of light energy

photosystem

group of proteins, chlorophyll, and other pigments that are used in the light-dependent reactions of photosynthesis to absorb light energy and convert it into chemical energy

photosystem I

integral pigment and protein complex in thylakoid membranes that uses light energy to transport electrons from plastocyanin to $NADP^+$ (which becomes reduced to NADPH in the process)

photosystem II

integral protein and pigment complex in thylakoid membranes that transports electrons from water to the electron transport chain; oxygen is a product of PSII

primary electron acceptor

pigment or other organic molecule in the reaction center that accepts an energized electron from the reaction center

reaction center

complex of chlorophyll molecules and other organic molecules that is assembled around a special pair of chlorophyll molecules and a primary electron acceptor; capable of undergoing oxidation and reduction

spectrophotometer

instrument that can measure transmitted light and compute the absorption

wavelength

distance between consecutive points of equal position (two crests or two troughs) of a wave in a graphic representation; inversely proportional to the energy of the radiation

---

This page titled 2.5.3: The Light-Dependent Reactions of Photosynthesis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **8.2: The Light-Dependent Reactions of Photosynthesis** by OpenStax is licensed CC BY 4.0.

2.5.4: Using Light Energy to Make Organic Molecules

Skills to Develop

- Describe the Calvin cycle
- Define carbon fixation
- Explain how photosynthesis works in the energy cycle of all living organisms

After the energy from the sun is converted into chemical energy and temporarily stored in ATP and NADPH molecules, the cell has the fuel needed to build carbohydrate molecules for long-term energy storage. The products of the light-dependent reactions, ATP and NADPH, have lifespans in the range of millionths of seconds, whereas the products of the light-independent reactions (carbohydrates and other forms of reduced carbon) can survive for hundreds of millions of years. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? It comes from carbon dioxide, the gas that is a waste product of respiration in microbes, fungi, plants, and animals.

The Calvin Cycle

In plants, carbon dioxide (CO_2) enters the leaves through stomata, where it diffuses over short distances through intercellular spaces until it reaches the mesophyll cells. Once in the mesophyll cells, CO_2 diffuses into the stroma of the chloroplast—the site of light-independent reactions of photosynthesis. These reactions actually have several names associated with them. Another term, the Calvin cycle, is named for the man who discovered it, and because these reactions function as a cycle. Others call it the Calvin-Benson cycle to include the name of another scientist involved in its discovery. The most outdated name is dark reactions, because light is not directly required (Figure 2.5.4.1). However, the term dark reaction can be misleading because it implies incorrectly that the reaction only occurs at night or is independent of light, which is why most scientists and instructors no longer use it.

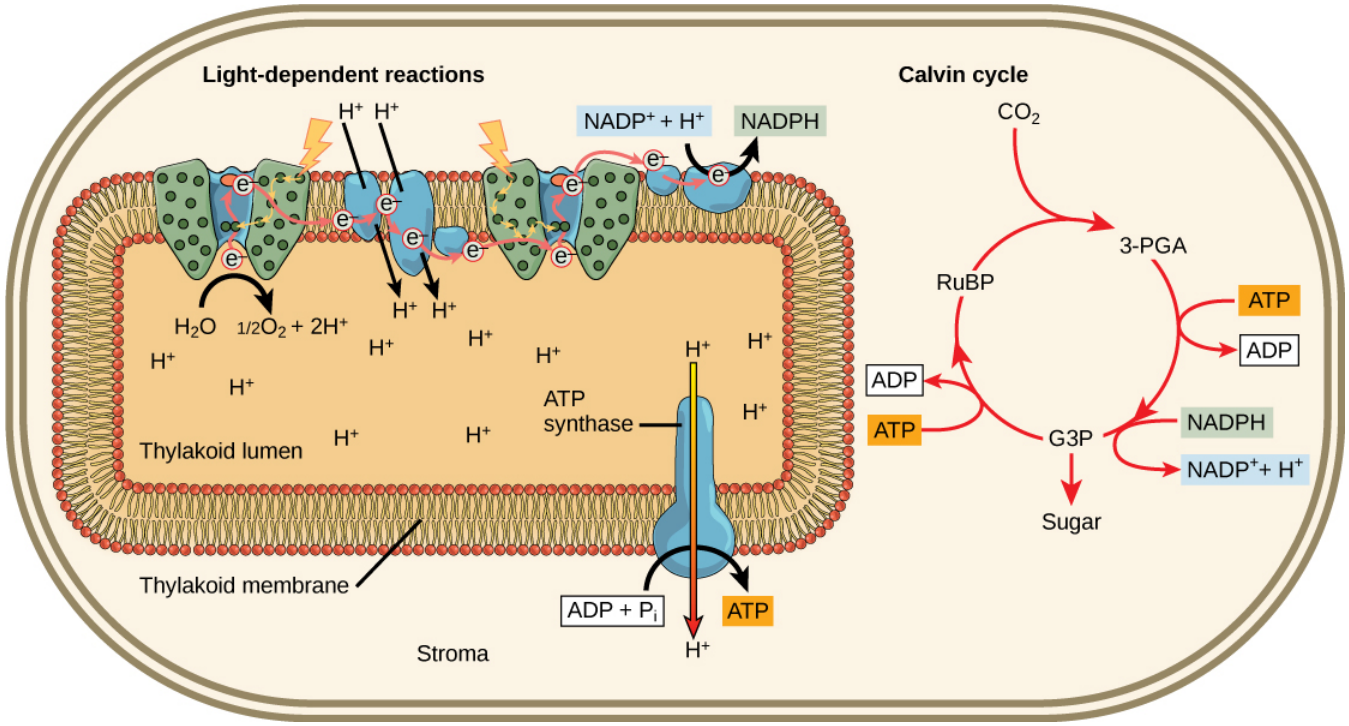


Figure 2.5.4.1: Light reactions harness energy from the sun to produce chemical bonds, ATP, and NADPH. These energy-carrying molecules are made in the stroma where carbon fixation takes place.

The light-independent reactions of the Calvin cycle can be organized into three basic stages: fixation, reduction, and regeneration.

Stage 1: Fixation

In the stroma, in addition to CO_2,two other components are present to initiate the light-independent reactions: an enzyme called ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), and three molecules of ribulose bisphosphate (RuBP), as shown in Figure 2.5.4.2. RuBP has five atoms of carbon, flanked by two phosphates.

Art Connection

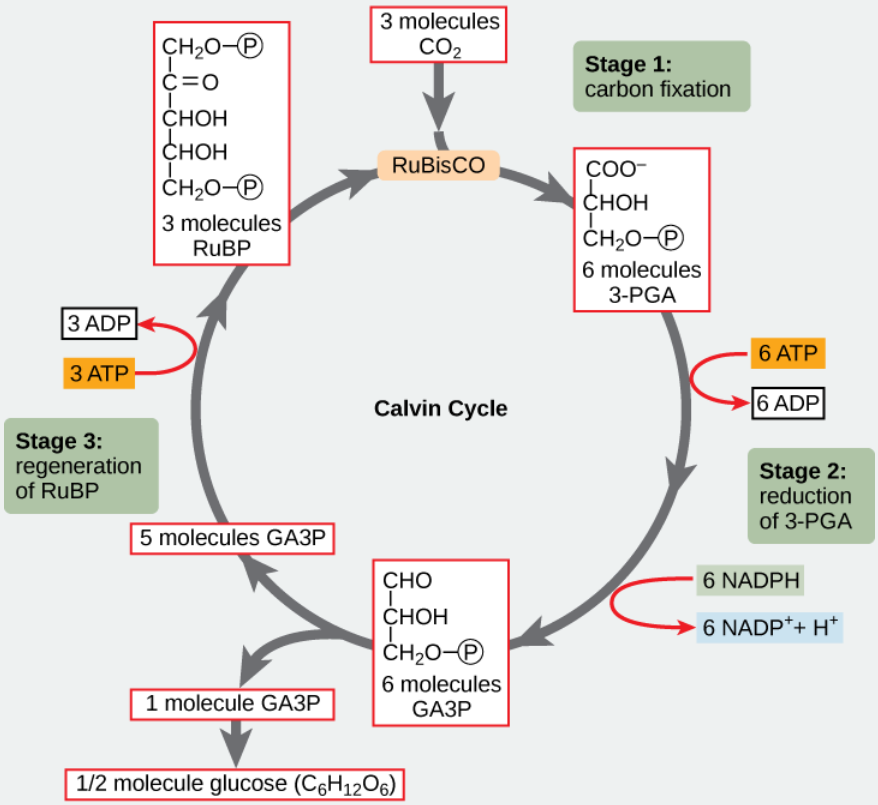


Figure 2.5.4.2: The Calvin cycle has three stages. In stage 1, the enzyme RuBisCO incorporates carbon dioxide into an organic molecule, 3-PGA. In stage 2, the organic molecule is reduced using electrons supplied by NADPH. In stage 3, RuBP, the molecule that starts the cycle, is regenerated so that the cycle can continue. Only one carbon dioxide molecule is incorporated at a time, so the cycle must be completed three times to produce a single three-carbon GA3P molecule, and six times to produce a six-carbon glucose molecule.

Which of the following statements is true?

A. In photosynthesis, oxygen, carbon dioxide, ATP, and NADPH are reactants. GA3P and water are products.
B. In photosynthesis, chlorophyll, water, and carbon dioxide are reactants. GA3P and oxygen are products.
C. In photosynthesis, water, carbon dioxide, ATP, and NADPH are reactants. RuBP and oxygen are products.
D. In photosynthesis, water and carbon dioxide are reactants. GA3P and oxygen are products.

RuBisCO catalyzes a reaction between CO_2 and RuBP. For each CO_2 molecule that reacts with one RuBP, two molecules of another compound (3-PGA) form. PGA has three carbons and one phosphate. Each turn of the cycle involves only one RuBP and one carbon dioxide and forms two molecules of 3-PGA. The number of carbon atoms remains the same, as the atoms move to form new bonds during the reactions (3 atoms from $3CO_2$ + 15 atoms from 3RuBP = 18 atoms in 3 atoms of 3-PGA). This process is called carbon fixation, because CO_2 is "fixed" from an inorganic form into organic molecules.

Stage 2: Reduction

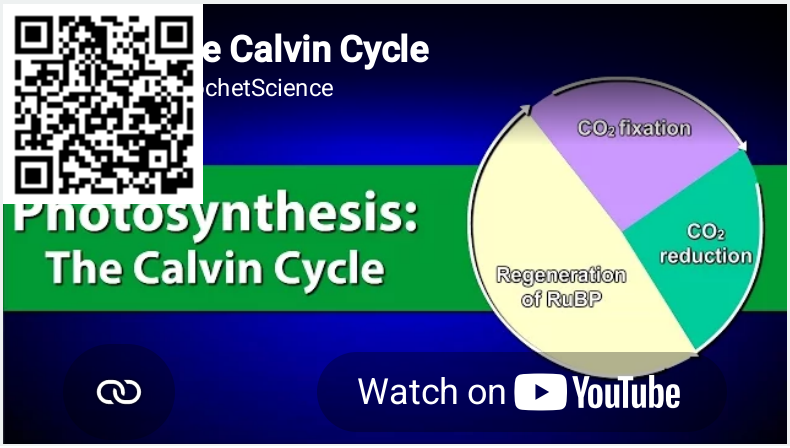
ATP and NADPH are used to convert the six molecules of 3-PGA into six molecules of a chemical called glyceraldehyde 3-phosphate (G3P). That is a reduction reaction because it involves the gain of electrons by 3-PGA. Recall that a reduction is the gain of an electron by an atom or molecule. Six molecules of both ATP and NADPH are used. For ATP, energy is released with the loss

of the terminal phosphate atom, converting it into ADP; for NADPH, both energy and a hydrogen atom are lost, converting it into $NADP^+$. Both of these molecules return to the nearby light-dependent reactions to be reused and reenergized.

Stage 3: Regeneration

Interestingly, at this point, only one of the G3P molecules leaves the Calvin cycle and is sent to the cytoplasm to contribute to the formation of other compounds needed by the plant. Because the G3P exported from the chloroplast has three carbon atoms, it takes three "turns" of the Calvin cycle to fix enough net carbon to export one G3P. But each turn makes two G3Ps, thus three turns make six G3Ps. One is exported while the remaining five G3P molecules remain in the cycle and are used to regenerate RuBP, which enables the system to prepare for more CO_2 to be fixed. Three more molecules of ATP are used in these regeneration reactions.

Video



Evolution Connection: Photosynthesis

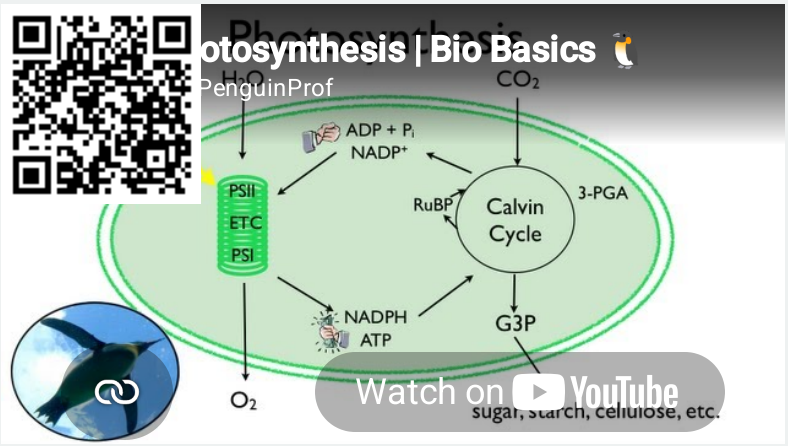
During the evolution of photosynthesis, a major shift occurred from the bacterial type of photosynthesis that involves only one photosystem and is typically anoxygenic (does not generate oxygen) into modern oxygenic (does generate oxygen) photosynthesis, employing two photosystems. This modern oxygenic photosynthesis is used by many organisms—from giant tropical leaves in the rainforest to tiny cyanobacterial cells—and the process and components of this photosynthesis remain largely the same. Photosystems absorb light and use electron transport chains to convert energy into the chemical energy of ATP and NADH. The subsequent light-independent reactions then assemble carbohydrate molecules with this energy.

Photosynthesis in desert plants has evolved adaptations that conserve water. In the harsh dry heat, every drop of water must be used to survive. Because stomata must open to allow for the uptake of CO_2, water escapes from the leaf during active photosynthesis. Desert plants have evolved processes to conserve water and deal with harsh conditions. A more efficient use of CO_2 allows plants to adapt to living with less water. Some plants such as cacti (Figure 2.5.4.3) can prepare materials for photosynthesis during the night by a temporary carbon fixation/storage process, because opening the stomata at this time conserves water due to cooler temperatures. In addition, cacti have evolved the ability to carry out low levels of photosynthesis without opening stomata at all, an extreme mechanism to face extremely dry periods.



Figure 2.5.4.3: The harsh conditions of the desert have led plants like these cacti to evolve variations of the light-independent reactions of photosynthesis. These variations increase the efficiency of water usage, helping to conserve water and energy. (credit: Piotr Wojtkowski)

Video



The Energy Cycle

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. In addition, an organism can either make its own food or eat another organism—either way, the food still needs to be broken down. Finally, in the process of breaking down food, called cellular respiration, heterotrophs release needed energy and produce "waste" in the form of CO_2 gas.

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 2.5.4.4).

CO_2 is no more a form of waste than oxygen is wasteful to photosynthesis. Both 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.

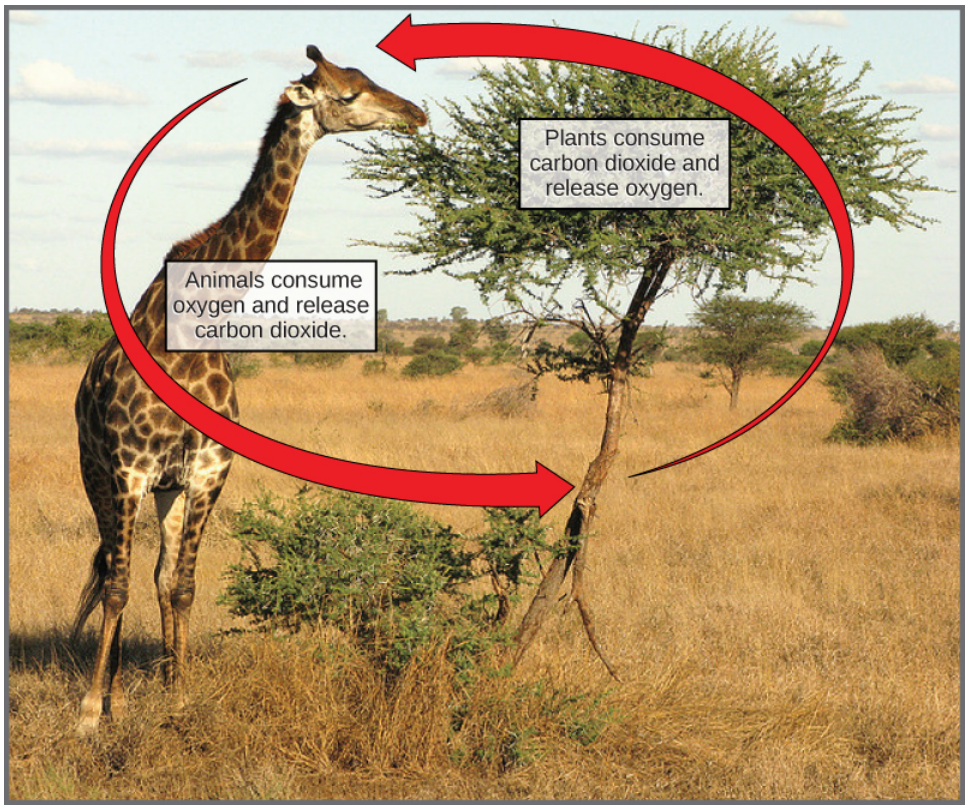


Figure 2.5.4.4: Photosynthesis consumes carbon dioxide and produces oxygen. Aerobic respiration consumes oxygen and produces carbon dioxide. These two processes play an important role in the carbon cycle. (credit: modification of work by Stuart Bassil)

Summary

Using the energy carriers formed in the first steps of photosynthesis, the light-independent reactions, or the Calvin cycle, take in CO_2 from the environment. An enzyme, RuBisCO, catalyzes a reaction with CO_2 and another molecule, RuBP. After three cycles, a three-carbon molecule of G3P leaves the cycle to become part of a carbohydrate molecule. The remaining G3P molecules stay in the cycle to be regenerated into RuBP, which is then ready to react with more CO_2. Photosynthesis forms an energy cycle with the process of cellular respiration. Plants need both photosynthesis and respiration for their ability to function in both the light and dark, and to be able to interconvert essential metabolites. Therefore, plants contain both chloroplasts and mitochondria.

Art Connections

Figure 2.5.4.2: Which of the following statements is true?

A. In photosynthesis, oxygen, carbon dioxide, ATP, and NADPH are reactants. G3P and water are products.
B. In photosynthesis, chlorophyll, water, and carbon dioxide are reactants. G3P and oxygen are products.
C. In photosynthesis, water, carbon dioxide, ATP, and NADPH are reactants. RuBP and oxygen are products.
D. In photosynthesis, water and carbon dioxide are reactants. G3P and oxygen are products.

Answer

D

Glossary

Calvin cycle

light-independent reactions of photosynthesis that convert carbon dioxide from the atmosphere into carbohydrates using the energy and reducing power of ATP and NADPH

carbon fixation

process of converting inorganic CO_2 gas into organic compounds

reduction

gain of electron(s) by an atom or molecule

This page titled 2.5.4: Using Light Energy to Make Organic Molecules is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **8.3: Using Light Energy to Make Organic Molecules** by OpenStax is licensed CC BY 4.0.

2.5.E: Photosynthesis (Exercises)

8.1: Overview of Photosynthesis

Photosynthesis is essential to all life on earth; both plants and animals depend on it. It is the only biological process that can capture energy that originates in outer space (sunlight) and convert it into chemical compounds (carbohydrates) that every organism uses to power its metabolism. In brief, the energy of sunlight is captured and used to energize electrons, which are then stored in the covalent bonds of sugar molecules.

Review Questions

Which of the following components is *not* used by both plants and cyanobacteria to carry out photosynthesis?

A. chloroplasts
B. chlorophyll
C. carbon dioxide
D. water

Answer

A

What two main products result from photosynthesis?

A. oxygen and carbon dioxide
B. chlorophyll and oxygen
C. sugars/carbohydrates and oxygen
D. sugars/carbohydrates and carbon dioxide

Answer

C

In which compartment of the plant cell do the light-independent reactions of photosynthesis take place?

A. thylakoid
B. stroma
C. outer membrane
D. mesophyll

Answer

B

Which statement about thylakoids in eukaryotes is *not* correct?

A. Thylakoids are assembled into stacks.
B. Thylakoids exist as a maze of folded membranes.
C. The space surrounding thylakoids is called stroma.
D. Thylakoids contain chlorophyll.

Answer

B

Free Response

What is the overall outcome of the light reactions in photosynthesis?

Answer

The outcome of light reactions in photosynthesis is the conversion of solar energy into chemical energy that the chloroplasts can use to do work (mostly anabolic production of carbohydrates from carbon dioxide).

Why are carnivores, such as lions, dependent on photosynthesis to survive?

Answer

Because lions eat animals that eat plants.

Why are energy carriers thought of as either “full” or “empty”?

Answer

The energy carriers that move from the light-dependent reaction to the light-independent one are “full” because they bring energy. After the energy is released, the “empty” energy carriers return to the light-dependent reaction to obtain more energy. There is not much actual movement involved. Both ATP and NADPH are produced in the stroma where they are also used and reconverted into ADP, Pi, and $NADP^+$.

8.2: The Light-Dependent Reactions of Photosynthesis

Like all other forms of kinetic energy, light can travel, change form, and be harnessed to do work. In the case of photosynthesis, light energy is converted into chemical energy, which photoautotrophs use to build carbohydrate molecules. However, autotrophs only use a few specific components of sunlight.

Review Questions

Which of the following structures is *not* a component of a photosystem?

A. ATP synthase
B. antenna molecule
C. reaction center
D. primary electron acceptor

Answer

A

How many photons does it take to fully reduce one molecule of $NADP^+$ to NADPH?

A. 1
B. 2
C. 4
D. 8

Answer

B

Which complex is *not* involved in the establishment of conditions for ATP synthesis?

A. photosystem I

B. ATP synthase
C. photosystem II
D. cytochrome complex

Answer

C

From which component of the light-dependent reactions does NADPH form most directly?

A. photosystem II
B. photosystem I
C. cytochrome complex
D. ATP synthase

Answer

B

Free Response

Describe the pathway of electron transfer from photosystem II to photosystem I in light-dependent reactions.

Answer

A photon of light hits an antenna molecule in photosystem II, and the energy released by it travels through other antenna molecules to the reaction center. The energy causes an electron to leave a molecule of chlorophyll *a* to a primary electron acceptor protein. The electron travels through the electron transport chain and is accepted by a pigment molecule in photosystem I.

What are the roles of ATP and NADPH in photosynthesis?

Answer

Both of these molecules carry energy; in the case of NADPH, it has reducing power that is used to fuel the process of making carbohydrate molecules in light-independent reactions.

8.3: Using Light Energy to Make Organic Molecules

The products of the light-dependent reactions, ATP and NADPH, have lifespans in the range of millionths of seconds, whereas the products of the light-independent reactions (carbohydrates and other forms of reduced carbon) can survive for hundreds of millions of years. The carbohydrate molecules made will have a backbone of carbon atoms. Where does the carbon come from? It comes from carbon dioxide, the gas that is a waste product of respiration in microbes, fungi, plants, and animals.

Review Questions

Which molecule must enter the Calvin cycle continually for the light-independent reactions to take place?

A. RuBisCO
B. RuBP
C. 3-PGA
D. CO_2

Answer

D

Which order of molecular conversions is correct for the Calvin cycle?

A. $\text{RuBP} + \text{G3P} \rightarrow \text{3-PGA} \rightarrow \text{sugar}$
B. $\text{RuBisCo} \rightarrow \text{CO}_2 \rightarrow \text{RuBP} \rightarrow \text{G3P}$
C. $\text{RuBP} + \text{CO}_2 \rightarrow [\text{RuBisCo}]\ \text{3-PGA} \rightarrow \text{G3P}$
D. $\text{CO}_2 \rightarrow \text{3-PGA} \rightarrow \text{RuBP} \rightarrow \text{G3P}$

Answer

C

Where in eukaryotic cells does the Calvin cycle take place?

A. thylakoid membrane
B. thylakoid lumen
C. chloroplast stroma
D. granum

Answer

C

Which statement correctly describes carbon fixation?

A. the conversion of CO_2 into an organic compound
B. the use of RuBisCO to form 3-PGA
C. the production of carbohydrate molecules from G3P
D. the formation of RuBP from G3P molecules
E. the use of ATP and NADPH to reduce CO_2

Answer

A

Free Response

Why is the third stage of the Calvin cycle called the regeneration stage?

Answer

Because RuBP, the molecule needed at the start of the cycle, is regenerated from G3P.

Which part of the light-independent reactions would be affected if a cell could not produce the enzyme RuBisCO?

Answer

None of the cycle could take place, because RuBisCO is essential in fixing carbon dioxide. Specifically, RuBisCO catalyzes the reaction between carbon dioxide and RuBP at the start of the cycle.

Why does it take three turns of the Calvin cycle to produce G3P, the initial product of photosynthesis?

Answer

Because G3P has three carbon atoms, and each turn of the cycle takes in one carbon atom in the form of carbon dioxide.

This page titled 2.5.E: Photosynthesis (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **8.E: Photosynthesis (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

2.6: Cell Communication

While the necessity for cellular communication in larger organisms seems obvious, even single-celled organisms communicate with each other. Yeast cells signal each other to aid mating. Some forms of bacteria coordinate their actions in order to form large complexes called biofilms or to organize the production of toxins to remove competing organisms. The ability of cells to communicate through chemical signals originated in single cells and was essential for the evolution of multicellular organisms. The efficient and error-free function of communication systems is vital for all life as we know it.

2.6.1: Prelude to Cell Communication

2.6.2: Signaling Molecules and Cellular Receptors

2.6.3: Propagation of the Signal

2.6.4: Response to the Signal

2.6.5: Signaling in Single-Celled Organisms

2.6.E: Cell Communication (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.6: Cell Communication is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

2.6.1: Prelude to Cell Communication



Figure 2.6.1.1: Have you ever become separated from a friend while in a crowd? If so, you know the challenge of searching for someone when surrounded by thousands of other people. If you and your friend have cell phones, your chances of finding each other are good. A cell phone's ability to send and receive messages makes it an ideal communication device. (credit: modification of work by Vincent and Bella Productions)

Imagine what life would be like if you and the people around you could not communicate. You would not be able to express your wishes to others, nor could you ask questions to find out more about your environment. Social organization is dependent on communication between the individuals that comprise that society; without communication, society would fall apart.

As with people, it is vital for individual cells to be able to interact with their environment. This is true whether a cell is growing by itself in a pond or is one of many cells that form a larger organism. In order to properly respond to external stimuli, cells have developed complex mechanisms of communication that can receive a message, transfer the information across the plasma membrane, and then produce changes within the cell in response to the message.

In multicellular organisms, cells send and receive chemical messages constantly to coordinate the actions of distant organs, tissues, and cells. The ability to send messages quickly and efficiently enables cells to coordinate and fine-tune their functions.

While the necessity for cellular communication in larger organisms seems obvious, even single-celled organisms communicate with each other. Yeast cells signal each other to aid mating. Some forms of bacteria coordinate their actions in order to form large complexes called biofilms or to organize the production of toxins to remove competing organisms. The ability of cells to communicate through chemical signals originated in single cells and was essential for the evolution of multicellular organisms. The efficient and error-free function of communication systems is vital for all life as we know it.

This page titled 2.6.1: Prelude to Cell Communication is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **9.0: Prelude to Cell Communication** by OpenStax is licensed CC BY 4.0.

2.6.2: Signaling Molecules and Cellular Receptors

Skills to Develop

- Describe four types of signaling found in multicellular organisms
- Compare internal receptors with cell-surface receptors
- Recognize the relationship between a ligand's structure and its mechanism of action

There are two kinds of communication in the world of living cells. Communication between cells is called intercellular signaling, and communication within a cell is called intracellular signaling. An easy way to remember the distinction is by understanding the Latin origin of the prefixes: inter- means "between" (for example, intersecting lines are those that cross each other) and intra- means "inside" (like intravenous).

Chemical signals are released by signaling cells in the form of small, usually volatile or soluble molecules called ligands. A ligand is a molecule that binds another specific molecule, in some cases, delivering a signal in the process. Ligands can thus be thought of as signaling molecules. Ligands interact with proteins in target cells, which are cells that are affected by chemical signals; these proteins are also called receptors. Ligands and receptors exist in several varieties; however, a specific ligand will have a specific receptor that typically binds only that ligand.

Video



Forms of Signaling

There are four categories of chemical signaling found in multicellular organisms: paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions (Figure 2.6.2.1). The main difference between the different categories of signaling is the distance that the signal travels through the organism to reach the target cell. Not all cells are affected by the same signals.

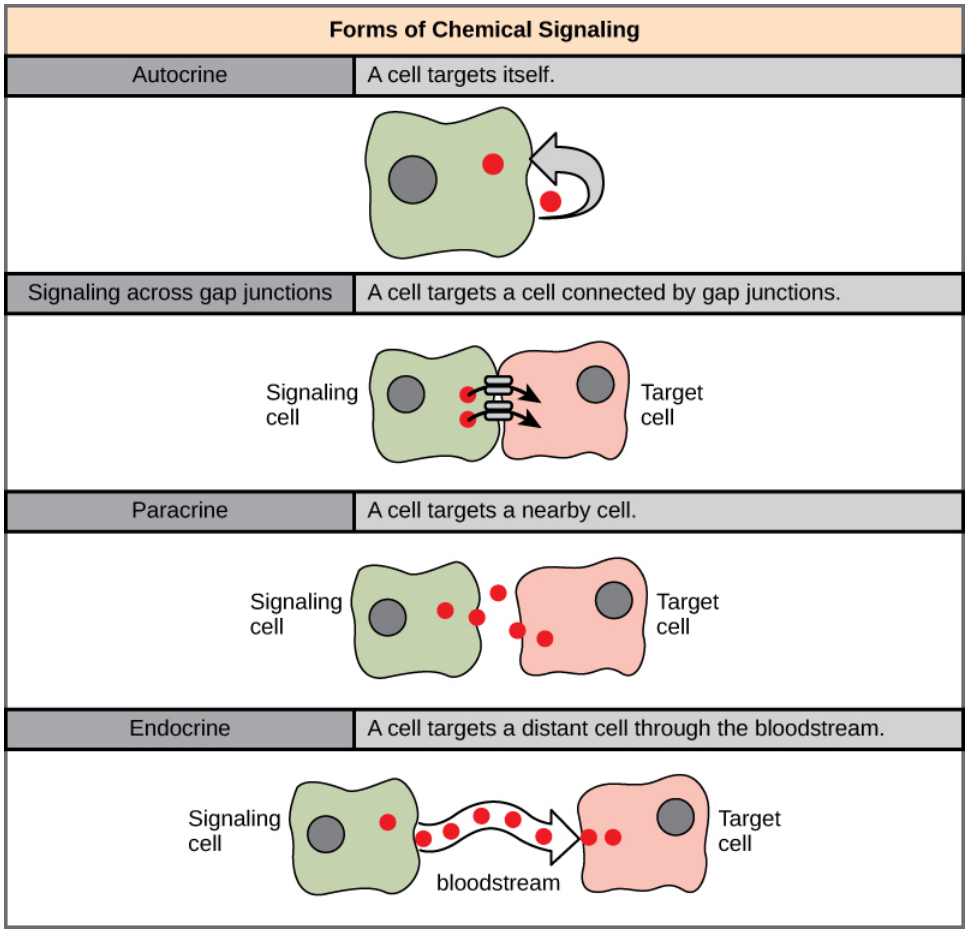


Figure 2.6.2.1: In chemical signaling, a cell may target itself (autocrine signaling), a cell connected by gap junctions, a nearby cell (paracrine signaling), or a distant cell (endocrine signaling). Paracrine signaling acts on nearby cells, endocrine signaling uses the circulatory system to transport ligands, and autocrine signaling acts on the signaling cell. Signaling via gap junctions involves signaling molecules moving directly between adjacent cells.

Paracrine Signaling

Signals that act locally between cells that are close together are called *paracrine signals*. Paracrine signals move by diffusion through the extracellular matrix. These types of signals usually elicit quick responses that last only a short amount of time. In order to keep the response localized, paracrine ligand molecules are normally quickly degraded by enzymes or removed by neighboring cells. Removing the signals will reestablish the concentration gradient for the signal, allowing them to quickly diffuse through the intracellular space if released again.

One example of paracrine signaling is the transfer of signals across synapses between nerve cells. A nerve cell consists of a cell body, several short, branched extensions called dendrites that receive stimuli, and a long extension called an axon, which transmits signals to other nerve cells or muscle cells. The junction between nerve cells where signal transmission occurs is called a synapse. A synaptic signal is a chemical signal that travels between nerve cells. Signals within the nerve cells are propagated by fast-moving electrical impulses. When these impulses reach the end of the axon, the signal continues on to a dendrite of the next cell by the release of chemical ligands called neurotransmitters by the presynaptic cell (the cell emitting the signal). The neurotransmitters are transported across the very small distances between nerve cells, which are called chemical synapses (Figure 2.6.2.2). The small distance between nerve cells allows the signal to travel quickly; this enables an immediate response, such as, Take your hand off the stove!

When the neurotransmitter binds the receptor on the surface of the postsynaptic cell, the electrochemical potential of the target cell changes, and the next electrical impulse is launched. The neurotransmitters that are released into the chemical synapse are degraded quickly or get reabsorbed by the presynaptic cell so that the recipient nerve cell can recover quickly and be prepared to respond rapidly to the next synaptic signal.

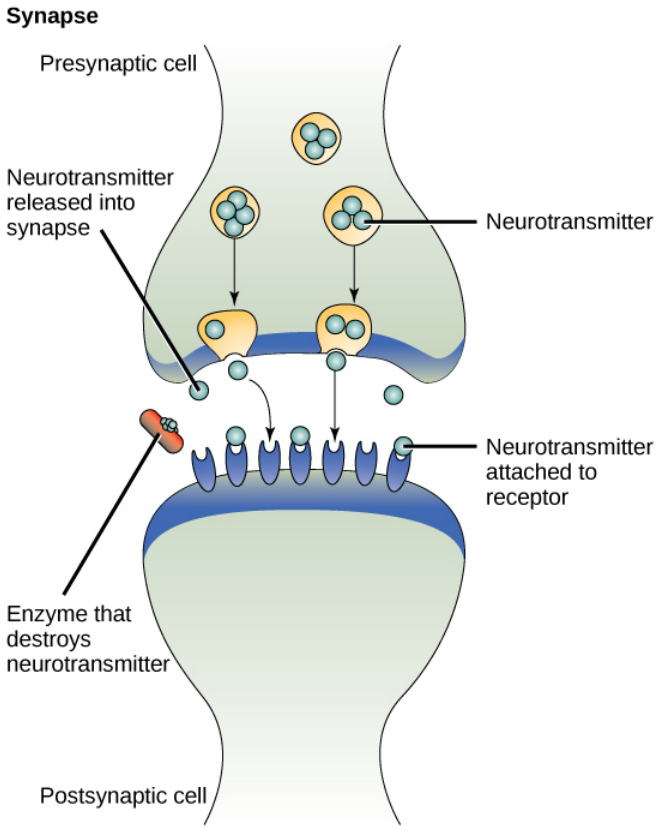


Figure 2.6.2.2: The distance between the presynaptic cell and the postsynaptic cell—called the synaptic gap—is very small and allows for rapid diffusion of the neurotransmitter. Enzymes in the synapatic cleft degrade some types of neurotransmitters to terminate the signal.

Endocrine Signaling

Signals from distant cells are called endocrine signals, and they originate from endocrine cells. (In the body, many endocrine cells are located in endocrine glands, such as the thyroid gland, the hypothalamus, and the pituitary gland.) These types of signals usually produce a slower response but have a longer-lasting effect. The ligands released in endocrine signaling are called hormones, signaling molecules that are produced in one part of the body but affect other body regions some distance away.

Hormones travel the large distances between endocrine cells and their target cells via the bloodstream, which is a relatively slow way to move throughout the body. Because of their form of transport, hormones get diluted and are present in low concentrations when they act on their target cells. This is different from paracrine signaling, in which local concentrations of ligands can be very high.

Autocrine Signaling

Autocrine signals are produced by signaling cells that can also bind to the ligand that is released. This means the signaling cell and the target cell can be the same or a similar cell (the prefix *auto-* means self, a reminder that the signaling cell sends a signal to itself). This type of signaling often occurs during the early development of an organism to ensure that cells develop into the correct tissues and take on the proper function. Autocrine signaling also regulates pain sensation and inflammatory responses. Further, if a cell is infected with a virus, the cell can signal itself to undergo programmed cell death, killing the virus in the process. In some cases, neighboring cells of the same type are also influenced by the released ligand. In embryological development, this process of stimulating a group of neighboring cells may help to direct the differentiation of identical cells into the same cell type, thus ensuring the proper developmental outcome.

Direct Signaling Across Gap Junctions

Gap junctions in animals and plasmodesmata in plants are connections between the plasma membranes of neighboring cells. These water-filled channels allow small signaling molecules, called intracellular mediators, to diffuse between the two cells. Small

molecules, such as calcium ions (Ca^{2+}), are able to move between cells, but large molecules like proteins and DNA cannot fit through the channels. The specificity of the channels ensures that the cells remain independent but can quickly and easily transmit signals. The transfer of signaling molecules communicates the current state of the cell that is directly next to the target cell; this allows a group of cells to coordinate their response to a signal that only one of them may have received. In plants, plasmodesmata are ubiquitous, making the entire plant into a giant, communication network.

Types of Receptors

Receptors are protein molecules in the target cell or on its surface that bind ligand. There are two types of receptors, internal receptors and cell-surface receptors.

Internal receptors

Internal receptors, also known as intracellular or cytoplasmic receptors, are found in the cytoplasm of the cell and respond to hydrophobic ligand molecules that are able to travel across the plasma membrane. Once inside the cell, many of these molecules bind to proteins that act as regulators of mRNA synthesis (transcription) to mediate gene expression. Gene expression is the cellular process of transforming the information in a cell's DNA into a sequence of amino acids, which ultimately forms a protein. When the ligand binds to the internal receptor, a conformational change is triggered that exposes a DNA-binding site on the protein. The ligand-receptor complex moves into the nucleus, then binds to specific regulatory regions of the chromosomal DNA and promotes the initiation of transcription (Figure 2.6.2.3). Transcription is the process of copying the information in a cells DNA into a special form of RNA called messenger RNA (mRNA); the cell uses information in the mRNA (which moves out into the cytoplasm and associates with ribosomes) to link specific amino acids in the correct order, producing a protein. Internal receptors can directly influence gene expression without having to pass the signal on to other receptors or messengers.

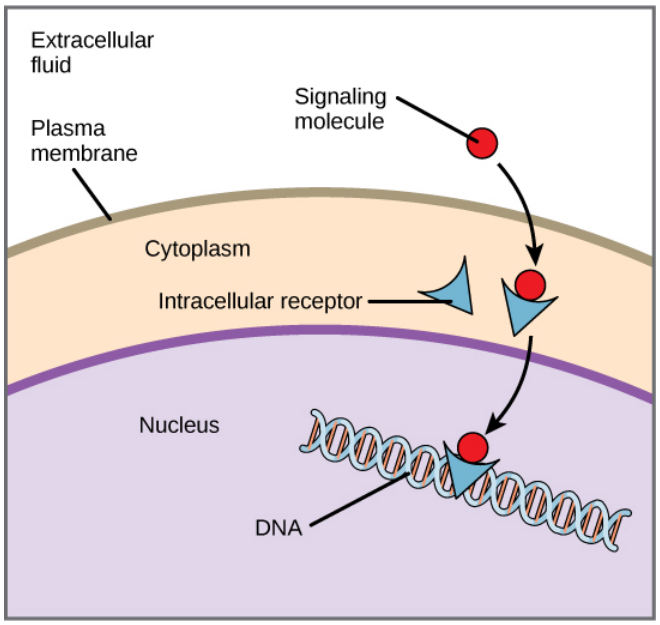


Figure 2.6.2.3: Hydrophobic signaling molecules typically diffuse across the plasma membrane and interact with intracellular receptors in the cytoplasm. Many intracellular receptors are transcription factors that interact with DNA in the nucleus and regulate gene expression.

Cell-Surface Receptors

Cell-surface receptors, also known as transmembrane receptors, are cell surface, membrane-anchored (integral) proteins that bind to external ligand molecules. This type of receptor spans the plasma membrane and performs signal transduction, in which an extracellular signal is converted into an intercellular signal. Ligands that interact with cell-surface receptors do not have to enter the cell that they affect. Cell-surface receptors are also called cell-specific proteins or markers because they are specific to individual cell types.

Because cell-surface receptor proteins are fundamental to normal cell functioning, it should come as no surprise that a malfunction in any one of these proteins could have severe consequences. Errors in the protein structures of certain receptor molecules have

been shown to play a role in hypertension (high blood pressure), asthma, heart disease, and cancer.

Each cell-surface receptor has three main components: an external ligand-binding domain, a hydrophobic membrane-spanning region, and an intracellular domain inside the cell. The ligand-binding domain is also called the extracellular domain. The size and extent of each of these domains vary widely, depending on the type of receptor.

Evolution Connection: How Viruses Recognize a Host

Unlike living cells, many viruses do not have a plasma membrane or any of the structures necessary to sustain life. Some viruses are simply composed of an inert protein shell containing DNA or RNA. To reproduce, viruses must invade a living cell, which serves as a host, and then take over the hosts cellular apparatus. But how does a virus recognize its host?

Viruses often bind to cell-surface receptors on the host cell. For example, the virus that causes human influenza (flu) binds specifically to receptors on membranes of cells of the respiratory system. Chemical differences in the cell-surface receptors among hosts mean that a virus that infects a specific species (for example, humans) cannot infect another species (for example, chickens).

However, viruses have very small amounts of DNA or RNA compared to humans, and, as a result, viral reproduction can occur rapidly. Viral reproduction invariably produces errors that can lead to changes in newly produced viruses; these changes mean that the viral proteins that interact with cell-surface receptors may evolve in such a way that they can bind to receptors in a new host. Such changes happen randomly and quite often in the reproductive cycle of a virus, but the changes only matter if a virus with new binding properties comes into contact with a suitable host. In the case of influenza, this situation can occur in settings where animals and people are in close contact, such as poultry and swine farms.[1] Once a virus jumps to a new host, it can spread quickly. Scientists watch newly appearing viruses (called emerging viruses) closely in the hope that such monitoring can reduce the likelihood of global viral epidemics.

Cell-surface receptors are involved in most of the signaling in multicellular organisms. There are three general categories of cell-surface receptors: ion channel-linked receptors, G-protein-linked receptors, and enzyme-linked receptors.

Ion channel-linked receptors bind a ligand and open a channel through the membrane that allows specific ions to pass through. To form a channel, this type of cell-surface receptor has an extensive membrane-spanning region. In order to interact with the phospholipid fatty acid tails that form the center of the plasma membrane, many of the amino acids in the membrane-spanning region are hydrophobic in nature. Conversely, the amino acids that line the inside of the channel are hydrophilic to allow for the passage of water or ions. When a ligand binds to the extracellular region of the channel, there is a conformational change in the proteins structure that allows ions such as sodium, calcium, magnesium, and hydrogen to pass through (Figure 2.6.2.4).

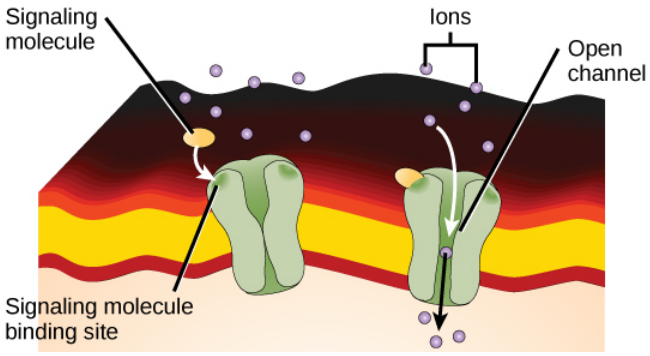


Figure 2.6.2.4: Gated ion channels form a pore through the plasma membrane that opens when the signaling molecule binds. The open pore then allows ions to flow into or out of the cell.

G-protein-linked receptors bind a ligand and activate a membrane protein called a G-protein. The activated G-protein then interacts with either an ion channel or an enzyme in the membrane (Figure 2.6.2.5). All G-protein-linked receptors have seven transmembrane domains, but each receptor has its own specific extracellular domain and G-protein-binding site.

Cell signaling using G-protein-linked receptors occurs as a cyclic series of events. Before the ligand binds, the inactive G-protein can bind to a newly revealed site on the receptor specific for its binding. Once the G-protein binds to the receptor, the resultant

shape change activates the G-protein, which releases GDP and picks up GTP. The subunits of the G-protein then split into the α subunit and the $\beta\gamma$ subunit. One or both of these G-protein fragments may be able to activate other proteins as a result. After awhile, the GTP on the active α subunit of the G-protein is hydrolyzed to GDP and the $\beta\gamma$ subunit is deactivated. The subunits reassociate to form the inactive G-protein and the cycle begins anew.

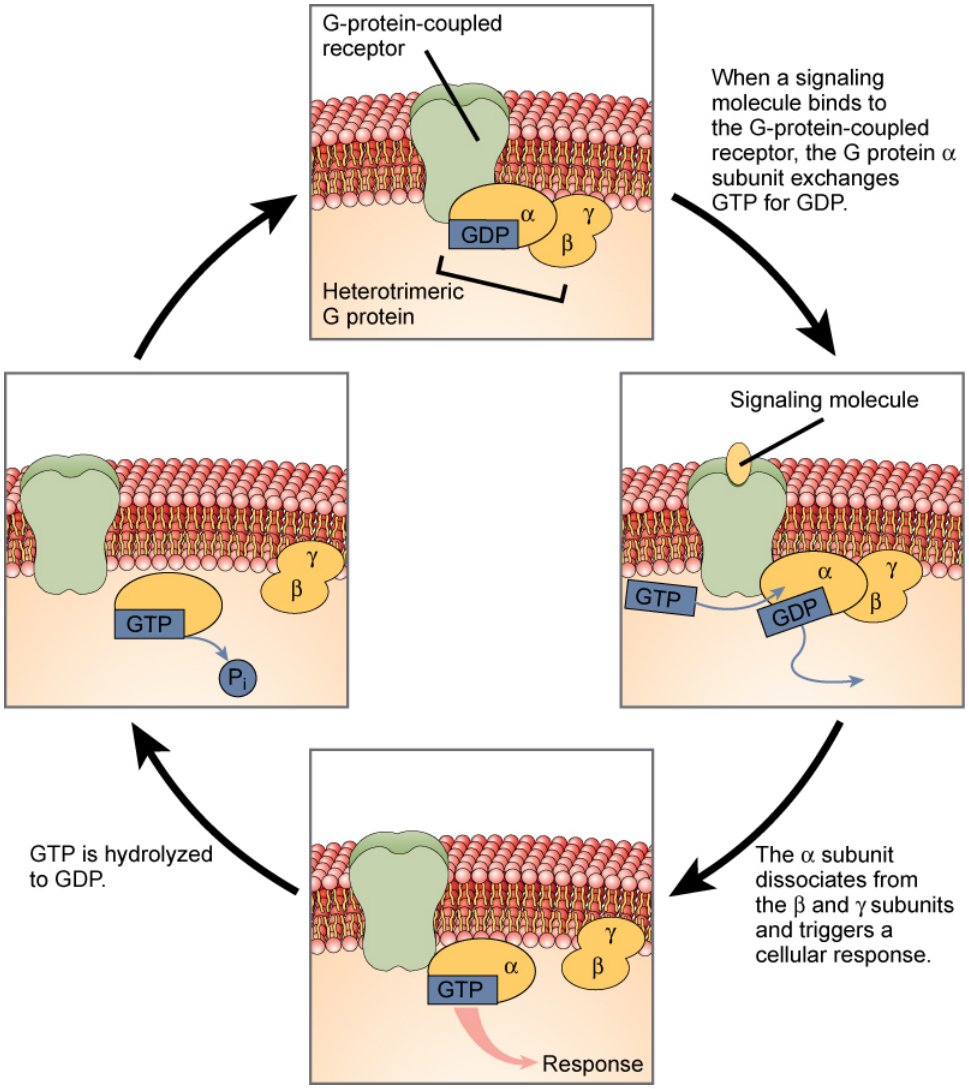
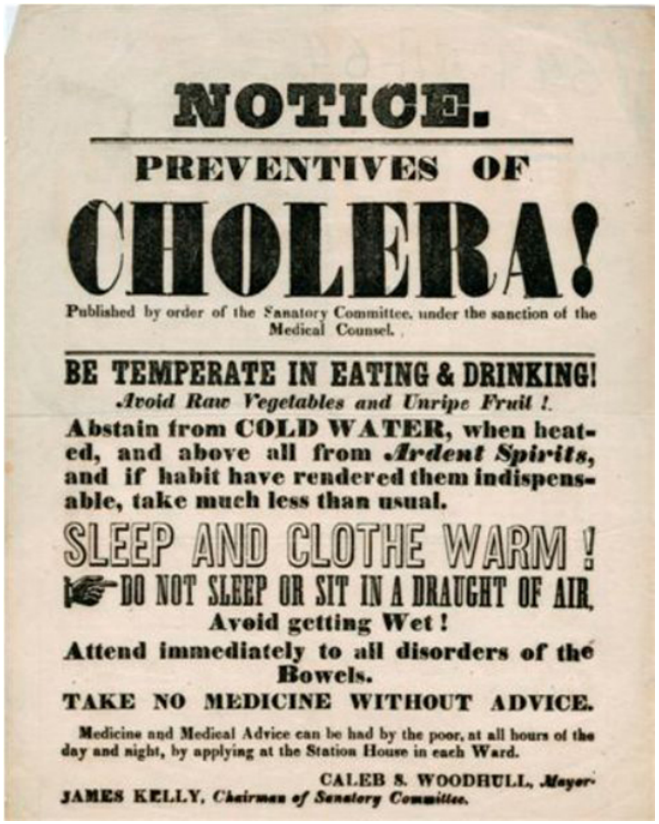


Figure 2.6.2.5: Heterotrimeric G proteins have three subunits: α, β, and γ. When a signaling molecule binds to a G-protein-coupled receptor in the plasma membrane, a GDP molecule associated with the α subunit is exchanged for GTP. The β and γ subunits dissociate from the α subunit, and a cellular response is triggered either by the α subunit or the dissociated $\beta\gamma$ pair. Hydrolysis of GTP to GDP terminates the signal.

G-protein-linked receptors have been extensively studied and much has been learned about their roles in maintaining health. Bacteria that are pathogenic to humans can release poisons that interrupt specific G-protein-linked receptor function, leading to illnesses such as pertussis, botulism, and cholera. In cholera (Figure 2.6.2.6), for example, the water-borne bacterium *Vibrio cholerae* produces a toxin, choleragen, that binds to cells lining the small intestine. The toxin then enters these intestinal cells, where it modifies a G-protein that controls the opening of a chloride channel and causes it to remain continuously active, resulting in large losses of fluids from the body and potentially fatal dehydration as a result.



NOTICE.

PREVENTIVES OF

CHOLERA!

Published by order of the Sanatory Committee, under the sanction of the Medical Counsel.

BE TEMPERATE IN EATING & DRINKING!

Avoid Raw Vegetables and Unripe Fruit !.

Abstain from COLD WATER, when heated, and above all from *Ardent Spirits*, and if habit have rendered them indispensable, take much less than usual.

SLEEP AND CLOTHE WARM !

DO NOT SLEEP OR SIT IN A DRAUGHT OF AIR.

Avoid getting Wet !

Attend immediately to all disorders of the Bowels.

TAKE NO MEDICINE WITHOUT ADVICE.

Medicine and Medical Advice can be had by the poor, at all hours of the day and night, by applying at the Station House in each Ward.

CALEB S. WOODHULL, *Mayor.*

JAMES KELLY, *Chairman of Sanatory Committee.*

Figure 2.6.2.6: Transmitted primarily through contaminated drinking water, cholera is a major cause of death in the developing world and in areas where natural disasters interrupt the availability of clean water. The cholera bacterium, *Vibrio cholerae*, creates a toxin that modifies G-protein-mediated cell signaling pathways in the intestines. Modern sanitation eliminates the threat of cholera outbreaks, such as the one that swept through New York City in 1866. This poster from that era shows how, at that time, the way that the disease was transmitted was not understood. (credit: New York City Sanitary Commission)

Enzyme-linked receptors are cell-surface receptors with intracellular domains that are associated with an enzyme. In some cases, the intracellular domain of the receptor itself is an enzyme. Other enzyme-linked receptors have a small intracellular domain that interacts directly with an enzyme. The enzyme-linked receptors normally have large extracellular and intracellular domains, but the membrane-spanning region consists of a single alpha-helical region of the peptide strand. When a ligand binds to the extracellular domain, a signal is transferred through the membrane, activating the enzyme. Activation of the enzyme sets off a chain of events within the cell that eventually leads to a response. One example of this type of enzyme-linked receptor is the tyrosine kinase receptor (Figure 2.6.2.7). A kinase is an enzyme that transfers phosphate groups from ATP to another protein. The tyrosine kinase receptor transfers phosphate groups to tyrosine molecules (tyrosine residues). First, signaling molecules bind to the extracellular domain of two nearby tyrosine kinase receptors. The two neighboring receptors then bond together, or dimerize. Phosphates are then added to tyrosine residues on the intracellular domain of the receptors (phosphorylation). The phosphorylated residues can then transmit the signal to the next messenger within the cytoplasm.

Art Connection

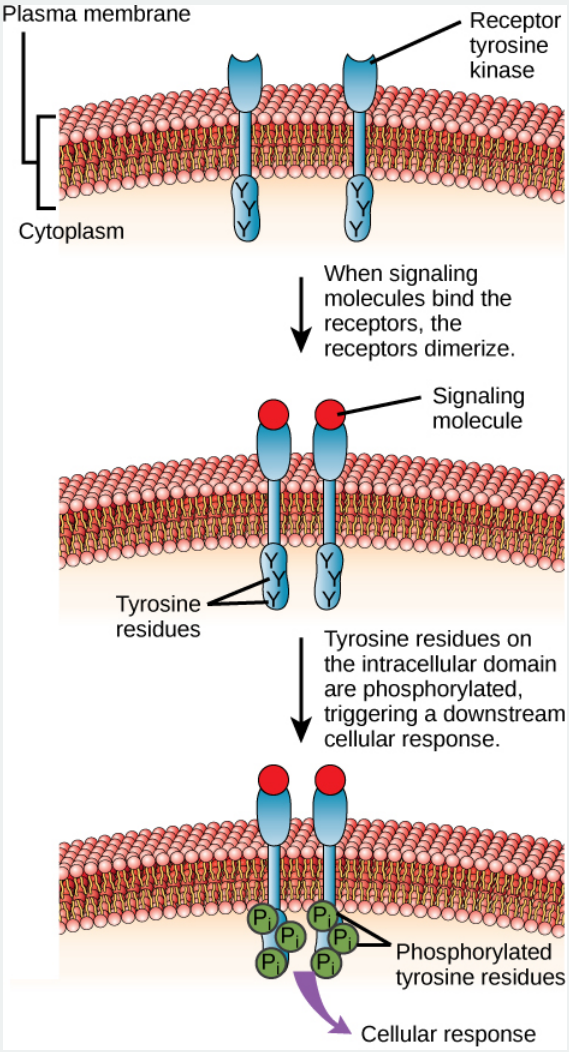


Figure 2.6.2.7: A receptor tyrosine kinase is an enzyme-linked receptor with a single transmembrane region, and extracellular and intracellular domains. Binding of a signaling molecule to the extracellular domain causes the receptor to dimerize. Tyrosine residues on the intracellular domain are then autophosphorylated, triggering a downstream cellular response. The signal is terminated by a phosphatase that removes the phosphates from the phosphotyrosine residues.

Figure 2.6.2.7: HER2 is a receptor tyrosine kinase. In 30 percent of human breast cancers, HER2 is permanently activated, resulting in unregulated cell division. Lapatinib, a drug used to treat breast cancer, inhibits HER2 receptor tyrosine kinase autophosphorylation (the process by which the receptor adds phosphates onto itself), thus reducing tumor growth by 50 percent. Besides autophosphorylation, which of the following steps would be inhibited by Lapatinib?

A. Signaling molecule binding, dimerization, and the downstream cellular response.
B. Dimerization, and the downstream cellular response.
C. The downstream cellular response.
D. Phosphatase activity, dimerization, and the downsteam cellular response.

Answer

C. The downstream cellular response would be inhibited.

Signaling Molecules

Produced by signaling cells and the subsequent binding to receptors in target cells, ligands act as chemical signals that travel to the target cells to coordinate responses. The types of molecules that serve as ligands are incredibly varied and range from small

proteins to small ions like calcium (Ca^{2+}).

Small Hydrophobic Ligands

Small hydrophobic ligands can directly diffuse through the plasma membrane and interact with internal receptors. Important members of this class of ligands are the steroid hormones. Steroids are lipids that have a hydrocarbon skeleton with four fused rings; different steroids have different functional groups attached to the carbon skeleton. Steroid hormones include the female sex hormone, estradiol, which is a type of estrogen; the male sex hormone, testosterone; and cholesterol, which is an important structural component of biological membranes and a precursor of steroid hormones (Figure 2.6.2.8). Other hydrophobic hormones include thyroid hormones and vitamin D. In order to be soluble in blood, hydrophobic ligands must bind to carrier proteins while they are being transported through the bloodstream.

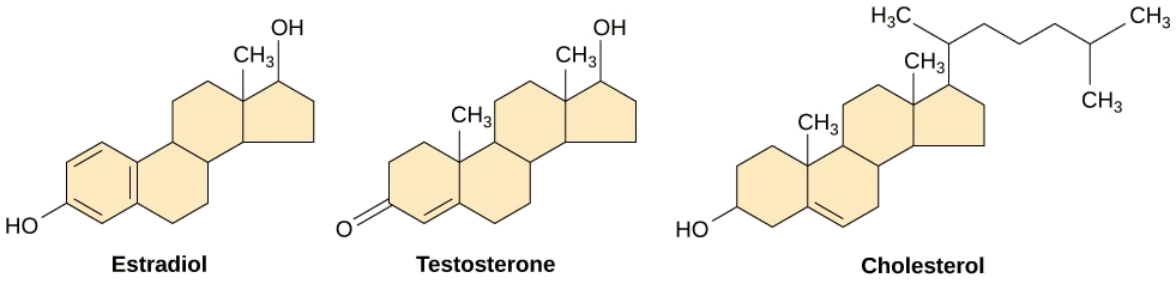


Figure 2.6.2.8: Steroid hormones have similar chemical structures to their precursor, cholesterol. Because these molecules are small and hydrophobic, they can diffuse directly across the plasma membrane into the cell, where they interact with internal receptors.

Water-Soluble Ligands

Water-soluble ligands are polar and therefore cannot pass through the plasma membrane unaided; sometimes, they are too large to pass through the membrane at all. Instead, most water-soluble ligands bind to the extracellular domain of cell-surface receptors. This group of ligands is quite diverse and includes small molecules, peptides, and proteins.

Other Ligands

Nitric oxide (NO) is a gas that also acts as a ligand. It is able to diffuse directly across the plasma membrane, and one of its roles is to interact with receptors in smooth muscle and induce relaxation of the tissue. NO has a very short half-life and therefore only functions over short distances. Nitroglycerin, a treatment for heart disease, acts by triggering the release of NO, which causes blood vessels to dilate (expand), thus restoring blood flow to the heart. NO has become better known recently because the pathway that it affects is targeted by prescription medications for erectile dysfunction, such as Viagra (erection involves dilated blood vessels).

Summary

Cells communicate by both inter- and intracellular signaling. Signaling cells secrete ligands that bind to target cells and initiate a chain of events within the target cell. The four categories of signaling in multicellular organisms are paracrine signaling, endocrine signaling, autocrine signaling, and direct signaling across gap junctions. Paracrine signaling takes place over short distances. Endocrine signals are carried long distances through the bloodstream by hormones, and autocrine signals are received by the same cell that sent the signal or other nearby cells of the same kind. Gap junctions allow small molecules, including signaling molecules, to flow between neighboring cells.

Internal receptors are found in the cell cytoplasm. Here, they bind ligand molecules that cross the plasma membrane; these receptor-ligand complexes move to the nucleus and interact directly with cellular DNA. Cell-surface receptors transmit a signal from outside the cell to the cytoplasm. Ion channel-linked receptors, when bound to their ligands, form a pore through the plasma membrane through which certain ions can pass. G-protein-linked receptors interact with a G-protein on the cytoplasmic side of the plasma membrane, promoting the exchange of bound GDP for GTP and interacting with other enzymes or ion channels to transmit a signal. Enzyme-linked receptors transmit a signal from outside the cell to an intracellular domain of a membrane-bound enzyme. Ligand binding causes activation of the enzyme. Small hydrophobic ligands (like steroids) are able to penetrate the plasma membrane and bind to internal receptors. Water-soluble hydrophilic ligands are unable to pass through the membrane; instead, they bind to cell-surface receptors, which transmit the signal to the inside of the cell.

Footnotes

1. 1 A. B. Sigalov, The School of Nature. IV. Learning from Viruses, *Self/Nonself* 1, no. 4 (2010): 282-298. Y. Cao, X. Koh, L. Dong, X. Du, A. Wu, X. Ding, H. Deng, Y. Shu, J. Chen, T. Jiang, Rapid Estimation of Binding Activity of Influenza Virus Hemagglutinin to Human and Avian Receptors, *PLoS One* 6, no. 4 (2011): e18664.

Glossary

autocrine signal
signal that is sent and received by the same or similar nearby cells

cell-surface receptor
cell-surface protein that transmits a signal from the exterior of the cell to the interior, even though the ligand does not enter the cell

chemical synapse
small space between axon terminals and dendrites of nerve cells where neurotransmitters function

endocrine cell
cell that releases ligands involved in endocrine signaling (hormones)

endocrine signal
long-distance signal that is delivered by ligands (hormones) traveling through an organisms circulatory system from the signaling cell to the target cell

enzyme-linked receptor
cell-surface receptor with intracellular domains that are associated with membrane-bound enzymes

extracellular domain
region of a cell-surface receptor that is located on the cell surface

G-protein-linked receptor
cell-surface receptor that activates membrane-bound G-proteins to transmit a signal from the receptor to nearby membrane components

intercellular signaling
communication between cells

internal receptor
(also, intracellular receptor) receptor protein that is located in the cytosol of a cell and binds to ligands that pass through the plasma membrane

intracellular mediator
(also, second messenger) small molecule that transmits signals within a cell

intracellular signaling
communication within cells

ion channel-linked receptor
cell-surface receptor that forms a plasma membrane channel, which opens when a ligand binds to the extracellular domain (ligand-gated channels)

ligand

molecule produced by a signaling cell that binds with a specific receptor, delivering a signal in the process

neurotransmitter

chemical ligand that carries a signal from one nerve cell to the next

paracrine signal

signal between nearby cells that is delivered by ligands traveling in the liquid medium in the space between the cells

receptor

protein in or on a target cell that bind to ligands

signaling cell

cell that releases signal molecules that allow communication with another cell

synaptic signal

chemical signal (neurotransmitter) that travels between nerve cells

target cell

cell that has a receptor for a signal or ligand from a signaling cell

---

This page titled 2.6.2: Signaling Molecules and Cellular Receptors is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **9.1: Signaling Molecules and Cellular Receptors** by OpenStax is licensed CC BY 4.0.

2.6.3: Propagation of the Signal

Skills to Develop

- Explain how the binding of a ligand initiates signal transduction throughout a cell
- Recognize the role of phosphorylation in the transmission of intracellular signals
- Evaluate the role of second messengers in signal transmission

Once a ligand binds to a receptor, the signal is transmitted through the membrane and into the cytoplasm. Continuation of a signal in this manner is called signal transduction. Signal transduction only occurs with cell-surface receptors because internal receptors are able to interact directly with DNA in the nucleus to initiate protein synthesis.

When a ligand binds to its receptor, conformational changes occur that affect the receptor's intracellular domain. Conformational changes of the extracellular domain upon ligand binding can propagate through the membrane region of the receptor and lead to activation of the intracellular domain or its associated proteins. In some cases, binding of the ligand causes dimerization of the receptor, which means that two receptors bind to each other to form a stable complex called a dimer. A dimer is a chemical compound formed when two molecules (often identical) join together. The binding of the receptors in this manner enables their intracellular domains to come into close contact and activate each other.

Binding Initiates a Signaling Pathway

After the ligand binds to the cell-surface receptor, the activation of the receptor's intracellular components sets off a chain of events that is called a signaling pathway or a signaling cascade. In a signaling pathway, second messengers, enzymes, and activated proteins interact with specific proteins, which are in turn activated in a chain reaction that eventually leads to a change in the cell's environment (Figure 2.6.3.1). The events in the cascade occur in a series, much like a current flows in a river. Interactions that occur before a certain point are defined as upstream events, and events after that point are called downstream events.

Art Connection

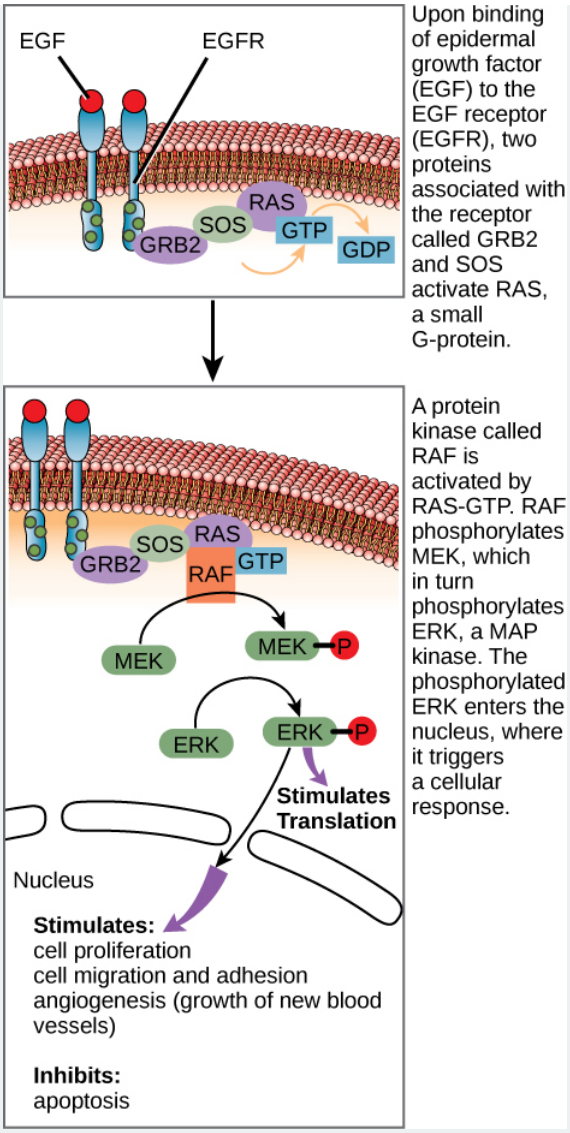


Figure 2.6.3.1: The epidermal growth factor (EGF) receptor (EGFR) is a receptor tyrosine kinase involved in the regulation of cell growth, wound healing, and tissue repair. When EGF binds to the EGFR, a cascade of downstream events causes the cell to grow and divide. If EGFR is activated at inappropriate times, uncontrolled cell growth (cancer) may occur.

In certain cancers, the GTPase activity of the RAS G-protein is inhibited. This means that the RAS protein can no longer hydrolyze GTP into GDP. What effect would this have on downstream cellular events?

Signaling pathways can get very complicated very quickly because most cellular proteins can affect different downstream events, depending on the conditions within the cell. A single pathway can branch off toward different endpoints based on the interplay between two or more signaling pathways, and the same ligands are often used to initiate different signals in different cell types. This variation in response is due to differences in protein expression in different cell types. Another complicating element is signal integration of the pathways, in which signals from two or more different cell-surface receptors merge to activate the same response in the cell. This process can ensure that multiple external requirements are met before a cell commits to a specific response.

The effects of extracellular signals can also be amplified by enzymatic cascades. At the initiation of the signal, a single ligand binds to a single receptor. However, activation of a receptor-linked enzyme can activate many copies of a component of the signaling cascade, which amplifies the signal.

Methods of Intracellular Signaling

The induction of a signaling pathway depends on the modification of a cellular component by an enzyme. There are numerous enzymatic modifications that can occur, and they are recognized in turn by the next component downstream. The following are some of the more common events in intracellular signaling.

Phosphorylation

One of the most common chemical modifications that occurs in signaling pathways is the addition of a phosphate group (PO_4^{-3}) to a molecule such as a protein in a process called phosphorylation. The phosphate can be added to a nucleotide such as GMP to form GDP or GTP. Phosphates are also often added to serine, threonine, and tyrosine residues of proteins, where they replace the hydroxyl group of the amino acid (Figure 2.6.3.2). The transfer of the phosphate is catalyzed by an enzyme called a kinase. Various kinases are named for the substrate they phosphorylate. Phosphorylation of serine and threonine residues often activates enzymes. Phosphorylation of tyrosine residues can either affect the activity of an enzyme or create a binding site that interacts with downstream components in the signaling cascade. Phosphorylation may activate or inactivate enzymes, and the reversal of phosphorylation, dephosphorylation by a phosphatase, will reverse the effect.

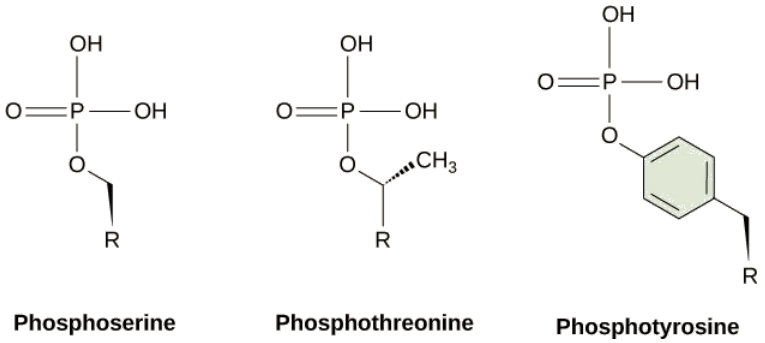


Figure 2.6.3.2: In protein phosphorylation, a phosphate group (PO_4^{-3}) is added to residues of the amino acids serine, threonine, and tyrosine.

Second Messengers

Second messengers are small molecules that propagate a signal after it has been initiated by the binding of the signaling molecule to the receptor. These molecules help to spread a signal through the cytoplasm by altering the behavior of certain cellular proteins.

Calcium ion is a widely used second messenger. The free concentration of calcium ions (Ca^{2+}) within a cell is very low because ion pumps in the plasma membrane continuously use adenosine-5'-triphosphate (ATP) to remove it. For signaling purposes, Ca^{2+} is stored in cytoplasmic vesicles, such as the endoplasmic reticulum, or accessed from outside the cell. When signaling occurs, ligand-gated calcium ion channels allow the higher levels of Ca^{2+} that are present outside the cell (or in intracellular storage compartments) to flow into the cytoplasm, which raises the concentration of cytoplasmic Ca^{2+}. The response to the increase in Ca^{2+} varies, depending on the cell type involved. For example, in the β-cells of the pancreas, Ca^{2+} signaling leads to the release of insulin, and in muscle cells, an increase in Ca^{2+} leads to muscle contractions.

Another second messenger utilized in many different cell types is cyclic AMP (cAMP). Cyclic AMP is synthesized by the enzyme adenylyl cyclase from ATP (Figure 2.6.3.3). The main role of cAMP in cells is to bind to and activate an enzyme called cAMP-dependent kinase (A-kinase). A-kinase regulates many vital metabolic pathways: It phosphorylates serine and threonine residues of its target proteins, activating them in the process. A-kinase is found in many different types of cells, and the target proteins in each kind of cell are different. Differences give rise to the variation of the responses to cAMP in different cells.

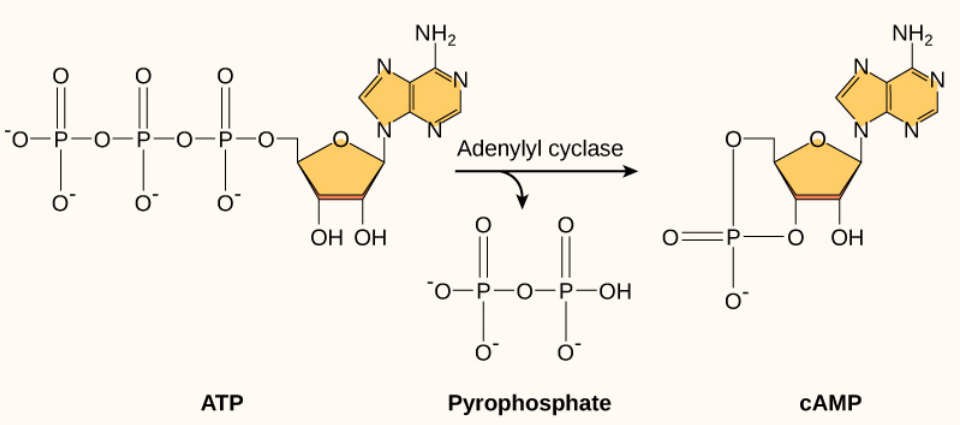


Figure 2.6.3.3: This diagram shows the mechanism for the formation of cyclic AMP (cAMP). cAMP serves as a second messenger to activate or inactivate proteins within the cell. Termination of the signal occurs when an enzyme called phosphodiesterase converts cAMP into AMP.

Present in small concentrations in the plasma membrane, inositol phospholipids are lipids that can also be converted into second messengers. Because these molecules are membrane components, they are located near membrane-bound receptors and can easily interact with them. Phosphatidylinositol (PI) is the main phospholipid that plays a role in cellular signaling. Enzymes known as kinases phosphorylate PI to form PI-phosphate (PIP) and PI-bisphosphate (PIP_2).

The enzyme phospholipase C cleaves PIP_2 to form diacylglycerol (DAG) and inositol triphosphate (IP_3) (Figure 2.6.3.4). These products of the cleavage of PIP_2 serve as second messengers. Diacylglycerol (DAG) remains in the plasma membrane and activates protein kinase C (PKC), which then phosphorylates serine and threonine residues in its target proteins. IP_3 diffuses into the cytoplasm and binds to ligand-gated calcium channels in the endoplasmic reticulum to release Ca^{2+} that continues the signal cascade.

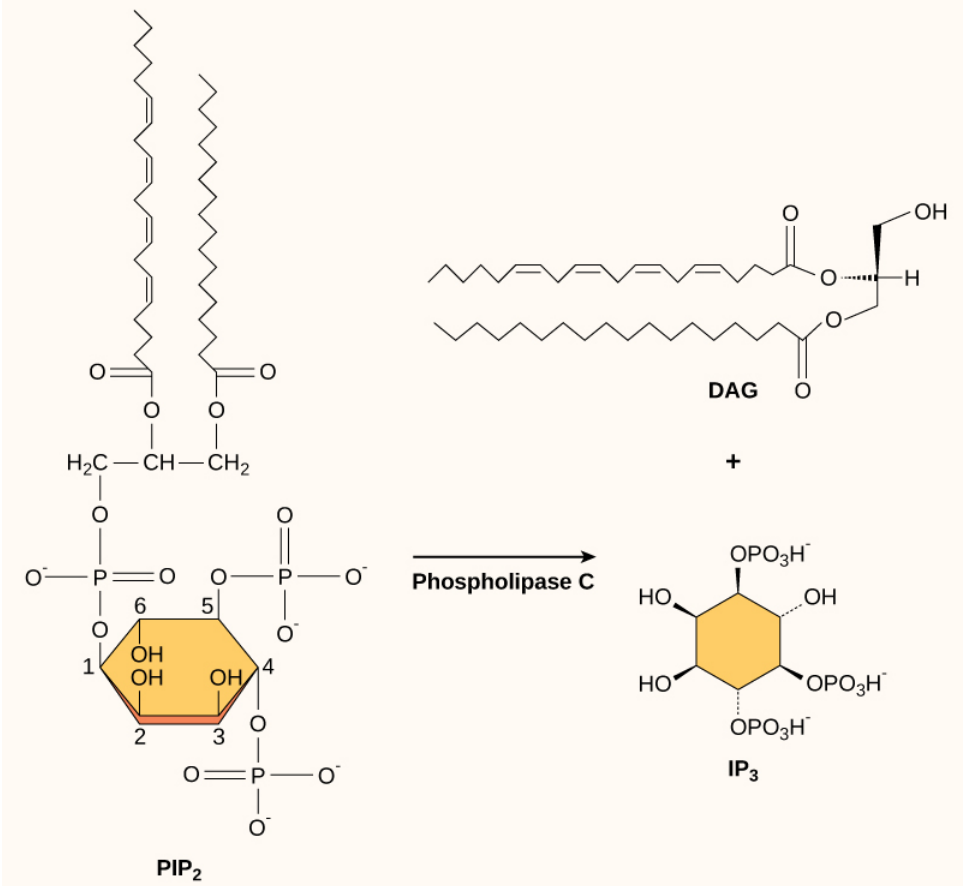


Figure 2.6.3.4: The enzyme phospholipase C breaks down PIP_2 into IP_3 and DAG, both of which serve as second messengers.

Summary

Ligand binding to the receptor allows for signal transduction through the cell. The chain of events that conveys the signal through the cell is called a signaling pathway or cascade. Signaling pathways are often very complex because of the interplay between different proteins. A major component of cell signaling cascades is the phosphorylation of molecules by enzymes known as kinases. Phosphorylation adds a phosphate group to serine, threonine, and tyrosine residues in a protein, changing their shapes, and activating or inactivating the protein. Small molecules like nucleotides can also be phosphorylated. Second messengers are small, non-protein molecules that are used to transmit a signal within a cell. Some examples of second messengers are calcium ions (Ca^{2+}), cyclic AMP (cAMP), diacylglycerol (DAG), and inositol triphosphate (IP_3).

Art Connections

Figure 2.6.3.1: In certain cancers, the GTPase activity of the RAS G-protein is inhibited. This means that the RAS protein can no longer hydrolyze GTP into GDP. What effect would this have on downstream cellular events?

Answer

ERK would become permanently activated, resulting in cell proliferation, migration, adhesion, and the growth of new blood vessels. Apoptosis would be inhibited.

Glossary

cyclic AMP (cAMP)

second messenger that is derived from ATP

cyclic AMP-dependent kinase

(also, protein kinase A, or PKA) kinase that is activated by binding to cAMP

diacylglycerol (DAG)
cleavage product of PIP_2 that is used for signaling within the plasma membrane

dimer
chemical compound formed when two molecules join together

dimerization
(of receptor proteins) interaction of two receptor proteins to form a functional complex called a dimer

inositol phospholipid
lipid present at small concentrations in the plasma membrane that is converted into a second messenger; it has inositol (a carbohydrate) as its hydrophilic head group

inositol triphosphate (IP_3)
cleavage product of PIP_2 that is used for signaling within the cell

kinase
enzyme that catalyzes the transfer of a phosphate group from ATP to another molecule

second messenger
small, non-protein molecule that propagates a signal within the cell after activation of a receptor causes its release

signal integration
interaction of signals from two or more different cell-surface receptors that merge to activate the same response in the cell

signal transduction
propagation of the signal through the cytoplasm (and sometimes also the nucleus) of the cell

signaling pathway
(also signaling cascade) chain of events that occurs in the cytoplasm of the cell to propagate the signal from the plasma membrane to produce a response

---

This page titled 2.6.3: Propagation of the Signal is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **9.2: Propagation of the Signal** by OpenStax is licensed CC BY 4.0.

2.6.4: Response to the Signal

Skills to Develop

- Describe how signaling pathways direct protein expression, cellular metabolism, and cell growth
- Identify the function of PKC in signal transduction pathways
- Recognize the role of apoptosis in the development and maintenance of a healthy organism

Inside the cell, ligands bind to their internal receptors, allowing them to directly affect the cell's DNA and protein-producing machinery. Using signal transduction pathways, receptors in the plasma membrane produce a variety of effects on the cell. The results of signaling pathways are extremely varied and depend on the type of cell involved as well as the external and internal conditions. A small sampling of responses is described below.

Gene Expression

Some signal transduction pathways regulate the transcription of RNA. Others regulate the translation of proteins from mRNA. An example of a protein that regulates translation in the nucleus is the MAP kinase ERK. ERK is activated in a phosphorylation cascade when epidermal growth factor (EGF) binds the EGF receptor (see Figure 9.2.1). Upon phosphorylation, ERK enters the nucleus and activates a protein kinase that, in turn, regulates protein translation (Figure 2.6.4.1).

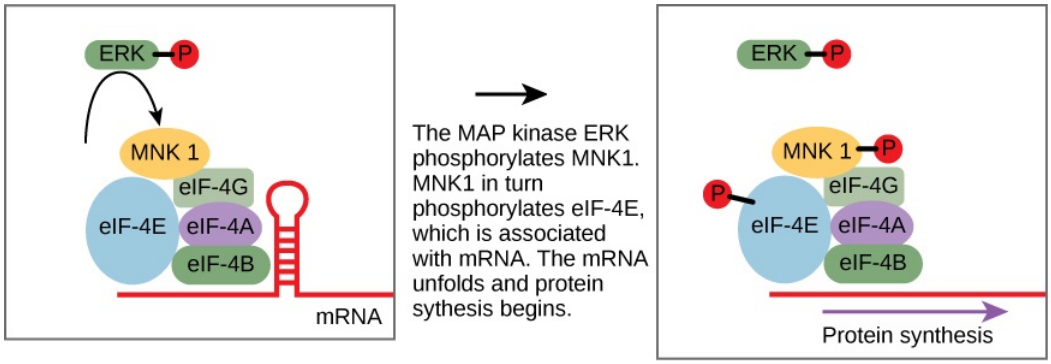


Figure 2.6.4.1: ERK is a MAP kinase that activates translation when it is phosphorylated. ERK phosphorylates MNK1, which in turn phosphorylates eIF-4E, an elongation initiation factor that, with other initiation factors, is associated with mRNA. When eIF-4E becomes phosphorylated, the mRNA unfolds, allowing protein synthesis in the nucleus to begin. (See Figure 9.2.1 for the phosphorylation pathway that activates ERK.)

The second kind of protein with which PKC can interact is a protein that acts as an inhibitor. An inhibitor is a molecule that binds to a protein and prevents it from functioning or reduces its function. In this case, the inhibitor is a protein called Iκ-B, which binds to the regulatory protein NF-κB. (The symbol κ represents the Greek letter kappa.) When Iκ-B is bound to NF-κB, the complex cannot enter the nucleus of the cell, but when Iκ-B is phosphorylated by PKC, it can no longer bind NF-κB, and NF-κB (a transcription factor) can enter the nucleus and initiate RNA transcription. In this case, the effect of phosphorylation is to inactivate an inhibitor and thereby activate the process of transcription.

Increase in Cellular Metabolism

The result of another signaling pathway affects muscle cells. The activation of β-adrenergic receptors in muscle cells by adrenaline leads to an increase in cyclic AMP (cAMP) inside the cell. Also known as epinephrine, adrenaline is a hormone (produced by the adrenal gland attached to the kidney) that readies the body for short-term emergencies. Cyclic AMP activates PKA (protein kinase A), which in turn phosphorylates two enzymes. The first enzyme promotes the degradation of glycogen by activating intermediate glycogen phosphorylase kinase (GPK) that in turn activates glycogen phosphorylase (GP) that catabolizes glycogen into glucose. (Recall that your body converts excess glucose to glycogen for short-term storage. When energy is needed, glycogen is quickly reconverted to glucose.) Phosphorylation of the second enzyme, glycogen synthase (GS), inhibits its ability to form glycogen from glucose. In this manner, a muscle cell obtains a ready pool of glucose by activating its formation via glycogen degradation and by inhibiting the use of glucose to form glycogen, thus preventing a futile cycle of glycogen degradation and synthesis. The glucose is then available for use by the muscle cell in response to a sudden surge of adrenaline—the "fight or flight" reflex.

Cell Growth

Cell signaling pathways also play a major role in cell division. Cells do not normally divide unless they are stimulated by signals from other cells. The ligands that promote cell growth are called growth factors. Most growth factors bind to cell-surface receptors that are linked to tyrosine kinases. These cell-surface receptors are called receptor tyrosine kinases (RTKs). Activation of RTKs initiates a signaling pathway that includes a G-protein called RAS, which activates the MAP kinase pathway described earlier. The enzyme MAP kinase then stimulates the expression of proteins that interact with other cellular components to initiate cell division.

Career Connection: Cancer Biologist

Cancer biologists study the molecular origins of cancer with the goal of developing new prevention methods and treatment strategies that will inhibit the growth of tumors without harming the normal cells of the body. As mentioned earlier, signaling pathways control cell growth. These signaling pathways are controlled by signaling proteins, which are, in turn, expressed by genes. Mutations in these genes can result in malfunctioning signaling proteins. This prevents the cell from regulating its cell cycle, triggering unrestricted cell division and cancer. The genes that regulate the signaling proteins are one type of oncogene which is a gene that has the potential to cause cancer. The gene encoding RAS is an oncogene that was originally discovered when mutations in the RAS protein were linked to cancer. Further studies have indicated that 30 percent of cancer cells have a mutation in the RAS gene that leads to uncontrolled growth. If left unchecked, uncontrolled cell division can lead tumor formation and metastasis, the growth of cancer cells in new locations in the body.

Cancer biologists have been able to identify many other oncogenes that contribute to the development of cancer. For example, HER2 is a cell-surface receptor that is present in excessive amounts in 20 percent of human breast cancers. Cancer biologists realized that gene duplication led to HER2 overexpression in 25 percent of breast cancer patients and developed a drug called Herceptin (trastuzumab). Herceptin is a monoclonal antibody that targets HER2 for removal by the immune system. Herceptin therapy helps to control signaling through HER2. The use of Herceptin in combination with chemotherapy has helped to increase the overall survival rate of patients with metastatic breast cancer.

Cell Death

When a cell is damaged, superfluous, or potentially dangerous to an organism, a cell can initiate a mechanism to trigger programmed cell death, or apoptosis. Apoptosis allows a cell to die in a controlled manner that prevents the release of potentially damaging molecules from inside the cell. There are many internal checkpoints that monitor a cell's health; if abnormalities are observed, a cell can spontaneously initiate the process of apoptosis. However, in some cases, such as a viral infection or uncontrolled cell division due to cancer, the cell's normal checks and balances fail. External signaling can also initiate apoptosis. For example, most normal animal cells have receptors that interact with the extracellular matrix, a network of glycoproteins that provides structural support for cells in an organism. The binding of cellular receptors to the extracellular matrix initiates a signaling cascade within the cell. However, if the cell moves away from the extracellular matrix, the signaling ceases, and the cell undergoes apoptosis. This system keeps cells from traveling through the body and proliferating out of control, as happens with tumor cells that metastasize.

Another example of external signaling that leads to apoptosis occurs in T-cell development. T-cells are immune cells that bind to foreign macromolecules and particles, and target them for destruction by the immune system. Normally, T-cells do not target "self" proteins (those of their own organism), a process that can lead to autoimmune diseases. In order to develop the ability to discriminate between self and non-self, immature T-cells undergo screening to determine whether they bind to so-called self proteins. If the T-cell receptor binds to self proteins, the cell initiates apoptosis to remove the potentially dangerous cell.

Apoptosis is also essential for normal embryological development. In vertebrates, for example, early stages of development include the formation of web-like tissue between individual fingers and toes (Figure 2.6.4.2). During the course of normal development, these unneeded cells must be eliminated, enabling fully separated fingers and toes to form. A cell signaling mechanism triggers apoptosis, which destroys the cells between the developing digits.



Figure 2.6.4.2: The histological section of a foot of a 15-day-old mouse embryo, visualized using light microscopy, reveals areas of tissue between the toes, which apoptosis will eliminate before the mouse reaches its full gestational age at 27 days. (credit: modification of work by Michal Mañas)

Termination of the Signal Cascade

The aberrant signaling often seen in tumor cells is proof that the termination of a signal at the appropriate time can be just as important as the initiation of a signal. One method of stopping a specific signal is to degrade the ligand or remove it so that it can no longer access its receptor. One reason that hydrophobic hormones like estrogen and testosterone trigger long-lasting events is because they bind carrier proteins. These proteins allow the insoluble molecules to be soluble in blood, but they also protect the hormones from degradation by circulating enzymes.

Inside the cell, many different enzymes reverse the cellular modifications that result from signaling cascades. For example, phosphatases are enzymes that remove the phosphate group attached to proteins by kinases in a process called dephosphorylation. Cyclic AMP (cAMP) is degraded into AMP by phosphodiesterase, and the release of calcium stores is reversed by the Ca^{2+} pumps that are located in the external and internal membranes of the cell.

Summary

The initiation of a signaling pathway is a response to external stimuli. This response can take many different forms, including protein synthesis, a change in the cell's metabolism, cell growth, or even cell death. Many pathways influence the cell by initiating gene expression, and the methods utilized are quite numerous. Some pathways activate enzymes that interact with DNA transcription factors. Others modify proteins and induce them to change their location in the cell. Depending on the status of the organism, cells can respond by storing energy as glycogen or fat, or making it available in the form of glucose. A signal transduction pathway allows muscle cells to respond to immediate requirements for energy in the form of glucose. Cell growth is

almost always stimulated by external signals called growth factors. Uncontrolled cell growth leads to cancer, and mutations in the genes encoding protein components of signaling pathways are often found in tumor cells. Programmed cell death, or apoptosis, is important for removing damaged or unnecessary cells. The use of cellular signaling to organize the dismantling of a cell ensures that harmful molecules from the cytoplasm are not released into the spaces between cells, as they are in uncontrolled death, necrosis. Apoptosis also ensures the efficient recycling of the components of the dead cell. Termination of the cellular signaling cascade is very important so that the response to a signal is appropriate in both timing and intensity. Degradation of signaling molecules and dephosphorylation of phosphorylated intermediates of the pathway by phosphatases are two ways to terminate signals within the cell.

Glossary

apoptosis
: programmed cell death

growth factor
: ligand that binds to cell-surface receptors and stimulates cell growth

inhibitor
: molecule that binds to a protein (usually an enzyme) and keeps it from functioning

phosphatase
: enzyme that removes the phosphate group from a molecule that has been previously phosphorylated

phosphodiesterase
: enzyme that degrades cAMP, producing AMP, to terminate signaling

---

This page titled 2.6.4: Response to the Signal is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **9.3: Response to the Signal** by OpenStax is licensed CC BY 4.0.

2.6.5: Signaling in Single-Celled Organisms

Skills to Develop

- Describe how single-celled yeasts use cell signaling to communicate with one another
- Relate the role of quorum sensing to the ability of some bacteria to form biofilms

Within-cell signaling allows bacteria to respond to environmental cues, such as nutrient levels, some single-celled organisms also release molecules to signal to each other.

Signaling in Yeast

Yeasts are eukaryotes (fungi), and the components and processes found in yeast signals are similar to those of cell-surface receptor signals in multicellular organisms. Budding yeasts (Figure 2.6.5.1) are able to participate in a process that is similar to sexual reproduction that entails two haploid cells (cells with one-half the normal number of chromosomes) combining to form a diploid cell (a cell with two sets of each chromosome, which is what normal body cells contain). In order to find another haploid yeast cell that is prepared to mate, budding yeasts secrete a signaling molecule called mating factor. When mating factor binds to cell-surface receptors in other yeast cells that are nearby, they stop their normal growth cycles and initiate a cell signaling cascade that includes protein kinases and GTP-binding proteins that are similar to G-proteins.

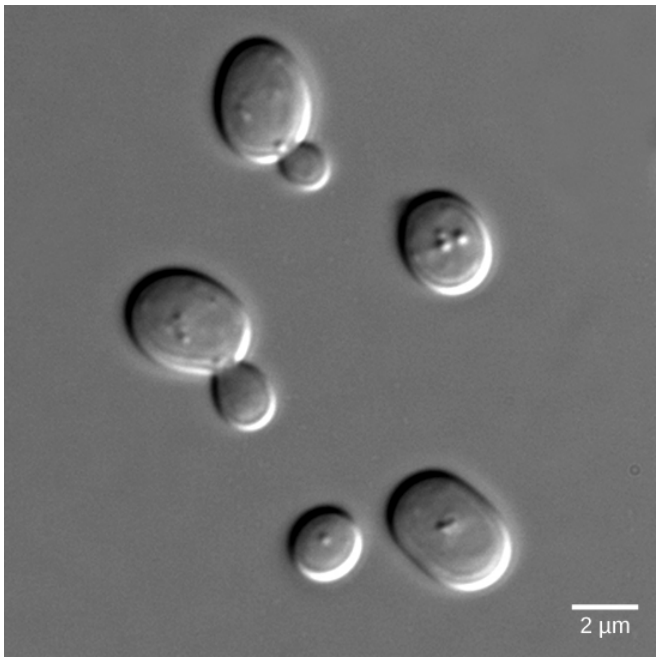


Figure 2.6.5.1: Budding *Saccharomyces cerevisiae* yeast cells can communicate by releasing a signaling molecule called mating factor. In this micrograph, they are visualized using differential interference contrast microscopy, a light microscopy technique that enhances the contrast of the sample.

Signaling in Bacteria

Signaling in bacteria enables bacteria to monitor extracellular conditions, ensure that there are sufficient amounts of nutrients, and ensure that hazardous situations are avoided. There are circumstances, however, when bacteria communicate with each other.

The first evidence of bacterial communication was observed in a bacterium that has a symbiotic relationship with Hawaiian bobtail squid. When the population density of the bacteria reaches a certain level, specific gene expression is initiated, and the bacteria produce bioluminescent proteins that emit light. Because the number of cells present in the environment (cell density) is the determining factor for signaling, bacterial signaling was named quorum sensing. In politics and business, a quorum is the minimum number of members required to be present to vote on an issue.

Quorum sensing uses autoinducers as signaling molecules. Autoinducers are signaling molecules secreted by bacteria to communicate with other bacteria of the same kind. The secreted autoinducers can be small, hydrophobic molecules such as acyl-homoserine lactone, (AHL) or larger peptide-based molecules; each type of molecule has a different mode of action. When AHL enters target bacteria, it binds to transcription factors, which then switch gene expression on or off (Figure 2.6.5.2). The peptide autoinducers stimulate more complicated signaling pathways that include bacterial kinases. The changes in bacteria following exposure to autoinducers can be quite extensive. The pathogenic bacterium *Pseudomonas aeruginosa* has 616 different genes that respond to autoinducers.

Art Connection

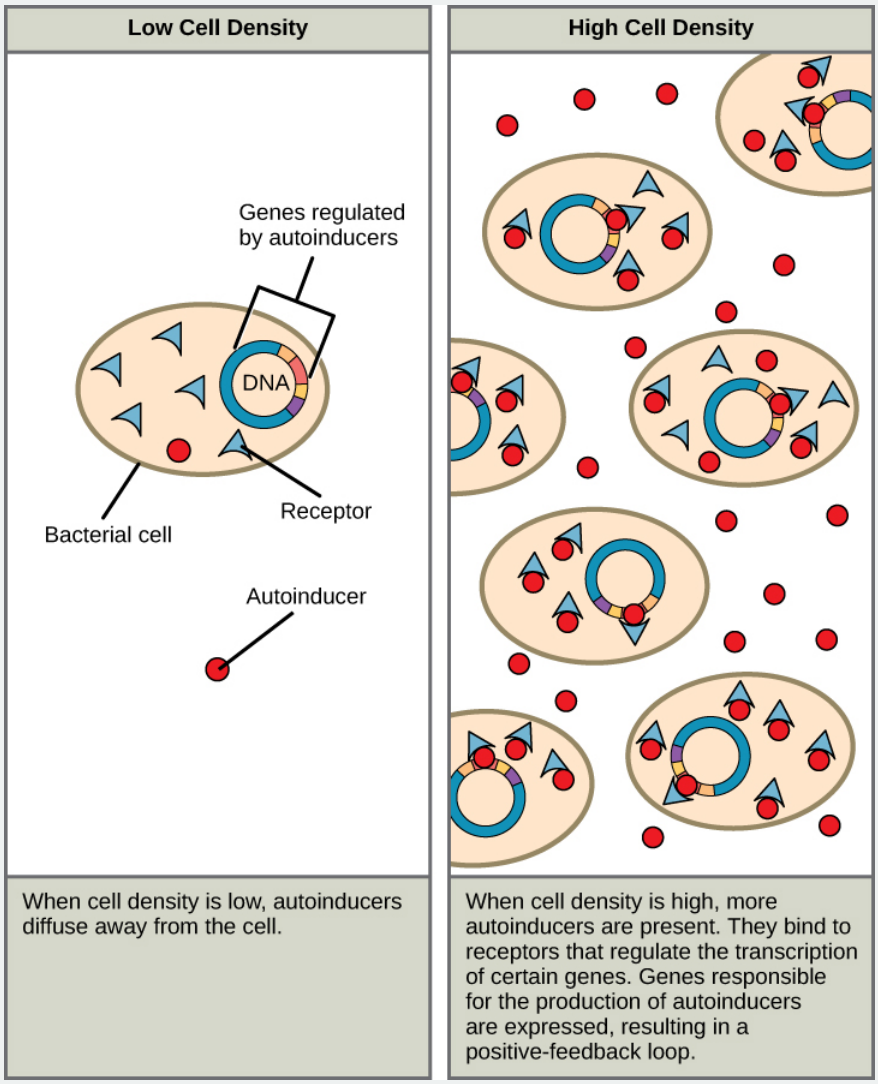


Figure 2.6.5.2: Autoinducers are small molecules or proteins produced by bacteria that regulate gene expression.

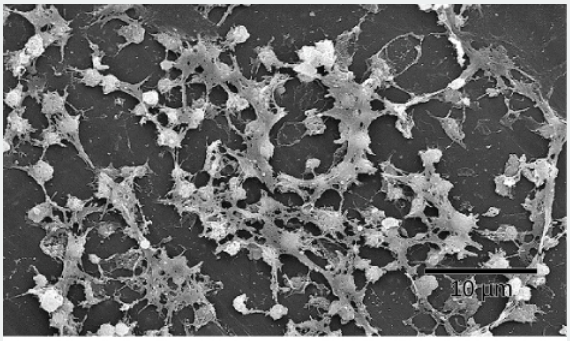
Which of the following statements about quorum sensing is false?

A. Autoinducer must bind to receptor to turn on transcription of genes responsible for the production of more autoinducer.
B. The receptor stays in the bacterial cell, but the autoinducer diffuses out.
C. Autoinducer can only act on a different cell: it cannot act on the cell in which it is made.
D. Autoinducer turns on genes that enable the bacteria to form a biofilm.

Some species of bacteria that use quorum sensing form biofilms, complex colonies of bacteria (often containing several species) that exchange chemical signals to coordinate the release of toxins that will attack the host. Bacterial biofilms (Figure 2.6.5.3) can

sometimes be found on medical equipment; when biofilms invade implants such as hip or knee replacements or heart pacemakers, they can cause life-threatening infections.

Art Connection



(a)



(b)

Figure 2.6.5.3: Cell-cell communication enables these (a) *Staphylococcus aureus* bacteria to work together to form a biofilm inside a hospital patient's catheter, seen here via scanning electron microscopy. *S. aureus* is the main cause of hospital-acquired infections. (b) Hawaiian bobtail squid have a symbiotic relationship with the bioluminescent bacteria *Vibrio fischeri*. The luminescence makes it difficult to see the squid from below because it effectively eliminates its shadow. In return for camouflage, the squid provides food for the bacteria. Free-living *V. fischeri* do not produce luciferase, the enzyme responsible for luminescence, but *V. fischeri* living in a symbiotic relationship with the squid do. Quorum sensing determines whether the bacteria should produce the luciferase enzyme. (credit a: modifications of work by CDC/Janice Carr; credit b: modifications of work by Cliff1066/Flickr)

What advantage might biofilm production confer on the *S. aureus* inside the catheter?

Research on the details of quorum sensing has led to advances in growing bacteria for industrial purposes. Recent discoveries suggest that it may be possible to exploit bacterial signaling pathways to control bacterial growth; this process could replace or supplement antibiotics that are no longer effective in certain situations.

Link to Learning

Watch geneticist Bonnie Bassler discuss her discovery of quorum sensing in biofilm bacteria in squid.

Evolution Connection: Cellular Communication in Yeasts

The first life on our planet consisted of single-celled prokaryotic organisms that had limited interaction with each other. While some external signaling occurs between different species of single-celled organisms, the majority of signaling within bacteria and yeasts concerns only other members of the same species. The evolution of cellular communication is an absolute necessity for the development of multicellular organisms, and this innovation is thought to have required approximately 2.5 billion years to appear in early life forms.

Yeasts are single-celled eukaryotes, and therefore have a nucleus and organelles characteristic of more complex life forms. Comparisons of the genomes of yeasts, nematode worms, fruit flies, and humans illustrate the evolution of increasingly complex signaling systems that allow for the efficient inner workings that keep humans and other complex life forms functioning correctly.

Kinases are a major component of cellular communication, and studies of these enzymes illustrate the evolutionary connectivity of different species. Yeasts have 130 types of kinases. More complex organisms such as nematode worms and fruit flies have 454 and 239 kinases, respectively. Of the 130 kinase types in yeast, 97 belong to the 55 subfamilies of kinases that are found in other eukaryotic organisms. The only obvious deficiency seen in yeasts is the complete absence of tyrosine kinases. It is hypothesized that phosphorylation of tyrosine residues is needed to control the more sophisticated functions of development, differentiation, and cellular communication used in multicellular organisms.

Because yeasts contain many of the same classes of signaling proteins as humans, these organisms are ideal for studying signaling cascades. Yeasts multiply quickly and are much simpler organisms than humans or other multicellular animals. Therefore, the signaling cascades are also simpler and easier to study, although they contain similar counterparts to human signaling.[1]

Link to Learning



Watch this collection of interview clips with biofilm researchers in “What Are Bacterial Biofilms?”

Summary

Yeasts and multicellular organisms have similar signaling mechanisms. Yeasts use cell-surface receptors and signaling cascades to communicate information on mating with other yeast cells. The signaling molecule secreted by yeasts is called mating factor.

Bacterial signaling is called quorum sensing. Bacteria secrete signaling molecules called autoinducers that are either small, hydrophobic molecules or peptide-based signals. The hydrophobic autoinducers, such as AHL, bind transcription factors and directly affect gene expression. The peptide-based molecules bind kinases and initiate signaling cascades in the cells.

Art Connections

Figure 2.6.5.2: Which of the following statements about quorum sensing is false?

A. Autoinducer must bind to receptor to turn on transcription of genes responsible for the production of more autoinducer.
B. The receptor stays in the bacterial cell, but the autoinducer diffuses out.
C. Autoinducer can only act on a different cell: it cannot act on the cell in which it is made.
D. Autoinducer turns on genes that enable the bacteria to form a biofilm.

Answer

C.

Figure 2.6.5.3: What advantage might biofilm production confer on the *S. aureus* inside the catheter?

Answer

S. aureus produces a biofilm because the higher cell density in the biofilm permits the formation of a dense surface that helps protect the bacteria from antibiotics.

Footnotes

1. 1 G. Manning, G.D. Plowman, T. Hunter, S. Sudarsanam, “Evolution of Protein Kinase Signaling from Yeast to Man,” *Trends in Biochemical Sciences* 27, no. 10 (2002): 514–520.

Glossary

autoinducer

signaling molecule secreted by bacteria to communicate with other bacteria of its kind and others

mating factor

signaling molecule secreted by yeast cells to communicate to nearby yeast cells that they are available to mate and communicating their mating orientation

quorum sensing

method of cellular communication used by bacteria that informs them of the abundance of similar (or different) bacteria in the environment

This page titled 2.6.5: Signaling in Single-Celled Organisms is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **9.4: Signaling in Single-Celled Organisms** by OpenStax is licensed CC BY 4.0.

2.6.E: Cell Communication (Exercises)

In multicellular organisms, cells send and receive chemical messages constantly to coordinate the actions of distant organs, tissues, and cells. The ability to send messages quickly and efficiently enables cells to coordinate and fine-tune their functions.

9.1: Signaling Molecules and Cellular Receptors

Chemical signals are released by signaling cells in the form of small, usually volatile or soluble molecules called ligands. A ligand is a molecule that binds another specific molecule, in some cases, delivering a signal in the process. Ligands can thus be thought of as signaling molecules. Ligands interact with proteins in target cells, which are cells that are affected by chemical signals; these proteins are also called receptors.

Review Questions

What property prevents the ligands of cell-surface receptors from entering the cell?

A. The molecules bind to the extracellular domain.
B. The molecules are hydrophilic and cannot penetrate the hydrophobic interior of the plasma membrane.
C. The molecules are attached to transport proteins that deliver them through the bloodstream to target cells.
D. The ligands are able to penetrate the membrane and directly influence gene expression upon receptor binding.

Answer

B

The secretion of hormones by the pituitary gland is an example of _____.

A. autocrine signaling
B. paracrine signaling
C. endocrine signaling
D. direct signaling across gap junctions

Answer

C

Why are ion channels necessary to transport ions into or out of a cell?

A. Ions are too large to diffuse through the membrane.
B. Ions are charged particles and cannot diffuse through the hydrophobic interior of the membrane.
C. Ions do not need ion channels to move through the membrane.
D. Ions bind to carrier proteins in the bloodstream, which must be removed before transport into the cell.

Answer

B

Endocrine signals are transmitted more slowly than paracrine signals because _____.

A. the ligands are transported through the bloodstream and travel greater distances
B. the target and signaling cells are close together
C. the ligands are degraded rapidly
D. the ligands don't bind to carrier proteins during transport

Answer

A

Free Response

What is the difference between intracellular signaling and intercellular signaling?

Answer

Intracellular signaling occurs within a cell, and intercellular signaling occurs between cells.

How are the effects of paracrine signaling limited to an area near the signaling cells?

Answer

The secreted ligands are quickly removed by degradation or reabsorption into the cell so that they cannot travel far.

What are the differences between internal receptors and cell-surface receptors?

Answer

Internal receptors are located inside the cell, and their ligands enter the cell to bind the receptor. The complex formed by the internal receptor and the ligand then enters the nucleus and directly affects protein production by binding to the chromosomal DNA and initiating the making of mRNA that codes for proteins. Cell-surface receptors, however, are embedded in the plasma membrane, and their ligands do not enter the cell. Binding of the ligand to the cell-surface receptor initiates a cell signaling cascade and does not directly influence the making of proteins; however, it may involve the activation of intracellular proteins.

Cells grown in the laboratory are mixed with a dye molecule that is unable to pass through the plasma membrane. If a ligand is added to the cells, observations show that the dye enters the cells. What type of receptor did the ligand bind to on the cell surface?

Answer

An ion channel receptor opened up a pore in the membrane, which allowed the ionic dye to move into the cell.

9.2: Propagation of the Signal

Once a ligand binds to a receptor, the signal is transmitted through the membrane and into the cytoplasm. Continuation of a signal in this manner is called signal transduction. Signal transduction only occurs with cell-surface receptors because internal receptors are able to interact directly with DNA in the nucleus to initiate protein synthesis. When a ligand binds to its receptor, conformational changes occur that affect the receptor's intracellular domain.

Review Questions

Where do DAG and IP_3 originate?

A. They are formed by phosphorylation of cAMP.
B. They are ligands expressed by signaling cells.
C. They are hormones that diffuse through the plasma membrane to stimulate protein production.
D. They are the cleavage products of the inositol phospholipid, PIP_2.

Answer

D

What property enables the residues of the amino acids serine, threonine, and tyrosine to be phosphorylated?

A. They are polar.

B. They are non-polar.
C. They contain a hydroxyl group.
D. They occur more frequently in the amino acid sequence of signaling proteins.

Answer

C

Free Response

The same second messengers are used in many different cells, but the response to second messengers is different in each cell. How is this possible?

Answer

Different cells produce different proteins, including cell-surface receptors and signaling pathway components. Therefore, they respond to different ligands, and the second messengers activate different pathways. Signal integration can also change the end result of signaling.

What would happen if the intracellular domain of a cell-surface receptor was switched with the domain from another receptor?

Answer

The binding of the ligand to the extracellular domain would activate the pathway normally activated by the receptor donating the intracellular domain.

9.3: Response to the Signal

Inside the cell, ligands bind to their internal receptors, allowing them to directly affect the cell's DNA and protein-producing machinery. Using signal transduction pathways, receptors in the plasma membrane produce a variety of effects on the cell. The results of signaling pathways are extremely varied and depend on the type of cell involved as well as the external and internal conditions. A small sampling of responses is described below.

Review Questions

What is the function of a phosphatase?

A. A phosphatase removes phosphorylated amino acids from proteins.
B. A phosphatase removes the phosphate group from phosphorylated amino acid residues in a protein.
C. A phosphatase phosphorylates serine, threonine, and tyrosine residues.
D. A phosphatase degrades second messengers in the cell.

Answer

B

How does NF-κB induce gene expression?

A. A small, hydrophobic ligand binds to NF-κB, activating it.
B. Phosphorylation of the inhibitor Iκ-B dissociates the complex between it and NF-κB, and allows NF-κB to enter the nucleus and stimulate transcription.
C. NF-κB is phosphorylated and is then free to enter the nucleus and bind DNA.
D. NF-κB is a kinase that phosphorylates a transcription factor that binds DNA and promotes protein production.

Answer

B

Apoptosis can occur in a cell when the cell is _____.

A. damaged
B. no longer needed
C. infected by a virus
D. all of the above

Answer

D

What is the effect of an inhibitor binding an enzyme?

A. The enzyme is degraded.
B. The enzyme is activated.
C. The enzyme is inactivated.
D. The complex is transported out of the cell.

Answer

C

Free Response

What is a possible result of a mutation in a kinase that controls a pathway that stimulates cell growth?

Answer

If a kinase is mutated so that it is always activated, it will continuously signal through the pathway and lead to uncontrolled growth and possibly cancer. If a kinase is mutated so that it cannot function, the cell will not respond to ligand binding.

How does the extracellular matrix control the growth of cells?

Answer

Receptors on the cell surface must be in contact with the extracellular matrix in order to receive positive signals that allow the cell to live. If the receptors are not activated by binding, the cell will undergo apoptosis. This ensures that cells are in the correct place in the body and helps to prevent invasive cell growth as occurs in metastasis in cancer.

9.4: Signaling in Single-Celled Organisms

Within-cell signaling allows bacteria to respond to environmental cues, such as nutrient levels, some single-celled organisms also release molecules to signal to each other.

Review Questions

Which type of molecule acts as a signaling molecule in yeasts?

A. steroid
B. autoinducer
C. mating factor
D. second messenger

Answer

C

Quorum sensing is triggered to begin when _____.

A. treatment with antibiotics occurs
B. bacteria release growth hormones
C. bacterial protein expression is switched on
D. a sufficient number of bacteria are present

Answer

D

Free Response

What characteristics make yeasts a good model for learning about signaling in humans?

Answer

Yeasts are eukaryotes and have many of the same systems that humans do; however, they are single-celled, so they are easy to grow, grow rapidly, have a short generation time, and are much simpler than humans.

Why is signaling in multicellular organisms more complicated than signaling in single-celled organisms?

Answer

Multicellular organisms must coordinate many different events in different cell types that may be very distant from each other. Single-celled organisms are only concerned with their immediate environment and the presence of other cells in the area.

This page titled 2.6.E: Cell Communication (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **9.E: Cell Communication (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

2.7: Cell Reproduction

2.7.1: Preface
2.7.2: Cell Division
2.7.3: The Cell Cycle
2.7.4: Control of the Cell Cycle
2.7.5: Cancer and the Cell Cycle
2.7.6: Prokaryotic Cell Division
2.7.E: Cell Reproduction (Exercises)

Contributors

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 2.7: Cell Reproduction is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

2.7.1: Preface

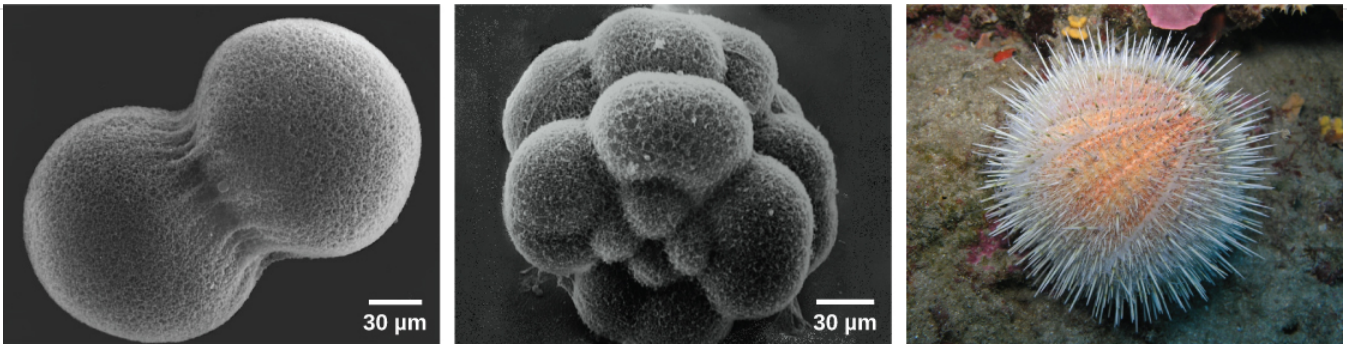


Figure 2.7.1.1: A sea urchin begins life as a single cell that (a) divides to form two cells, visible by scanning electron microscopy. After four rounds of cell division, (b) there are 16 cells, as seen in this SEM image. After many rounds of cell division, the individual develops into a complex, multicellular organism, as seen in this (c) mature sea urchin. (credit a: modification of work by Evelyn Spiegel, Louisa Howard; credit b: modification of work by Evelyn Spiegel, Louisa Howard; credit c: modification of work by Marco Busdraghi; scale-bar data from Matt Russell)

A human, as well as every sexually reproducing organism, begins life as a fertilized egg (embryo) or zygote. Trillions of cell divisions subsequently occur in a controlled manner to produce a complex, multicellular human. In other words, that original single cell is the ancestor of every other cell in the body. Once a being is fully grown, cell reproduction is still necessary to repair or regenerate tissues. For example, new blood and skin cells are constantly being produced. All multicellular organisms use cell division for growth and the maintenance and repair of cells and tissues. Cell division is tightly regulated, and the occasional failure of regulation can have life-threatening consequences. Single-celled organisms use cell division as their method of reproduction.

This page titled 2.7.1: Preface is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.0: Introduction** by OpenStax is licensed CC BY 4.0.

2.7.2: Cell Division

Skills to Develop

- Describe the structure of prokaryotic and eukaryotic genomes
- Distinguish between chromosomes, genes, and traits
- Describe the mechanisms of chromosome compaction

The continuity of life from one cell to another has its foundation in the reproduction of cells by way of the cell cycle. The cell cycle is an orderly sequence of events that describes the stages of a cell's life from the division of a single parent cell to the production of two new daughter cells. The mechanisms involved in the cell cycle are highly regulated.

Genomic DNA

Before discussing the steps a cell must undertake to replicate, a deeper understanding of the structure and function of a cell's genetic information is necessary. A cell's DNA, packaged as a double-stranded DNA molecule, is called its genome. In prokaryotes, the genome is composed of a single, double-stranded DNA molecule in the form of a loop or circle (Figure 2.7.2.1). The region in the cell containing this genetic material is called a nucleoid. Some prokaryotes also have smaller loops of DNA called plasmids that are not essential for normal growth. Bacteria can exchange these plasmids with other bacteria, sometimes receiving beneficial new genes that the recipient can add to their chromosomal DNA. Antibiotic resistance is one trait that often spreads through a bacterial colony through plasmid exchange.

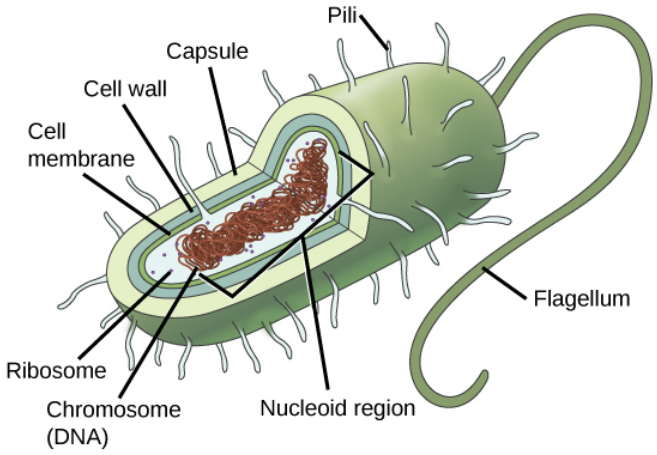


Figure 2.7.2.1: Prokaryotes, including bacteria and archaea, have a single, circular chromosome located in a central region called the nucleoid.

In eukaryotes, the genome consists of several double-stranded linear DNA molecules (Figure 2.7.2.2). Each species of eukaryotes has a characteristic number of chromosomes in the nuclei of its cells. Human body cells have 46 chromosomes, while human gametes (sperm or eggs) have 23 chromosomes each. A typical body cell, or somatic cell, contains two matched sets of chromosomes, a configuration known as diploid. The letter *n* is used to represent a single set of chromosomes; therefore, a diploid organism is designated 2*n*. Human cells that contain one set of chromosomes are called gametes, or sex cells; these are eggs and sperm, and are designated 1*n*, or haploid.

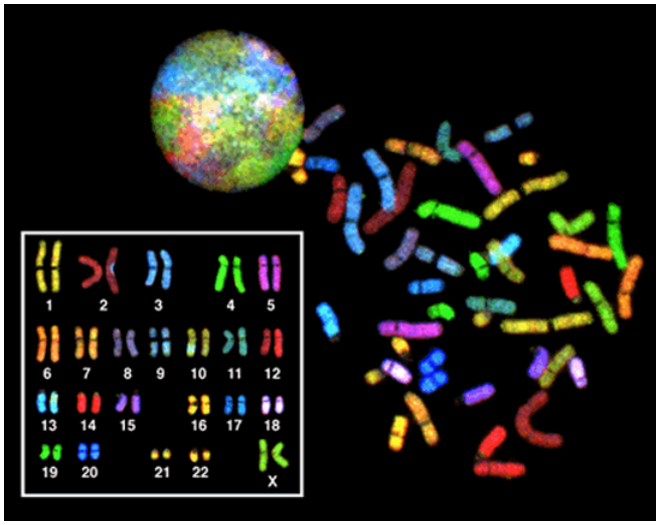


Figure 2.7.2.2: There are 23 pairs of homologous chromosomes in a female human somatic cell. The condensed chromosomes are viewed within the nucleus (top), removed from a cell in mitosis and spread out on a slide (right), and artificially arranged according to length (left); an arrangement like this is called a karyotype. In this image, the chromosomes were exposed to fluorescent stains for differentiation of the different chromosomes. A method of staining called "chromosome painting" employs fluorescent dyes that highlight chromosomes in different colors. (credit: National Human Genome Project/NIH)

Matched pairs of chromosomes in a diploid organism are called homologous ("same knowledge") chromosomes. Homologous chromosomes are the same length and have specific nucleotide segments called genes in exactly the same location, or locus. Genes, the functional units of chromosomes, determine specific characteristics by coding for specific proteins. Traits are the variations of those characteristics. For example, hair color is a characteristic with traits that are blonde, brown, or black.

Each copy of a homologous pair of chromosomes originates from a different parent; therefore, the genes themselves are not identical. The variation of individuals within a species is due to the specific combination of the genes inherited from both parents. Even a slightly altered sequence of nucleotides within a gene can result in an alternative trait. For example, there are three possible gene sequences on the human chromosome that code for blood type: sequence A, sequence B, and sequence O. Because all diploid human cells have two copies of the chromosome that determines blood type, the blood type (the trait) is determined by which two versions of the marker gene are inherited. It is possible to have two copies of the same gene sequence on both homologous chromosomes, with one on each (for example, AA, BB, or OO), or two different sequences, such as AB.

Minor variations of traits, such as blood type, eye color, and handedness, contribute to the natural variation found within a species. However, if the entire DNA sequence from any pair of human homologous chromosomes is compared, the difference is less than one percent. The sex chromosomes, X and Y, are the single exception to the rule of homologous chromosome uniformity: Other than a small amount of homology that is necessary to accurately produce gametes, the genes found on the X and Y chromosomes are different.

Eukaryotic Chromosomal Structure and Compaction

If the DNA from all 46 chromosomes in a human cell nucleus was laid out end to end, it would measure approximately two meters; however, its diameter would be only 2 nm. Considering that the size of a typical human cell is about 10 µm (100,000 cells lined up to equal one meter), DNA must be tightly packaged to fit in the cell's nucleus. At the same time, it must also be readily accessible for the genes to be expressed. During some stages of the cell cycle, the long strands of DNA are condensed into compact chromosomes. There are a number of ways that chromosomes are compacted.

In the first level of compaction, short stretches of the DNA double helix wrap around a core of eight histone proteins at regular intervals along the entire length of the chromosome (Figure 2.7.2.3). The DNA-histone complex is called chromatin. The beadlike, histone DNA complex is called a nucleosome, and DNA connecting the nucleosomes is called linker DNA. A DNA molecule in this form is about seven times shorter than the double helix without the histones, and the beads are about 10 nm in diameter, in contrast with the 2-nm diameter of a DNA double helix. The next level of compaction occurs as the nucleosomes and the linker DNA between them are coiled into a 30-nm chromatin fiber. This coiling further shortens the chromosome so that it is now about 50 times shorter than the extended form. In the third level of packing, a variety of fibrous proteins is used to pack the chromatin. These

fibrous proteins also ensure that each chromosome in a non-dividing cell occupies a particular area of the nucleus that does not overlap with that of any other chromosome (see the top image in Figure 2.7.2.2).

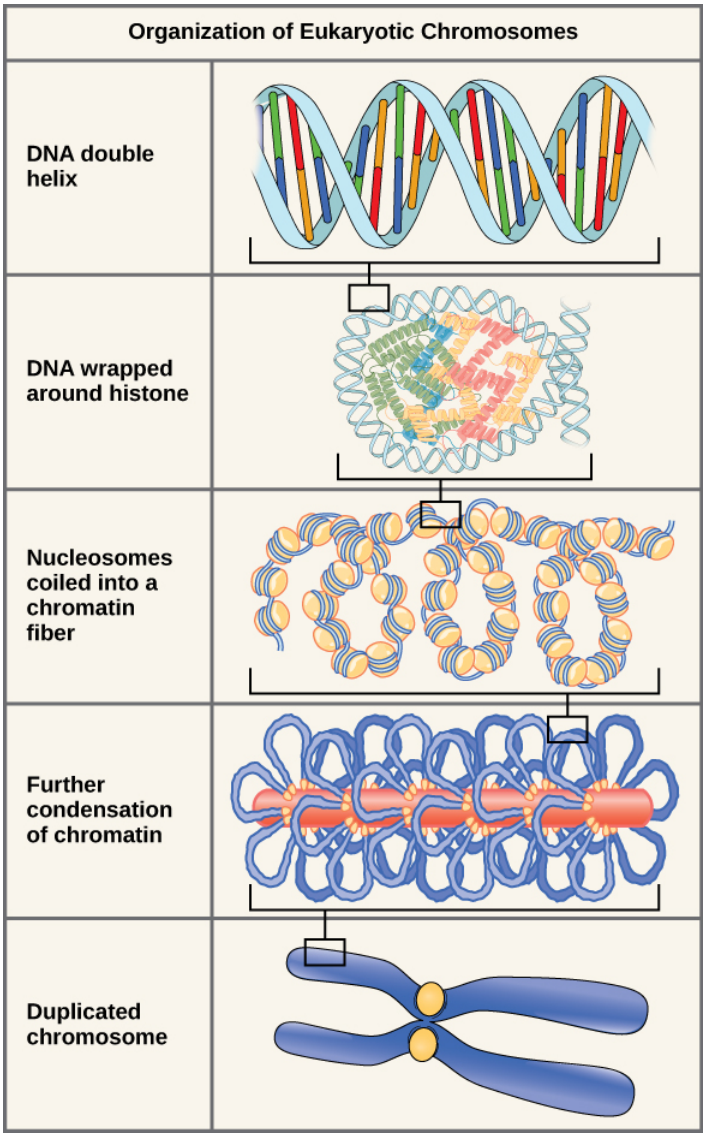


Figure 2.7.2.3: Double-stranded DNA wraps around histone proteins to form nucleosomes that have the appearance of "beads on a string." The nucleosomes are coiled into a 30-nm chromatin fiber. When a cell undergoes mitosis, the chromosomes condense even further.

DNA replicates in the S phase of interphase. After replication, the chromosomes are composed of two linked sister chromatids. When fully compact, the pairs of identically packed chromosomes are bound to each other by cohesin proteins. The connection between the sister chromatids is closest in a region called the centromere. The conjoined sister chromatids, with a diameter of about 1 µm, are visible under a light microscope. The centromeric region is highly condensed and thus will appear as a constricted area.

Link to Learning



This animation illustrates the different levels of chromosome packing.

Summary

Prokaryotes have a single circular chromosome composed of double-stranded DNA, whereas eukaryotes have multiple, linear chromosomes composed of chromatin surrounded by a nuclear membrane. The 46 chromosomes of human somatic cells are composed of 22 pairs of autosomes (matched pairs) and a pair of sex chromosomes, which may or may not be matched. This is the 2*n* or diploid state. Human gametes have 23 chromosomes or one complete set of chromosomes; a set of chromosomes is complete with either one of the sex chromosomes. This is the *n* or haploid state. Genes are segments of DNA that code for a specific protein. An organism's traits are determined by the genes inherited from each parent. Duplicated chromosomes are composed of two sister chromatids. Chromosomes are compacted using a variety of mechanisms during certain stages of the cell cycle. Several classes of protein are involved in the organization and packing of the chromosomal DNA into a highly condensed structure. The condensing complex compacts chromosomes, and the resulting condensed structure is necessary for chromosomal segregation during mitosis.

Glossary

cell cycle
ordered sequence of events that a cell passes through between one cell division and the next

centromere
region at which sister chromatids are bound together; a constricted area in condensed chromosomes

chromatid
single DNA molecule of two strands of duplicated DNA and associated proteins held together at the centromere

diploid
cell, nucleus, or organism containing two sets of chromosomes (2*n*)

gamete
haploid reproductive cell or sex cell (sperm, pollen grain, or egg)

gene
physical and functional unit of heredity, a sequence of DNA that codes for a protein.

genome
total genetic information of a cell or organism

haploid
cell, nucleus, or organism containing one set of chromosomes (*n*)

histone

one of several similar, highly conserved, low molecular weight, basic proteins found in the chromatin of all eukaryotic cells; associates with DNA to form nucleosomes

homologous chromosomes

chromosomes of the same morphology with genes in the same location; diploid organisms have pairs of homologous chromosomes (homologs), with each homolog derived from a different parent

locus

position of a gene on a chromosome

nucleosome

subunit of chromatin composed of a short length of DNA wrapped around a core of histone proteins

---

This page titled 2.7.2: Cell Division is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.1: Cell Division** by OpenStax is licensed CC BY 4.0.

2.7.3: The Cell Cycle

Learning Objectives

- Describe the three stages of interphase
- Discuss the behavior of chromosomes during karyokinesis
- Explain how the cytoplasmic content is divided during cytokinesis
- Define the quiescent G_0 phase

The cell cycle is an ordered series of events involving cell growth and cell division that produces two new daughter cells. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages of growth, DNA replication, and division that produces two identical (clone) cells. The cell cycle has two major phases: interphase and the mitotic phase (Figure 2.7.3.1). During interphase, the cell grows and DNA is replicated. During the mitotic phase, the replicated DNA and cytoplasmic contents are separated, and the cell divides.

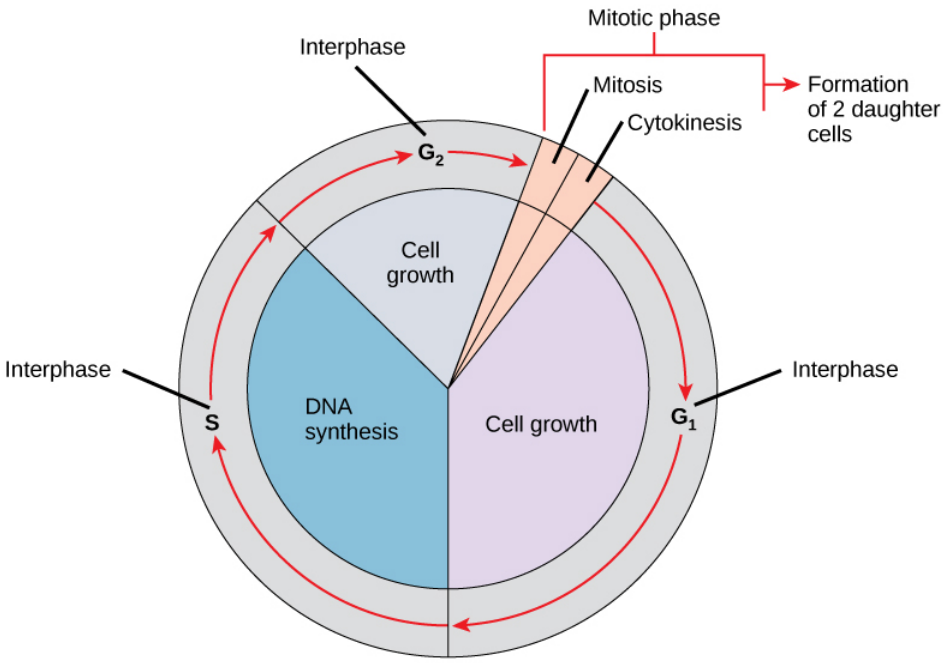
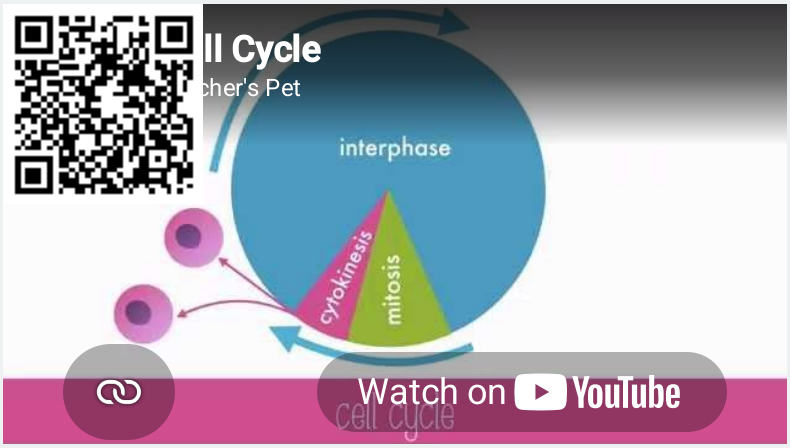


Figure 2.7.3.1: The cell cycle consists of interphase and the mitotic phase. During interphase, the cell grows and the nuclear DNA is duplicated. Interphase is followed by the mitotic phase. During the mitotic phase, the duplicated chromosomes are segregated and distributed into daughter nuclei. The cytoplasm is usually divided as well, resulting in two daughter cells.

Video



Interphase

During interphase, the cell undergoes normal growth processes while also preparing for cell division. In order for a cell to move from interphase into the mitotic phase, many internal and external conditions must be met. The three stages of interphase are called G_1, S, and G_2.

G_1 Phase (First Gap)

The first stage of interphase is called the G_1 phase (first gap) because, from a microscopic aspect, little change is visible. However, during the G_1 stage, the cell is quite active at the biochemical level. The cell is accumulating the building blocks of chromosomal DNA and the associated proteins as well as accumulating sufficient energy reserves to complete the task of replicating each chromosome in the nucleus.

S Phase (Synthesis of DNA)

Throughout interphase, nuclear DNA remains in a semi-condensed chromatin configuration. In the S phase, DNA replication can proceed through the mechanisms that result in the formation of identical pairs of DNA molecules—sister chromatids—that are firmly attached to the centromeric region. The centrosome is duplicated during the S phase. The two centrosomes will give rise to the mitotic spindle, the apparatus that orchestrates the movement of chromosomes during mitosis. At the center of each animal cell, the centrosomes of animal cells are associated with a pair of rod-like objects, the centrioles, which are at right angles to each other. Centrioles help organize cell division. Centrioles are not present in the centrosomes of other eukaryotic species, such as plants and most fungi.

G_2 Phase (Second Gap)

In the G_2 phase, the cell replenishes its energy stores and synthesizes proteins necessary for chromosome manipulation. Some cell organelles are duplicated, and the cytoskeleton is dismantled to provide resources for the mitotic phase. There may be additional cell growth during G_2. The final preparations for the mitotic phase must be completed before the cell is able to enter the first stage of mitosis.

The Mitotic Phase

The mitotic phase is a multistep process during which the duplicated chromosomes are aligned, separated, and move into two new, identical daughter cells. The first portion of the mitotic phase is called karyokinesis, or nuclear division. The second portion of the mitotic phase, called cytokinesis, is the physical separation of the cytoplasmic components into the two daughter cells.

Mitosis

Mitosis is divided into a series of phases—prophase, prometaphase, metaphase, anaphase, and telophase—that result in the division of the cell nucleus (Figure 2.7.3.2).

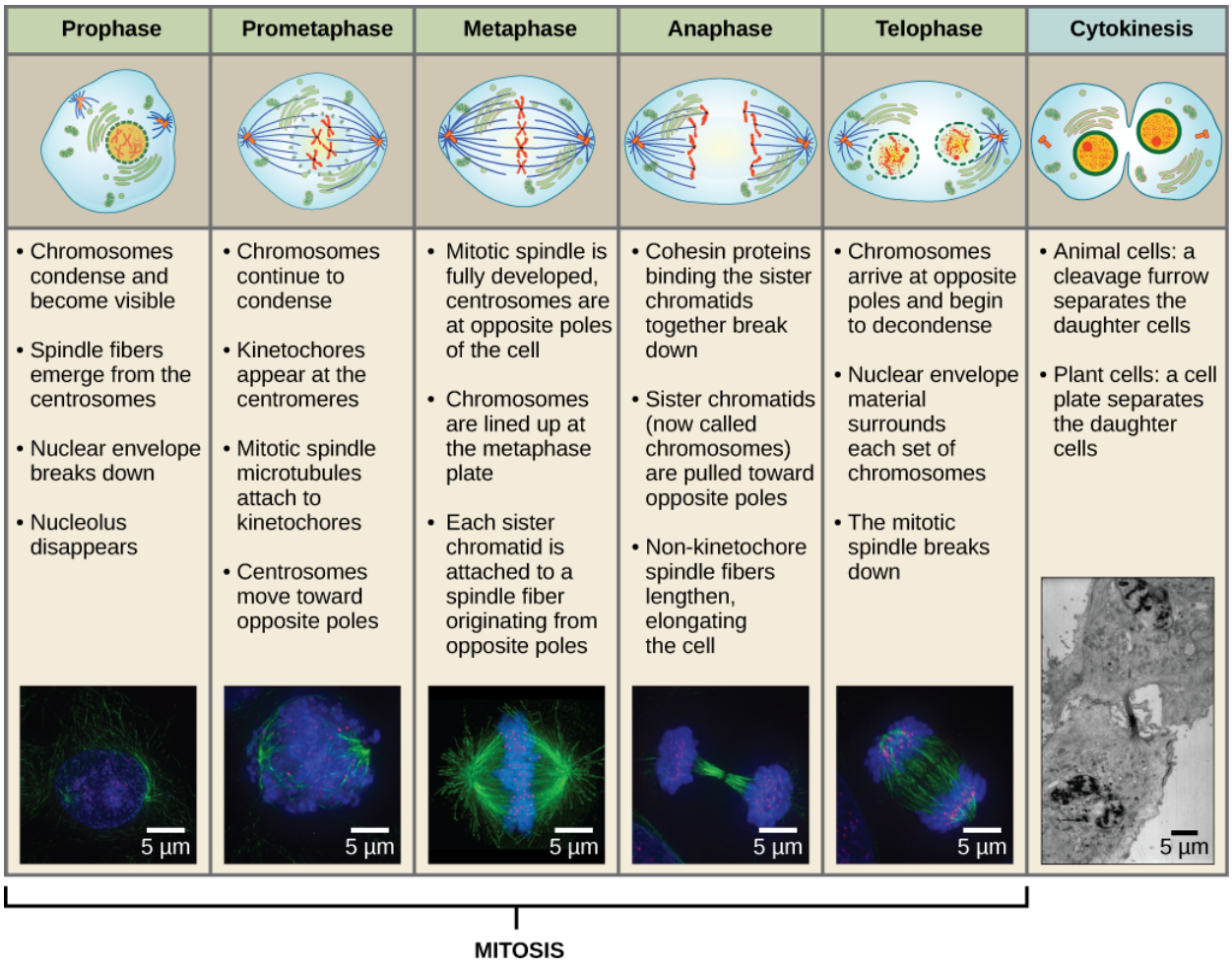


Figure 2.7.3.2: Mitosis is divided into five stages—prophase, prometaphase, metaphase, anaphase, and telophase. The pictures at the bottom were taken by fluorescence microscopy (hence, the black background) of cells artificially stained by fluorescent dyes: blue fluorescence indicates DNA (chromosomes) and green fluorescence indicates microtubules (spindle apparatus). (credit "mitosis drawings": modification of work by Mariana Ruiz Villareal; credit "micrographs": modification of work by Roy van Heesbeen; credit "cytokinesis micrograph": Wadsworth Center/New York State Department of Health; scale-bar data from Matt Russell)

? Exercise 2.7.3.1

Which of the following is the correct order of events in mitosis?

A. Sister chromatids line up at the metaphase plate. The kinetochore becomes attached to the mitotic spindle. The nucleus reforms and the cell divides. Cohesin proteins break down and the sister chromatids separate.

B. The kinetochore becomes attached to the mitotic spindle. Cohesin proteins break down and the sister chromatids separate. Sister chromatids line up at the metaphase plate. The nucleus reforms and the cell divides.

C. The kinetochore becomes attached to the cohesin proteins. Sister chromatids line up at the metaphase plate. The kinetochore breaks down and the sister chromatids separate. The nucleus reforms and the cell divides.

D. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. Cohesin proteins break down and the sister chromatids separate. The nucleus reforms and the cell divides.

Answer

D. The kinetochore becomes attached to the mitotic spindle. Sister chromatids line up at the metaphase plate. Cohesin proteins break down and the sister chromatids separate. The nucleus reforms and the cell divides.

During prophase, the “first phase,” the nuclear envelope starts to dissociate into small vesicles, and the membranous organelles (such as the Golgi complex or Golgi apparatus, and endoplasmic reticulum), fragment and disperse toward the periphery of the cell. The nucleolus disappears (disperses). The centrosomes begin to move to opposite poles of the cell. Microtubules that will form the mitotic spindle extend between the centrosomes, pushing them farther apart as the microtubule fibers lengthen. The sister chromatids begin to coil more tightly with the aid of condensin proteins and become visible under a light microscope.

During prometaphase, the “first change phase,” many processes that were begun in prophase continue to advance. The remnants of the nuclear envelope fragment. The mitotic spindle continues to develop as more microtubules assemble and stretch across the length of the former nuclear area. Chromosomes become more condensed and discrete. Each sister chromatid develops a protein structure called a kinetochore in the centromeric region (Figure 2.7.3.3). The proteins of the kinetochore attract and bind mitotic spindle microtubules. As the spindle microtubules extend from the centrosomes, some of these microtubules come into contact with and firmly bind to the kinetochores. Once a mitotic fiber attaches to a chromosome, the chromosome will be oriented until the kinetochores of sister chromatids face the opposite poles. Eventually, all the sister chromatids will be attached via their kinetochores to microtubules from opposing poles. Spindle microtubules that do not engage the chromosomes are called polar microtubules. These microtubules overlap each other midway between the two poles and contribute to cell elongation. Astral microtubules are located near the poles, aid in spindle orientation, and are required for the regulation of mitosis.

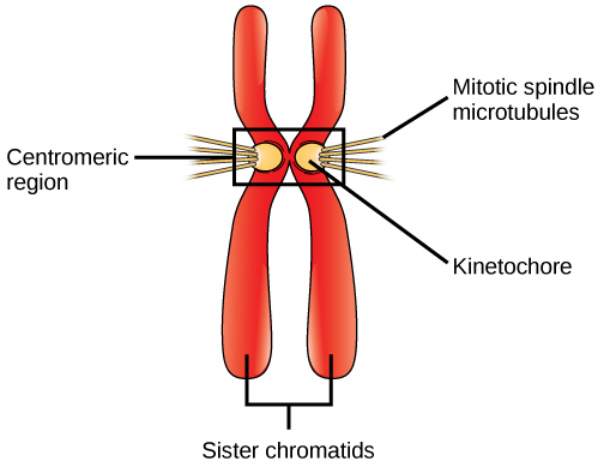


Figure 2.7.3.3: During prometaphase, mitotic spindle microtubules from opposite poles attach to each sister chromatid at the kinetochore. In anaphase, the connection between the sister chromatids breaks down, and the microtubules pull the chromosomes toward opposite poles.

During metaphase, the “change phase,” all the chromosomes are aligned in a plane called the metaphase plate, or the equatorial plane, midway between the two poles of the cell. The sister chromatids are still tightly attached to each other by cohesin proteins. At this time, the chromosomes are maximally condensed.

During anaphase, the “upward phase,” the cohesin proteins degrade, and the sister chromatids separate at the centromere. Each chromatid, now called a chromosome, is pulled rapidly toward the centrosome to which its microtubule is attached. The cell becomes visibly elongated (oval shaped) as the polar microtubules slide against each other at the metaphase plate where they overlap.

During telophase, the “distance phase,” the chromosomes reach the opposite poles and begin to decondense (unravel), relaxing into a chromatin configuration. The mitotic spindles are depolymerized into tubulin monomers that will be used to assemble cytoskeletal components for each daughter cell. Nuclear envelopes form around the chromosomes, and nucleosomes appear within the nuclear area.

Cytokinesis

Cytokinesis, or “cell motion,” is the second main stage of the mitotic phase during which cell division is completed via the physical separation of the cytoplasmic components into two daughter cells. Division is not complete until the cell components have been apportioned and completely separated into the two daughter cells. Although the stages of mitosis are similar for most eukaryotes, the process of cytokinesis is quite different for eukaryotes that have cell walls, such as plant cells.

In cells such as animal cells that lack cell walls, cytokinesis follows the onset of anaphase. A contractile ring composed of actin filaments forms just inside the plasma membrane at the former metaphase plate. The actin filaments pull the equator of the cell inward, forming a fissure. This fissure, or "crack," is called the cleavage furrow. The furrow deepens as the actin ring contracts, and eventually the membrane is cleaved in two (Figure 2.7.3.4).

In plant cells, a new cell wall must form between the daughter cells. During interphase, the Golgi apparatus accumulates enzymes, structural proteins, and glucose molecules prior to breaking into vesicles and dispersing throughout the dividing cell. During telophase, these Golgi vesicles are transported on microtubules to form a phragmoplast (a vesicular structure) at the metaphase plate. There, the vesicles fuse and coalesce from the center toward the cell walls; this structure is called a cell plate. As more vesicles fuse, the cell plate enlarges until it merges with the cell walls at the periphery of the cell. Enzymes use the glucose that has accumulated between the membrane layers to build a new cell wall. The Golgi membranes become parts of the plasma membrane on either side of the new cell wall (Figure 2.7.3.4).

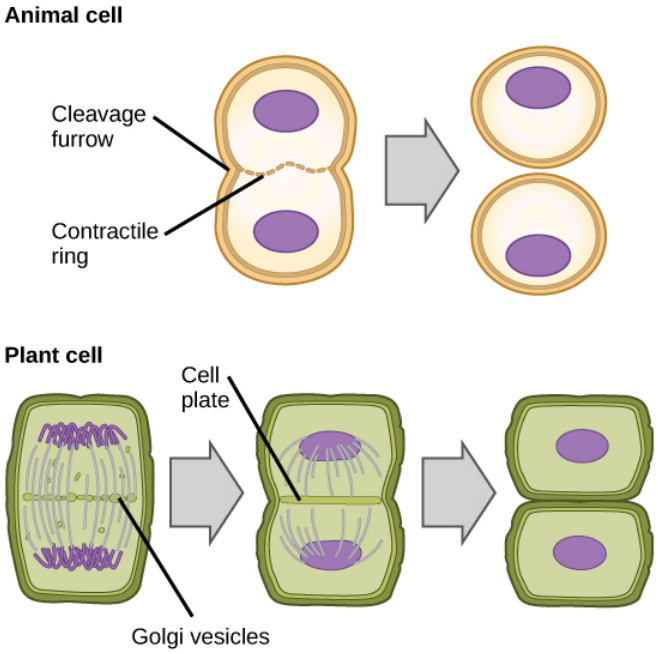
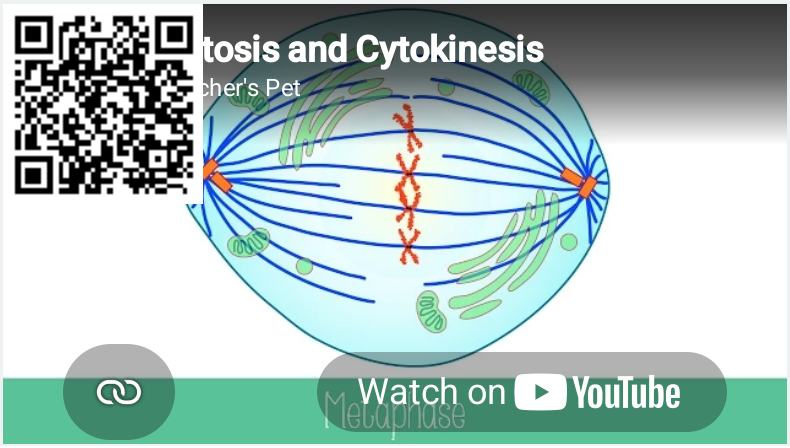


Figure 2.7.3.4: During cytokinesis in animal cells, a ring of actin filaments forms at the metaphase plate. The ring contracts, forming a cleavage furrow, which divides the cell in two. In plant cells, Golgi vesicles coalesce at the former metaphase plate, forming a phragmoplast. A cell plate formed by the fusion of the vesicles of the phragmoplast grows from the center toward the cell walls, and the membranes of the vesicles fuse to form a plasma membrane that divides the cell in two.

Video



G_0 Phase

Not all cells adhere to the classic cell cycle pattern in which a newly formed daughter cell immediately enters the preparatory phases of interphase, closely followed by the mitotic phase. Cells in G_0 phase are not actively preparing to divide. The cell is in a quiescent (inactive) stage that occurs when cells exit the cell cycle. Some cells enter G_0 temporarily until an external signal triggers the onset of G_1. Other cells that never or rarely divide, such as mature cardiac muscle and nerve cells, remain in G_0 permanently.

Summary

The cell cycle is an orderly sequence of events. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages. In eukaryotes, the cell cycle consists of a long preparatory period, called interphase. Interphase is divided into G_1, S, and G_2 phases. The mitotic phase begins with karyokinesis (mitosis), which consists of five stages: prophase, prometaphase, metaphase, anaphase, and telophase. The final stage of the mitotic phase is cytokinesis, during which the cytoplasmic components of the daughter cells are separated either by an actin ring (animal cells) or by cell plate formation (plant cells).

Glossary

anaphase
stage of mitosis during which sister chromatids are separated from each other

cell cycle
ordered series of events involving cell growth and cell division that produces two new daughter cells

cell plate
structure formed during plant cell cytokinesis by Golgi vesicles, forming a temporary structure (phragmoplast) and fusing at the metaphase plate; ultimately leads to the formation of cell walls that separate the two daughter cells

centriole
rod-like structure constructed of microtubules at the center of each animal cell centrosome

cleavage furrow
constriction formed by an actin ring during cytokinesis in animal cells that leads to cytoplasmic division

condensin
proteins that help sister chromatids coil during prophase

cytokinesis
division of the cytoplasm following mitosis that forms two daughter cells.

G_0 phase
distinct from the G_1 phase of interphase; a cell in G_0 is not preparing to divide

G_1 phase
(also, first gap) first phase of interphase centered on cell growth during mitosis

G_2 phase
(also, second gap) third phase of interphase during which the cell undergoes final preparations for mitosis

interphase
period of the cell cycle leading up to mitosis; includes G_1, S, and G_2 phases (the interim period between two consecutive cell divisions

karyokinesis
mitotic nuclear division

kinetochore
protein structure associated with the centromere of each sister chromatid that attracts and binds spindle microtubules during prometaphase

metaphase plate
equatorial plane midway between the two poles of a cell where the chromosomes align during metaphase

metaphase
stage of mitosis during which chromosomes are aligned at the metaphase plate

mitosis
(also, karyokinesis) period of the cell cycle during which the duplicated chromosomes are separated into identical nuclei; includes prophase, prometaphase, metaphase, anaphase, and telophase

mitotic phase
period of the cell cycle during which duplicated chromosomes are distributed into two nuclei and cytoplasmic contents are divided; includes karyokinesis (mitosis) and cytokinesis

mitotic spindle
apparatus composed of microtubules that orchestrates the movement of chromosomes during mitosis

prometaphase
stage of mitosis during which the nuclear membrane breaks down and mitotic spindle fibers attach to kinetochores

prophase
stage of mitosis during which chromosomes condense and the mitotic spindle begins to form

quiescent
refers to a cell that is performing normal cell functions and has not initiated preparations for cell division

S phase
second, or synthesis, stage of interphase during which DNA replication occurs

telophase
stage of mitosis during which chromosomes arrive at opposite poles, decondense, and are surrounded by a new nuclear envelope

---

This page titled 2.7.3: The Cell Cycle is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.2: The Cell Cycle** by OpenStax is licensed CC BY 4.0.

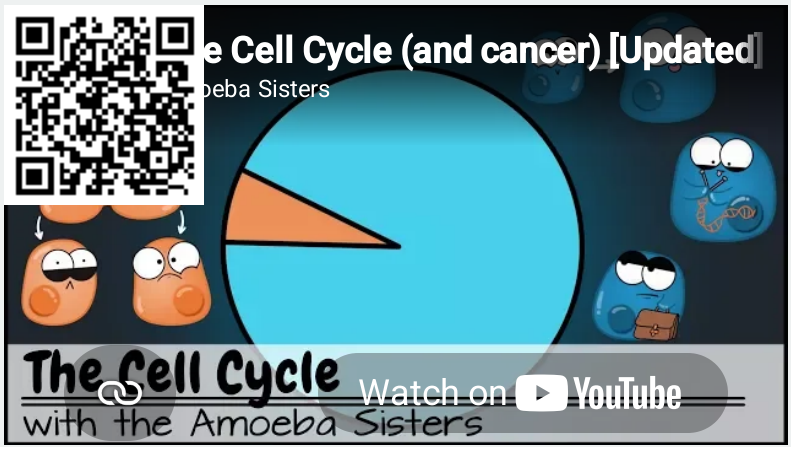
2.7.4: Control of the Cell Cycle

Learning Objectives

- Understand how the cell cycle is controlled by mechanisms both internal and external to the cell
- Explain how the three internal control checkpoints occur at the end of G_1, at the G_2/M transition, and during metaphase
- Describe the molecules that control the cell cycle through positive and negative regulation

The length of the cell cycle is highly variable, even within the cells of a single organism. In humans, the frequency of cell turnover ranges from a few hours in early embryonic development, to an average of two to five days for epithelial cells, and to an entire human lifetime spent in G_0 by specialized cells, such as cortical neurons or cardiac muscle cells. There is also variation in the time that a cell spends in each phase of the cell cycle. When fast-dividing mammalian cells are grown in culture (outside the body under optimal growing conditions), the length of the cycle is about 24 hours. In rapidly dividing human cells with a 24-hour cell cycle, the G_1 phase lasts approximately nine hours, the S phase lasts 10 hours, the G_2 phase lasts about four and one-half hours, and the M phase lasts approximately one-half hour. In early embryos of fruit flies, the cell cycle is completed in about eight minutes. The timing of events in the cell cycle is controlled by mechanisms that are both internal and external to the cell.

Video



Regulation of the Cell Cycle by External Events

Both the initiation and inhibition of cell division are triggered by events external to the cell when it is about to begin the replication process. An event may be as simple as the death of a nearby cell or as sweeping as the release of growth-promoting hormones, such as human growth hormone (HGH). A lack of HGH can inhibit cell division, resulting in dwarfism, whereas too much HGH can result in gigantism. Crowding of cells can also inhibit cell division. Another factor that can initiate cell division is the size of the cell; as a cell grows, it becomes inefficient due to its decreasing surface-to-volume ratio. The solution to this problem is to divide.

Whatever the source of the message, the cell receives the signal, and a series of events within the cell allows it to proceed into interphase. Moving forward from this initiation point, every parameter required during each cell cycle phase must be met or the cycle cannot progress.

Regulation at Internal Checkpoints

It is essential that the daughter cells produced be exact duplicates of the parent cell. Mistakes in the duplication or distribution of the chromosomes lead to mutations that may be passed forward to every new cell produced from an abnormal cell. To prevent a compromised cell from continuing to divide, there are internal control mechanisms that operate at three main cell cycle checkpoints. A checkpoint is one of several points in the eukaryotic cell cycle at which the progression of a cell to the next stage in the cycle can be halted until conditions are favorable. These checkpoints occur near the end of G_1, at the G_2/M transition, and during metaphase (Figure 2.7.4.1).

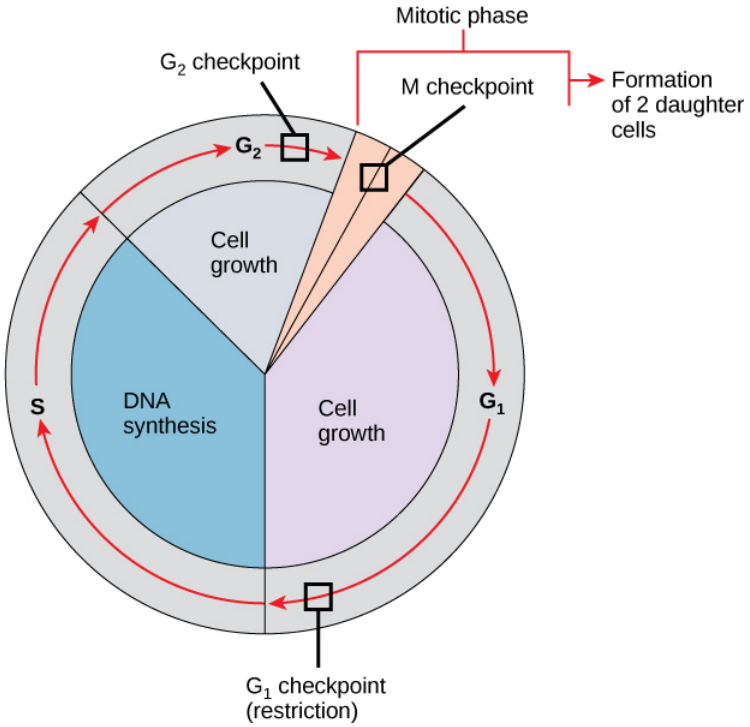


Figure 2.7.4.3: The cell cycle is controlled at three checkpoints. The integrity of the DNA is assessed at the G_1 checkpoint. Proper chromosome duplication is assessed at the G_2 checkpoint. Attachment of each kinetochore to a spindle fiber is assessed at the M checkpoint.

The G_1 Checkpoint

The G_1 checkpoint determines whether all conditions are favorable for cell division to proceed. The G_1 checkpoint, also called the restriction point (in yeast), is a point at which the cell irreversibly commits to the cell division process. External influences, such as growth factors, play a large role in carrying the cell past the G_1 checkpoint. In addition to adequate reserves and cell size, there is a check for genomic DNA damage at the G_1 checkpoint. A cell that does not meet all the requirements will not be allowed to progress into the S phase. The cell can halt the cycle and attempt to remedy the problematic condition, or the cell can advance into G_0 and await further signals when conditions improve.

The G_2 Checkpoint

The G_2 checkpoint bars entry into the mitotic phase if certain conditions are not met. As at the G_1 checkpoint, cell size and protein reserves are assessed. However, the most important role of the G_2 checkpoint is to ensure that all of the chromosomes have been replicated and that the replicated DNA is not damaged. If the checkpoint mechanisms detect problems with the DNA, the cell cycle is halted, and the cell attempts to either complete DNA replication or repair the damaged DNA.

The M Checkpoint

The M checkpoint occurs near the end of the metaphase stage of karyokinesis. The M checkpoint is also known as the spindle checkpoint, because it determines whether all the sister chromatids are correctly attached to the spindle microtubules. Because the separation of the sister chromatids during anaphase is an irreversible step, the cycle will not proceed until the kinetochores of each pair of sister chromatids are firmly anchored to at least two spindle fibers arising from opposite poles of the cell.

Link to Learning

Watch what occurs at the G_1, G_2, and M checkpoints by visiting this website to see an animation of the cell cycle.

Regulator Molecules of the Cell Cycle

In addition to the internally controlled checkpoints, there are two groups of intracellular molecules that regulate the cell cycle. These regulatory molecules either promote progress of the cell to the next phase (positive regulation) or halt the cycle (negative regulation). Regulator molecules may act individually, or they can influence the activity or production of other regulatory proteins. Therefore, the failure of a single regulator may have almost no effect on the cell cycle, especially if more than one mechanism controls the same event. Conversely, the effect of a deficient or non-functioning regulator can be wide-ranging and possibly fatal to the cell if multiple processes are affected.

Positive Regulation of the Cell Cycle

Two groups of proteins, called cyclins and cyclin-dependent kinases (Cdks), are responsible for the progress of the cell through the various checkpoints. The levels of the four cyclin proteins fluctuate throughout the cell cycle in a predictable pattern (Figure 2.7.4.2). Increases in the concentration of cyclin proteins are triggered by both external and internal signals. After the cell moves to the next stage of the cell cycle, the cyclins that were active in the previous stage are degraded.

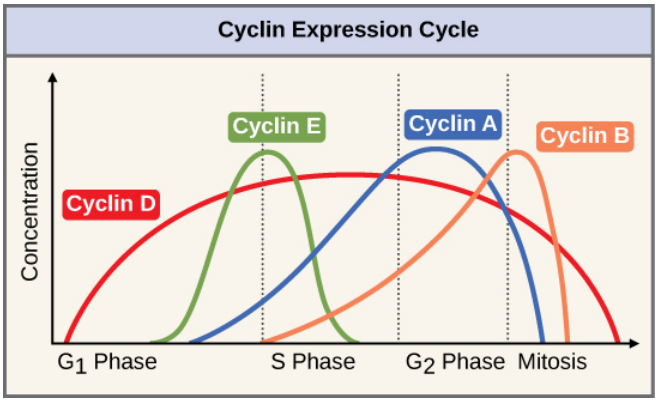


Figure 2.7.4.2: The concentrations of cyclin proteins change throughout the cell cycle. There is a direct correlation between cyclin accumulation and the three major cell cycle checkpoints. Also note the sharp decline of cyclin levels following each checkpoint (the transition between phases of the cell cycle), as cyclin is degraded by cytoplasmic enzymes. (credit: modification of work by "WikiMiMa"/Wikimedia Commons)

Cyclins regulate the cell cycle only when they are tightly bound to Cdks. To be fully active, the Cdk/cyclin complex must also be phosphorylated in specific locations. Like all kinases, Cdks are enzymes (kinases) that phosphorylate other proteins. Phosphorylation activates the protein by changing its shape. The proteins phosphorylated by Cdks are involved in advancing the cell to the next phase. (Figure 2.7.4.3). The levels of Cdk proteins are relatively stable throughout the cell cycle; however, the concentrations of cyclin fluctuate and determine when Cdk/cyclin complexes form. The different cyclins and Cdks bind at specific points in the cell cycle and thus regulate different checkpoints.

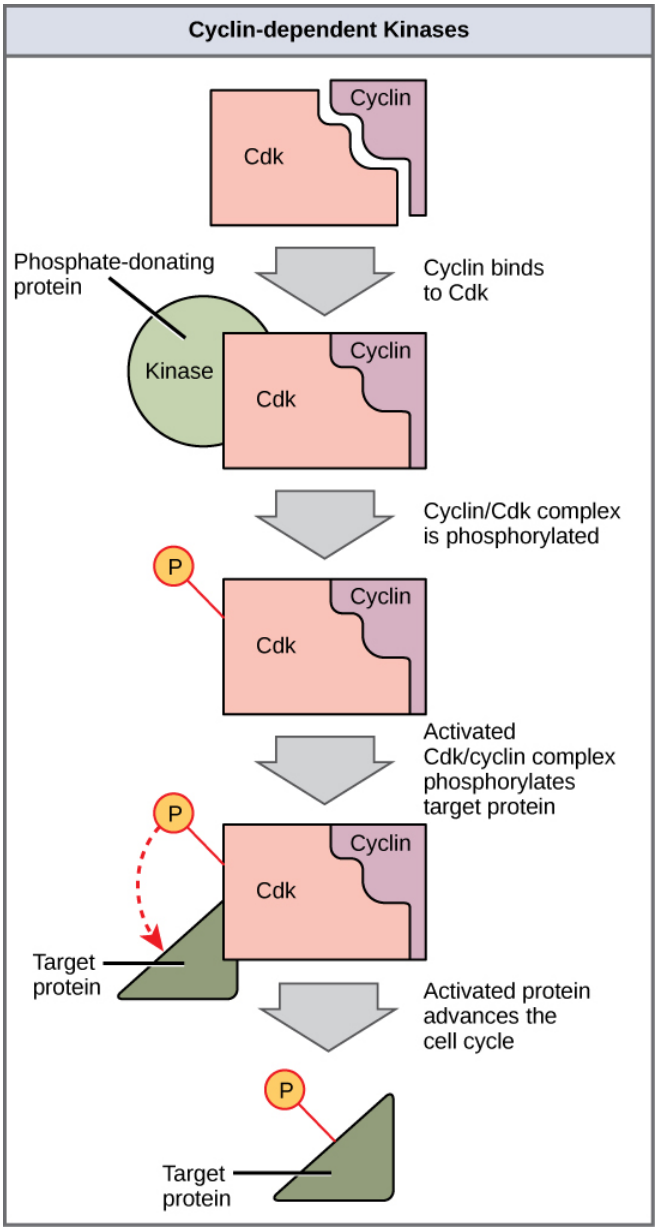


Figure 2.7.4.3: Cyclin-dependent kinases (Cdks) are protein kinases that, when fully activated, can phosphorylate and thus activate other proteins that advance the cell cycle past a checkpoint. To become fully activated, a Cdk must bind to a cyclin protein and then be phosphorylated by another kinase.

Since the cyclic fluctuations of cyclin levels are based on the timing of the cell cycle and not on specific events, regulation of the cell cycle usually occurs by either the Cdk molecules alone or the Cdk/cyclin complexes. Without a specific concentration of fully activated cyclin/Cdk complexes, the cell cycle cannot proceed through the checkpoints.

Although the cyclins are the main regulatory molecules that determine the forward momentum of the cell cycle, there are several other mechanisms that fine-tune the progress of the cycle with negative, rather than positive, effects. These mechanisms essentially block the progression of the cell cycle until problematic conditions are resolved. Molecules that prevent the full activation of Cdks are called Cdk inhibitors. Many of these inhibitor molecules directly or indirectly monitor a particular cell cycle event. The block placed on Cdks by inhibitor molecules will not be removed until the specific event that the inhibitor monitors is completed.

Negative Regulation of the Cell Cycle

The second group of cell cycle regulatory molecules are negative regulators. Negative regulators halt the cell cycle. Remember that in positive regulation, active molecules cause the cycle to progress.

The best understood negative regulatory molecules are retinoblastoma protein (Rb), p53, and p21. Retinoblastoma proteins are a group of tumor-suppressor proteins common in many cells. The 53 and 21 designations refer to the functional molecular masses of the proteins (p) in kilodaltons. Much of what is known about cell cycle regulation comes from research conducted with cells that have lost regulatory control. All three of these regulatory proteins were discovered to be damaged or non-functional in cells that had begun to replicate uncontrollably (became cancerous). In each case, the main cause of the unchecked progress through the cell cycle was a faulty copy of the regulatory protein.

Rb, p53, and p21 act primarily at the G_1 checkpoint. p53 is a multi-functional protein that has a major impact on the commitment of a cell to division because it acts when there is damaged DNA in cells that are undergoing the preparatory processes during G_1. If damaged DNA is detected, p53 halts the cell cycle and recruits enzymes to repair the DNA. If the DNA cannot be repaired, p53 can trigger apoptosis, or cell suicide, to prevent the duplication of damaged chromosomes. As p53 levels rise, the production of p21 is triggered. p21 enforces the halt in the cycle dictated by p53 by binding to and inhibiting the activity of the Cdk/cyclin complexes. As a cell is exposed to more stress, higher levels of p53 and p21 accumulate, making it less likely that the cell will move into the S phase.

Rb exerts its regulatory influence on other positive regulator proteins. Chiefly, Rb monitors cell size. In the active, dephosphorylated state, Rb binds to proteins called transcription factors, most commonly, E2F (Figure 2.7.4.4). Transcription factors "turn on" specific genes, allowing the production of proteins encoded by that gene. When Rb is bound to E2F, production of proteins necessary for the G_1/S transition is blocked. As the cell increases in size, Rb is slowly phosphorylated until it becomes inactivated. Rb releases E2F, which can now turn on the gene that produces the transition protein, and this particular block is removed. For the cell to move past each of the checkpoints, all positive regulators must be "turned on," and all negative regulators must be "turned off."

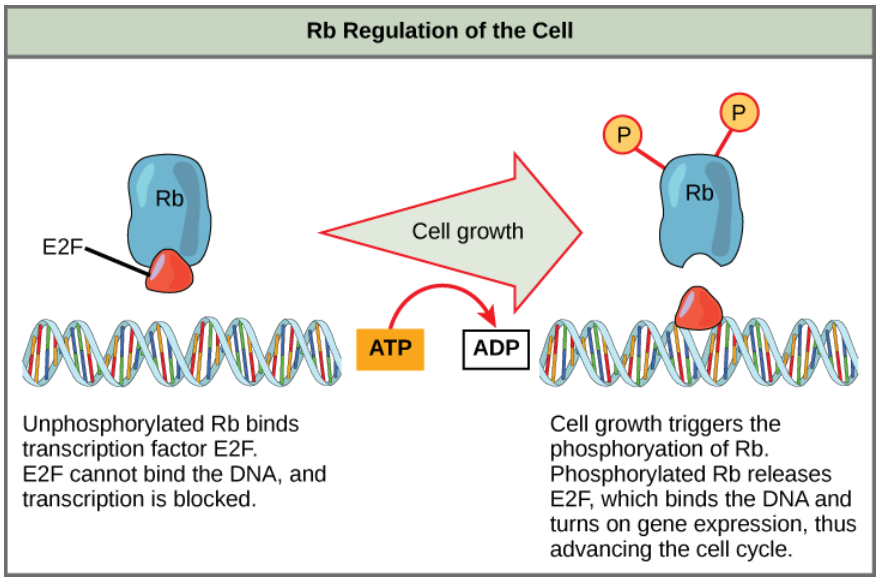


Figure 2.7.4.4: Rb halts the cell cycle and releases its hold in response to cell growth.

? Exercise 2.7.4.1

Rb and other proteins that negatively regulate the cell cycle are sometimes called tumor suppressors. Why do you think the name tumor suppressor might be appropriate for these proteins?

Answer

Rb and other negative regulatory proteins control cell division and therefore prevent the formation of tumors. Mutations that prevent these proteins from carrying out their function can result in cancer.

Summary

Each step of the cell cycle is monitored by internal controls called checkpoints. There are three major checkpoints in the cell cycle: one near the end of G_1, a second at the G_2/M transition, and the third during metaphase. Positive regulator molecules allow the cell cycle to advance to the next stage. Negative regulator molecules monitor cellular conditions and can halt the cycle until specific requirements are met.

Glossary

cell cycle checkpoint
: mechanism that monitors the preparedness of a eukaryotic cell to advance through the various cell cycle stages

cyclin
: one of a group of proteins that act in conjunction with cyclin-dependent kinases to help regulate the cell cycle by phosphorylating key proteins; the concentrations of cyclins fluctuate throughout the cell cycle

cyclin-dependent kinase
: one of a group of protein kinases that helps to regulate the cell cycle when bound to cyclin; it functions to phosphorylate other proteins that are either activated or inactivated by phosphorylation

p21
: cell cycle regulatory protein that inhibits the cell cycle; its levels are controlled by p53

p53
: cell cycle regulatory protein that regulates cell growth and monitors DNA damage; it halts the progression of the cell cycle in cases of DNA damage and may induce apoptosis

retinoblastoma protein (Rb)
: regulatory molecule that exhibits negative effects on the cell cycle by interacting with a transcription factor (E2F)

This page titled 2.7.4: Control of the Cell Cycle is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.3: Control of the Cell Cycle** by OpenStax is licensed CC BY 4.0.

2.7.5: Cancer and the Cell Cycle

Learning Objectives

- Describe how cancer is caused by uncontrolled cell growth
- Understand how proto-oncogenes are normal cell genes that, when mutated, become oncogenes
- Describe how tumor suppressors function
- Explain how mutant tumor suppressors cause cancer

Cancer comprises many different diseases caused by a common mechanism: uncontrolled cell growth. Despite the redundancy and overlapping levels of cell cycle control, errors do occur. One of the critical processes monitored by the cell cycle checkpoint surveillance mechanism is the proper replication of DNA during the S phase. Even when all of the cell cycle controls are fully functional, a small percentage of replication errors (mutations) will be passed on to the daughter cells. If changes to the DNA nucleotide sequence occur within a coding portion of a gene and are not corrected, a gene mutation results. All cancers start when a gene mutation gives rise to a faulty protein that plays a key role in cell reproduction. The change in the cell that results from the malformed protein may be minor: perhaps a slight delay in the binding of Cdk to cyclin or an Rb protein that detaches from its target DNA while still phosphorylated. Even minor mistakes, however, may allow subsequent mistakes to occur more readily. Over and over, small uncorrected errors are passed from the parent cell to the daughter cells and amplified as each generation produces more non-functional proteins from uncorrected DNA damage. Eventually, the pace of the cell cycle speeds up as the effectiveness of the control and repair mechanisms decreases. Uncontrolled growth of the mutated cells outpaces the growth of normal cells in the area, and a tumor (“-oma”) can result.

Note

Receiving news about cancer, whether for yourself or a loved one/friend, can be one of the most difficult diagnoses in a lifetime. However, having the most information possible is often the best way to understand the disease, as well as to remove a lot of the fear and mystery that goes along with the word "cancer". The videos in this section will lead you through what cancer is, how we diagnose/screen for cancer, how we know what stage the cancer is, how cancer is treated, and how to best cope with a diagnosis.

Video





Proto-oncogenes

The genes that code for the positive cell cycle regulators are called proto-oncogenes. Proto-oncogenes are normal genes that, when mutated in certain ways, become oncogenes, genes that cause a cell to become cancerous. Consider what might happen to the cell cycle in a cell with a recently acquired oncogene. In most instances, the alteration of the DNA sequence will result in a less functional (or non-functional) protein. The result is detrimental to the cell and will likely prevent the cell from completing the cell cycle; however, the organism is not harmed because the mutation will not be carried forward. If a cell cannot reproduce, the mutation is not propagated and the damage is minimal. Occasionally, however, a gene mutation causes a change that increases the activity of a positive regulator. For example, a mutation that allows Cdk to be activated without being partnered with cyclin could push the cell cycle past a checkpoint before all of the required conditions are met. If the resulting daughter cells are too damaged to undergo further cell divisions, the mutation would not be propagated and no harm would come to the organism. However, if the atypical daughter cells are able to undergo further cell divisions, subsequent generations of cells will probably accumulate even more mutations, some possibly in additional genes that regulate the cell cycle.

The Cdk gene in the above example is only one of many genes that are considered proto-oncogenes. In addition to the cell cycle regulatory proteins, any protein that influences the cycle can be altered in such a way as to override cell cycle checkpoints. An oncogene is any gene that, when altered, leads to an increase in the rate of cell cycle progression.

Tumor Suppressor Genes

Like proto-oncogenes, many of the negative cell cycle regulatory proteins were discovered in cells that had become cancerous. Tumor suppressor genes are segments of DNA that code for negative regulator proteins, the type of regulators that, when activated, can prevent the cell from undergoing uncontrolled division. The collective function of the best-understood tumor suppressor gene proteins, Rb, p53, and p21, is to put up a roadblock to cell cycle progression until certain events are completed. A cell that carries a mutated form of a negative regulator might not be able to halt the cell cycle if there is a problem. Tumor suppressors are similar to brakes in a vehicle: Malfunctioning brakes can contribute to a car crash.

Mutated p53 genes have been identified in more than one-half of all human tumor cells. This discovery is not surprising in light of the multiple roles that the p53 protein plays at the G_1 checkpoint. A cell with a faulty p53 may fail to detect errors present in the genomic DNA (Figure 2.7.5.1). Even if a partially functional p53 does identify the mutations, it may no longer be able to signal the necessary DNA repair enzymes. Either way, damaged DNA will remain uncorrected. At this point, a functional p53 will deem the cell unsalvageable and trigger programmed cell death (apoptosis). The damaged version of p53 found in cancer cells, however, cannot trigger apoptosis.

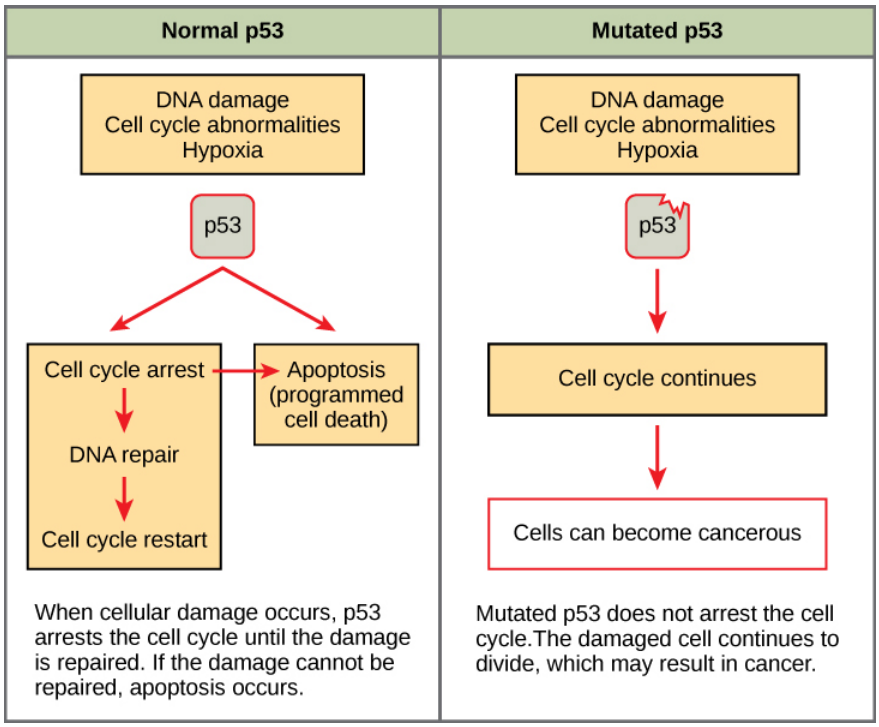


Figure 2.7.5.1: The role of normal p53 is to monitor DNA and the supply of oxygen (hypoxia is a condition of reduced oxygen supply). If damage is detected, p53 triggers repair mechanisms. If repairs are unsuccessful, p53 signals apoptosis. A cell with an abnormal p53 protein cannot repair damaged DNA and thus cannot signal apoptosis. Cells with abnormal p53 can become cancerous. (credit: modification of work by Thierry Soussi)

? Exercise 2.7.5.1

Human papillomavirus can cause cervical cancer. The virus encodes E6, a protein that binds p53. Based on this fact and what you know about p53, what effect do you think E6 binding has on p53 activity?

A. E6 activates p53
B. E6 inactivates p53
C. E6 mutates p53
D. E6 binding marks p53 for degradation

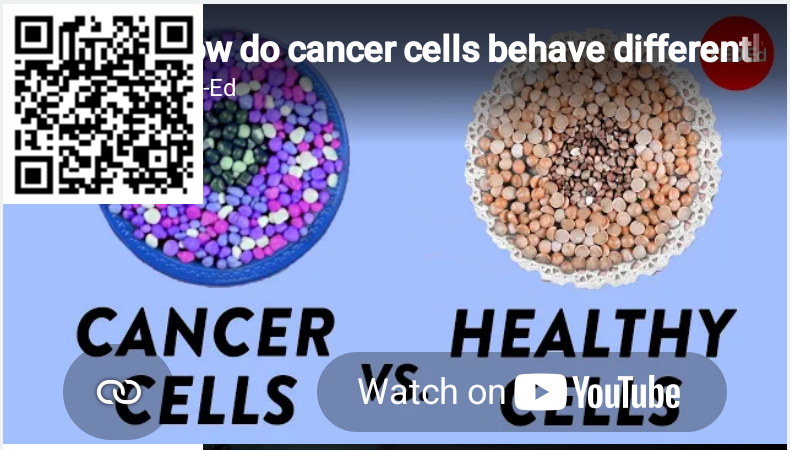
Answer

D. E6 binding marks p53 for degradation.

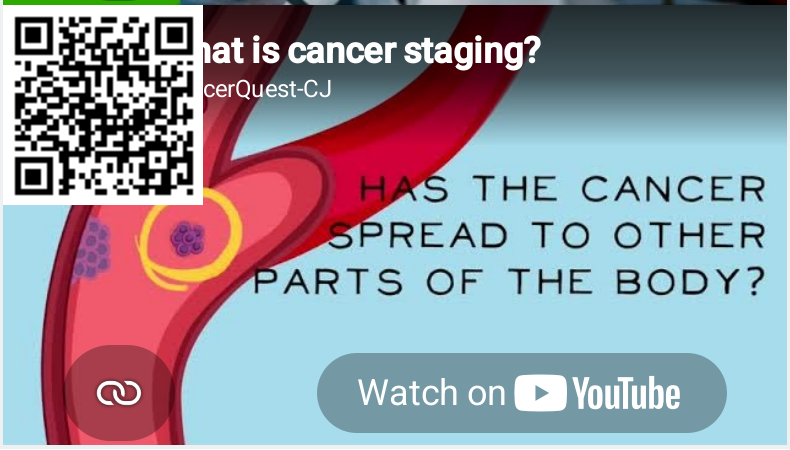
The loss of p53 function has other repercussions for the cell cycle. Mutated p53 might lose its ability to trigger p21 production. Without adequate levels of p21, there is no effective block on Cdk activation. Essentially, without a fully functional p53, the G_1 checkpoint is severely compromised and the cell proceeds directly from G_1 to S regardless of internal and external conditions. At the completion of this shortened cell cycle, two daughter cells are produced that have inherited the mutated p53 gene. Given the non-optimal conditions under which the parent cell reproduced, it is likely that the daughter cells will have acquired other mutations in addition to the faulty tumor suppressor gene. Cells such as these daughter cells quickly accumulate both oncogenes and non-functional tumor suppressor genes. Again, the result is tumor growth.

Approaches to Cancer

Video







Summary

Cancer is the result of unchecked cell division caused by a breakdown of the mechanisms that regulate the cell cycle. The loss of control begins with a change in the DNA sequence of a gene that codes for one of the regulatory molecules. Faulty instructions lead to a protein that does not function as it should. Any disruption of the monitoring system can allow other mistakes to be passed on to the daughter cells. Each successive cell division will give rise to daughter cells with even more accumulated damage. Eventually, all checkpoints become nonfunctional, and rapidly reproducing cells crowd out normal cells, resulting in a tumor or leukemia (blood cancer).

oncogene
mutated version of a normal gene involved in the positive regulation of the cell cycle

proto-oncogene
normal gene that when mutated becomes an oncogene

tumor suppressor gene
segment of DNA that codes for regulator proteins that prevent the cell from undergoing uncontrolled division

---

This page titled 2.7.5: Cancer and the Cell Cycle is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.4: Cancer and the Cell Cycle** by OpenStax is licensed CC BY 4.0.

2.7.6: Prokaryotic Cell Division

Skills to Develop

- Describe the process of binary fission in prokaryotes
- Explain how FtsZ and tubulin proteins are examples of homology

Prokaryotes, such as bacteria, propagate by binary fission. For unicellular organisms, cell division is the only method to produce new individuals. In both prokaryotic and eukaryotic cells, the outcome of cell reproduction is a pair of daughter cells that are genetically identical to the parent cell. In unicellular organisms, daughter cells are individuals.

To achieve the outcome of cloned offspring, certain steps are essential. The genomic DNA must be replicated and then allocated into the daughter cells; the cytoplasmic contents must also be divided to give both new cells the machinery to sustain life. In bacterial cells, the genome consists of a single, circular DNA chromosome; therefore, the process of cell division is simplified. Karyokinesis is unnecessary because there is no nucleus and thus no need to direct one copy of the multiple chromosomes into each daughter cell. This type of cell division is called binary (prokaryotic) fission.

Binary Fission

Due to the relative simplicity of the prokaryotes, the cell division process, called binary fission, is a less complicated and much more rapid process than cell division in eukaryotes. The single, circular DNA chromosome of bacteria is not enclosed in a nucleus, but instead occupies a specific location, the nucleoid, within the cell (Figure 2.7.6.1). Although the DNA of the nucleoid is associated with proteins that aid in packaging the molecule into a compact size, there are no histone proteins and thus no nucleosomes in prokaryotes. The packing proteins of bacteria are, however, related to the cohesin and condensin proteins involved in the chromosome compaction of eukaryotes.

The bacterial chromosome is attached to the plasma membrane at about the midpoint of the cell. The starting point of replication, the origin, is close to the binding site of the chromosome to the plasma membrane (Figure 2.7.6.1). Replication of the DNA is bidirectional, moving away from the origin on both strands of the loop simultaneously. As the new double strands are formed, each origin point moves away from the cell wall attachment toward the opposite ends of the cell. As the cell elongates, the growing membrane aids in the transport of the chromosomes. After the chromosomes have cleared the midpoint of the elongated cell, cytoplasmic separation begins. The formation of a ring composed of repeating units of a protein called FtsZ directs the partition between the nucleoids. Formation of the FtsZ ring triggers the accumulation of other proteins that work together to recruit new membrane and cell wall materials to the site. A septum is formed between the nucleoids, extending gradually from the periphery toward the center of the cell. When the new cell walls are in place, the daughter cells separate.

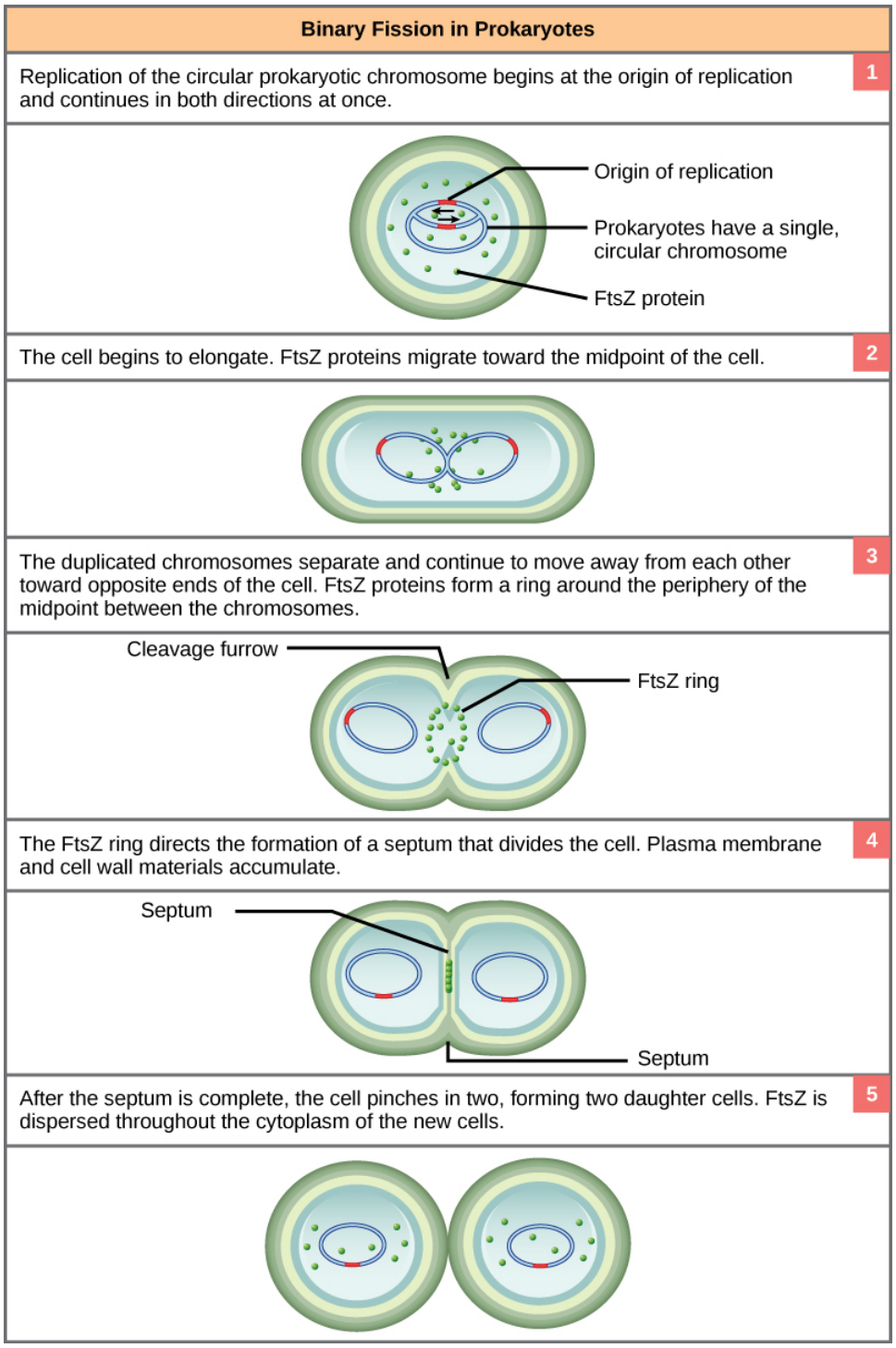


Figure 2.7.6.1: These images show the steps of binary fission in prokaryotes. (credit: modification of work by "Mcstrother"/Wikimedia Commons)

Evolution Connection: Mitotic Spindle Apparatus

The precise timing and formation of the mitotic spindle is critical to the success of eukaryotic cell division. Prokaryotic cells, on the other hand, do not undergo karyokinesis and therefore have no need for a mitotic spindle. However, the FtsZ protein that plays such a vital role in prokaryotic cytokinesis is structurally and functionally very similar to tubulin, the building block of the microtubules that make up the mitotic spindle fibers that are necessary for eukaryotes. FtsZ proteins can form filaments, rings, and other three-dimensional structures that resemble the way tubulin forms microtubules, centrioles, and various

cytoskeletal components. In addition, both FtsZ and tubulin employ the same energy source, GTP (guanosine triphosphate), to rapidly assemble and disassemble complex structures.

FtsZ and tubulin are homologous structures derived from common evolutionary origins. In this example, FtsZ is the ancestor protein to tubulin (a modern protein). While both proteins are found in extant organisms, tubulin function has evolved and diversified tremendously since evolving from its FtsZ prokaryotic origin. A survey of mitotic assembly components found in present-day unicellular eukaryotes reveals crucial intermediary steps to the complex membrane-enclosed genomes of multicellular eukaryotes.

Table 2.7.6.1: Cell Division Apparatus among Various Organisms

	Structure of genetic material	Division of nuclear material	Separation of daughter cells
Prokaryotes	There is no nucleus. The single, circular chromosome exists in a region of cytoplasm called the nucleoid.	Occurs through binary fission. As the chromosome is replicated, the two copies move to opposite ends of the cell by an unknown mechanism.	FtsZ proteins assemble into a ring that pinches the cell in two.
Some protists	Linear chromosomes exist in the nucleus.	Chromosomes attach to the nuclear envelope, which remains intact. The mitotic spindle passes through the envelope and elongates the cell. No centrioles exist.	Microfilaments form a cleavage furrow that pinches the cell in two.
Other protists	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrioles and passes through the nuclear membrane, which remains intact. Chromosomes attach to the mitotic spindle, which separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.
Animal cells	Linear chromosomes exist in the nucleus.	A mitotic spindle forms from the centrosomes. The nuclear envelope dissolves. Chromosomes attach to the mitotic spindle, which separates the chromosomes and elongates the cell.	Microfilaments form a cleavage furrow that pinches the cell in two.

Summary

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and then each copy is allocated into a daughter cell. In addition, the cytoplasmic contents are divided evenly and distributed to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome but no nucleus. Therefore, mitosis is not necessary in bacterial cell division. Bacterial cytokinesis is directed by a ring composed of a protein called FtsZ. Ingrowth of membrane and cell wall material from the periphery of the cells results in the formation of a septum that eventually constructs the separate cell walls of the daughter cells.

binary fission
prokaryotic cell division process

FtsZ
tubulin-like protein component of the prokaryotic cytoskeleton that is important in prokaryotic cytokinesis (name origin: **F**ilamenting **t**emperature-**s**ensitive mutant **Z**)

origin
(also, ORI) region of the prokaryotic chromosome where replication begins (origin of replication)

septum
structure formed in a bacterial cell as a precursor to the separation of the cell into two daughter cells

---

This page titled 2.7.6: Prokaryotic Cell Division is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.5: Prokaryotic Cell Division** by OpenStax is licensed CC BY 4.0.

2.7.E: Cell Reproduction (Exercises)

This page is a draft and is under active development.

10.1: Cell Division

The continuity of life from one cell to another has its foundation in the reproduction of cells by way of the cell cycle. The cell cycle is an orderly sequence of events that describes the stages of a cell's life from the division of a single parent cell to the production of two new daughter cells. The mechanisms involved in the cell cycle are highly regulated.

Review Questions

A diploid cell has_____ the number of chromosomes as a haploid cell.

A. one-fourth
B. half
C. twice
D. four times

Answer

C

An organism's traits are determined by the specific combination of inherited _____.

A. cells.
B. genes.
C. proteins.
D. chromatids.

Answer

B

The first level of DNA organization in a eukaryotic cell is maintained by which molecule?

A. cohesin
B. condensin
C. chromatin
D. histone

Answer

D

Identical copies of chromatin held together by cohesin at the centromere are called _____.

A. histones.
B. nucleosomes.
C. chromatin.
D. sister chromatids.

Answer

D

Free Response

Compare and contrast a human somatic cell to a human gamete.

Answer

Human somatic cells have 46 chromosomes: 22 pairs and 2 sex chromosomes that may or may not form a pair. This is the 2*n* or diploid condition. Human gametes have 23 chromosomes, one each of 23 unique chromosomes, one of which is a sex chromosome. This is the *n* or haploid condition.

What is the relationship between a genome, chromosomes, and genes?

Answer

The genome consists of the sum total of an organism's chromosomes. Each chromosome contains hundreds and sometimes thousands of genes, segments of DNA that code for a polypeptide or RNA, and a large amount of DNA with no known function.

Eukaryotic chromosomes are thousands of times longer than a typical cell. Explain how chromosomes can fit inside a eukaryotic nucleus.

Answer

The DNA double helix is wrapped around histone proteins to form structures called nucleosomes. Nucleosomes and the linker DNA in between them are coiled into a 30-nm fiber. During cell division, chromatin is further condensed by packing proteins.

10.2: The Cell Cycle

The cell cycle is an ordered series of events involving cell growth and cell division that produces two new daughter cells. Cells on the path to cell division proceed through a series of precisely timed and carefully regulated stages of growth, DNA replication, and division that produces two identical (clone) cells. The cell cycle has two major phases: interphase and the mitotic phase.

Review Questions

Chromosomes are duplicated during what stage of the cell cycle?

A. G_1 phase
B. S phase
C. prophase
D. prometaphase

Answer

B

Which of the following events does not occur during some stages of interphase?

A. DNA duplication
B. organelle duplication
C. increase in cell size
D. separation of sister chromatids

Answer

D

The mitotic spindles arise from which cell structure?

A. centromere
B. centrosome
C. kinetochore
D. cleavage furrow

Answer

B

Attachment of the mitotic spindle fibers to the kinetochores is a characteristic of which stage of mitosis?

A. prophase
B. prometaphase
C. metaphase
D. anaphase

Answer

B

Unpacking of chromosomes and the formation of a new nuclear envelope is a characteristic of which stage of mitosis?

A. prometaphase
B. metaphase
C. anaphase
D. telophase

Answer

D

Separation of the sister chromatids is a characteristic of which stage of mitosis?

A. prometaphase
B. metaphase
C. anaphase
D. telophase

Answer

C

The chromosomes become visible under a light microscope during which stage of mitosis?

A. prophase
B. prometaphase
C. metaphase
D. anaphase

Answer

A

The fusing of Golgi vesicles at the metaphase plate of dividing plant cells forms what structure?

https://bio.libretexts.org/@go/page/82908

A. cell plate
B. actin ring
C. cleavage furrow
D. mitotic spindle

Answer

A

Free Response

Briefly describe the events that occur in each phase of interphase.

Answer

During G_1, the cell increases in size, the genomic DNA is assessed for damage, and the cell stockpiles energy reserves and the components to synthesize DNA. During the S phase, the chromosomes, the centrosomes, and the centrioles (animal cells) duplicate. During the G_2 phase, the cell recovers from the S phase, continues to grow, duplicates some organelles, and dismantles other organelles.

Chemotherapy drugs such as vincristine and colchicine disrupt mitosis by binding to tubulin (the subunit of microtubules) and interfering with microtubule assembly and disassembly. Exactly what mitotic structure is targeted by these drugs and what effect would that have on cell division?

Answer

The mitotic spindle is formed of microtubules. Microtubules are polymers of the protein tubulin; therefore, it is the mitotic spindle that is disrupted by these drugs. Without a functional mitotic spindle, the chromosomes will not be sorted or separated during mitosis. The cell will arrest in mitosis and die.

Describe the similarities and differences between the cytokinesis mechanisms found in animal cells versus those in plant cells.

Answer

There are very few similarities between animal cell and plant cell cytokinesis. In animal cells, a ring of actin fibers is formed around the periphery of the cell at the former metaphase plate (cleavage furrow). The actin ring contracts inward, pulling the plasma membrane toward the center of the cell until the cell is pinched in two. In plant cells, a new cell wall must be formed between the daughter cells. Due to the rigid cell walls of the parent cell, contraction of the middle of the cell is not possible. Instead, a phragmoplast first forms. Subsequently, a cell plate is formed in the center of the cell at the former metaphase plate. The cell plate is formed from Golgi vesicles that contain enzymes, proteins, and glucose. The vesicles fuse and the enzymes build a new cell wall from the proteins and glucose. The cell plate grows toward and eventually fuses with the cell wall of the parent cell.

List some reasons why a cell that has just completed cytokinesis might enter the G_0 phase instead of the G_1 phase.

Answer

Many cells temporarily enter G_0 until they reach maturity. Some cells are only triggered to enter G_1 when the organism needs to increase that particular cell type. Some cells only reproduce following an injury to the tissue. Some cells never divide once they reach maturity.

What cell cycle events will be affected in a cell that produces mutated (non-functional) cohesin protein?

Answer

If cohesin is not functional, chromosomes are not packaged after DNA replication in the S phase of interphase. It is likely that the proteins of the centromeric region, such as the kinetochore, would not form. Even if the mitotic spindle fibers could attach to the chromatids without packing, the chromosomes would not be sorted or separated during mitosis.

10.3: Control of the Cell Cycle

The length of the cell cycle is highly variable, even within the cells of a single organism. In humans, the frequency of cell turnover ranges from a few hours in early embryonic development, to an average of two to five days for epithelial cells, and to an entire human lifetime spent in G0 by specialized cells, such as cortical neurons or cardiac muscle cells. There is also variation in the time that a cell spends in each phase of the cell cycle.

Review Questions

At which of the cell cycle checkpoints do external forces have the greatest influence?

A. G_1 checkpoint
B. G_2 checkpoint
C. M checkpoint
D. G_0 checkpoint

Answer

A

What is the main prerequisite for clearance at the G_2 checkpoint?

A. cell has reached a sufficient size
B. an adequate stockpile of nucleotides
C. accurate and complete DNA replication
D. proper attachment of mitotic spindle fibers to kinetochores

Answer

C

If the M checkpoint is not cleared, what stage of mitosis will be blocked?

A. prophase
B. prometaphase
C. metaphase
D. anaphase

Answer

D

Which protein is a positive regulator that phosphorylates other proteins when activated?

A. p53
B. retinoblastoma protein (Rb)
C. cyclin
D. cyclin-dependent kinase (Cdk)

Answer

D

Many of the negative regulator proteins of the cell cycle were discovered in what type of cells?

A. gametes
B. cells in G_0
C. cancer cells
D. stem cells

Answer

C

Which negative regulatory molecule can trigger cell suicide (apoptosis) if vital cell cycle events do not occur?

A. p53
B. p21
C. retinoblastoma protein (Rb)
D. cyclin-dependent kinase (Cdk)

Answer

A

Free Response

Describe the general conditions that must be met at each of the three main cell cycle checkpoints.

Answer

The G_1 checkpoint monitors adequate cell growth, the state of the genomic DNA, adequate stores of energy, and materials for S phase. At the G_2 checkpoint, DNA is checked to ensure that all chromosomes were duplicated and that there are no mistakes in newly synthesized DNA. Additionally, cell size and energy reserves are evaluated. The M checkpoint confirms the correct attachment of the mitotic spindle fibers to the kinetochores.

Explain the roles of the positive cell cycle regulators compared to the negative regulators.

Answer

Positive cell regulators such as cyclin and Cdk perform tasks that advance the cell cycle to the next stage. Negative regulators such as Rb, p53, and p21 block the progression of the cell cycle until certain events have occurred.

What steps are necessary for Cdk to become fully active?

Answer

Cdk must bind to a cyclin, and it must be phosphorylated in the correct position to become fully active.

Rb is a negative regulator that blocks the cell cycle at the G_1 checkpoint until the cell achieves a requisite size. What molecular mechanism does Rb employ to halt the cell cycle?

Answer

Rb is active when it is dephosphorylated. In this state, Rb binds to E2F, which is a transcription factor required for the transcription and eventual translation of molecules required for the G_1/S transition. E2F cannot transcribe certain genes when it is bound to Rb. As the cell increases in size, Rb becomes phosphorylated, inactivated, and releases E2F. E2F can then promote the transcription of the genes it controls, and the transition proteins will be produced.

10.4: Cancer and the Cell Cycle

Cancer is the result of unchecked cell division caused by a breakdown of the mechanisms that regulate the cell cycle. The loss of control begins with a change in the DNA sequence of a gene that codes for one of the regulatory molecules. Faulty instructions lead to a protein that does not function as it should. Any disruption of the monitoring system can allow other mistakes to be passed on to the daughter cells. Each successive cell division will give rise to daughter cells with even more damage

Review Questions

_____ are changes to the order of nucleotides in a segment of DNA that codes for a protein.

A. Proto-oncogenes
B. Tumor suppressor genes
C. Gene mutations
D. Negative regulators

Answer

C

A gene that codes for a positive cell cycle regulator is called a(n) _____.

A. kinase inhibitor.
B. tumor suppressor gene.
C. proto-oncogene.
D. oncogene.

Answer

C

A mutated gene that codes for an altered version of Cdk that is active in the absence of cyclin is a(n) _____.

A. kinase inhibitor.
B. tumor suppressor gene.
C. proto-oncogene.
D. oncogene.

Answer

D

Which molecule is a Cdk inhibitor that is controlled by p53?

A. cyclin
B. anti-kinase
C. Rb
D. p21

Answer

D

Free Response

Outline the steps that lead to a cell becoming cancerous.

Answer

If one of the genes that produces regulator proteins becomes mutated, it produces a malformed, possibly non-functional, cell cycle regulator, increasing the chance that more mutations will be left unrepaired in the cell. Each subsequent generation of cells sustains more damage. The cell cycle can speed up as a result of the loss of functional checkpoint proteins. The cells can lose the ability to self-destruct and eventually become "immortalized."

Explain the difference between a proto-oncogene and a tumor suppressor gene.

Answer

A proto-oncogene is a segment of DNA that codes for one of the positive cell cycle regulators. If that gene becomes mutated so that it produces a hyperactivated protein product, it is considered an oncogene. A tumor suppressor gene is a segment of DNA that codes for one of the negative cell cycle regulators. If that gene becomes mutated so that the protein product becomes less active, the cell cycle will run unchecked. A single oncogene can initiate abnormal cell divisions; however, tumor suppressors lose their effectiveness only when both copies of the gene are damaged.

List the regulatory mechanisms that might be lost in a cell producing faulty p53.

Answer

Regulatory mechanisms that might be lost include monitoring of the quality of the genomic DNA, recruiting of repair enzymes, and the triggering of apoptosis.

p53 can trigger apoptosis if certain cell cycle events fail. How does this regulatory outcome benefit a multicellular organism?

Answer

If a cell has damaged DNA, the likelihood of producing faulty proteins is higher. The daughter cells of such a damaged parent cell would also produce faulty proteins that might eventually become cancerous. If p53 recognizes this damage and triggers the cell to self-destruct, the damaged DNA is degraded and recycled. No further harm comes to the organism. Another healthy cell is triggered to divide instead.

10.5: Prokaryotic Cell Division

In both prokaryotic and eukaryotic cell division, the genomic DNA is replicated and then each copy is allocated into a daughter cell. In addition, the cytoplasmic contents are divided evenly and distributed to the new cells. However, there are many differences between prokaryotic and eukaryotic cell division. Bacteria have a single, circular DNA chromosome but no nucleus. Therefore, mitosis is not necessary in bacterial cell division.

Review Questions

Which eukaryotic cell cycle event is missing in binary fission?

A. cell growth
B. DNA duplication
C. karyokinesis
D. cytokinesis

Answer

C

FtsZ proteins direct the formation of a _____ that will eventually form the new cell walls of the daughter cells.

A. contractile ring
B. cell plate
C. cytoskeleton

D. septum

Answer

B

Free Response

Name the common components of eukaryotic cell division and binary fission.

Answer

The common components of eukaryotic cell division and binary fission are DNA duplication, segregation of duplicated chromosomes, and division of the cytoplasmic contents.

Describe how the duplicated bacterial chromosomes are distributed into new daughter cells without the direction of the mitotic spindle.

Answer

As the chromosome is being duplicated, each origin moves away from the starting point of replication. The chromosomes are attached to the cell membrane via proteins; the growth of the membrane as the cell elongates aids in their movement.

This page titled 2.7.E: Cell Reproduction (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **10.E: Cell Reproduction (Exercises)** is licensed CC BY 4.0.

SECTION OVERVIEW

3: Unit III- Genetics

Genetics is the study of genes, heredity, and genetic variation in living organisms. Our comprehensive genetics unit takes learners from the earliest experiments that revealed the basis of genetics through the intricacies of DNA to current applications in the emerging studies of biotechnology and genomics.

3.1: Meiosis and Sexual Reproduction

- 3.1.1: Prelude to Meiosis and Sexual Reproduction
- 3.1.2: The Process of Meiosis
- 3.1.3: Sexual Reproduction
- 3.1.E: Meiosis and Sexual Reproduction (Exercises)

3.2: Mendel's Experiments and Heredity

- 3.2.1: Prelude to Mendel's Experiments and Heredity
- 3.2.2: Mendel’s Experiments and the Laws of Probability
- 3.2.3: Characteristics and Traits
- 3.2.4: Laws of Inheritance
- 3.2.E: Mendel's Experiments and Heredity (Exercises)

3.3: Modern Understandings of Inheritance

- 3.3.1: Prelude to Modern Understandings of Inheritance
- 3.3.2: Chromosomal Theory and Genetic Linkage
- 3.3.3: Chromosomal Basis of Inherited Disorders
- 3.3.E: Modern Understandings of Inheritance (Exercises)

3.4: DNA Structure and Function

- 3.4.1: Prelude to DNA Structure and Function
- 3.4.2: Historical Basis of Modern Understanding
- 3.4.3: DNA Structure and Sequencing
- 3.4.4: Basics of DNA Replication
- 3.4.5: DNA Replication in Prokaryotes
- 3.4.6: DNA Replication in Eukaryotes
- 3.4.7: DNA Repair
- 3.4.E: DNA Structure and Function (Exercises)

3.5: Genes Expression

- 3.5.1: Prelude to Genes and Proteins
- 3.5.2: The Genetic Code
- 3.5.3: Prokaryotic Transcription
- 3.5.4: Eukaryotic Transcription
- 3.5.5: RNA Processing in Eukaryotes
- 3.5.6: Ribosomes and Protein Synthesis

3.5.E: Genes and Proteins (Exercises)

3.6: Gene Regulation

3.6.1: Prelude to Gene Expression
3.6.2: Regulation of Gene Expression
3.6.3: Prokaryotic Gene Regulation
3.6.4: Eukaryotic Epigenetic Gene Regulation
3.6.5: Eukaryotic Transcription Gene Regulation
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
3.6.8: Cancer and Gene Regulation
3.6.E: Gene Expression (Exercises)

3.7: Biotechnology and Genomics

3.7.1: Prelude
3.7.2: Biotechnology
3.7.3: Mapping Genomes
3.7.4: Whole-Genome Sequencing
3.7.5: Applying Genomics
3.7.6: Genomics and Proteomics
3.7.E: Biotechnology and Genomics (Exercises)

Contributors

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3: Unit III- Genetics is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

3.1: Meiosis and Sexual Reproduction

3.1.1: Prelude to Meiosis and Sexual Reproduction

3.1.2: The Process of Meiosis

3.1.3: Sexual Reproduction

3.1.E: Meiosis and Sexual Reproduction (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.1: Meiosis and Sexual Reproduction is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.1.1: Prelude to Meiosis and Sexual Reproduction



(a) (b) (c)

Figure 3.1.1.1: Each of us, like these other large multicellular organisms, begins life as a fertilized egg. After trillions of cell divisions, each of us develops into a complex, multicellular organism. (credit a: modification of work by Frank Wouters; credit b: modification of work by Ken Cole, USGS; credit c: modification of work by Martin Pettitt)

The ability to reproduce *in kind* is a basic characteristic of all living things. *In kind* means that the offspring of any organism closely resemble their parent or parents. Hippopotamuses give birth to hippopotamus calves, Joshua trees produce seeds from which Joshua tree seedlings emerge, and adult flamingos lay eggs that hatch into flamingo chicks. *In kind* does not generally mean *exactly the same*. Whereas many unicellular organisms and a few multicellular organisms can produce genetically identical clones of themselves through cell division, many single-celled organisms and most multicellular organisms reproduce regularly using another method. Sexual reproduction is the production by parents of two haploid cells and the fusion of two haploid cells to form a single, unique diploid cell. In most plants and animals, through tens of rounds of mitotic cell division, this diploid cell will develop into an adult organism. Haploid cells that are part of the sexual reproductive cycle are produced by a type of cell division called meiosis. Sexual reproduction, specifically meiosis and fertilization, introduces variation into offspring that may account for the evolutionary success of sexual reproduction. The vast majority of eukaryotic organisms, both multicellular and unicellular, can or must employ some form of meiosis and fertilization to reproduce.

This page titled 3.1.1: Prelude to Meiosis and Sexual Reproduction is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **11.0: Prelude to Meiosis and Sexual Reproduction** by OpenStax is licensed CC BY 4.0.

3.1.2: The Process of Meiosis

Learning Objectives

- Describe the behavior of chromosomes during meiosis
- Describe cellular events during meiosis
- Explain the differences between meiosis and mitosis
- Explain the mechanisms within meiosis that generate genetic variation among the products of meiosis

Video



Sexual reproduction requires fertilization, the union of two cells from two individual organisms. If those two cells each contain one set of chromosomes, then the resulting cell contains two sets of chromosomes. *Haploid* cells contain one set of chromosomes. Cells containing two sets of chromosomes are called *diploid*. The number of sets of chromosomes in a cell is called its *ploidy level*. If the reproductive cycle is to continue, then the diploid cell must somehow reduce its number of chromosome sets before fertilization can occur again, or there will be a continual doubling in the number of chromosome sets in every generation. So, in addition to fertilization, sexual reproduction includes a nuclear division that reduces the number of chromosome sets.

Most animals and plants are diploid, containing two sets of chromosomes. In each somatic cell of the organism (all cells of a multicellular organism except the gametes or reproductive cells), the nucleus contains two copies of each chromosome, called homologous chromosomes. Somatic cells are sometimes referred to as “body” cells. Homologous chromosomes are matched pairs containing the same genes in identical locations along their length. Diploid organisms inherit one copy of each homologous chromosome from each parent; all together, they are considered a full set of chromosomes. Haploid cells, containing a single copy of each homologous chromosome, are found only within structures that give rise to either gametes or spores. Spores are haploid cells that can produce a haploid organism or can fuse with another spore to form a diploid cell. All animals and most plants produce eggs and sperm, or gametes. Some plants and all fungi produce spores.

The nuclear division that forms haploid cells, which is called meiosis, is related to mitosis. As you have learned, mitosis is the part of a cell reproduction cycle that results in identical daughter nuclei that are also genetically identical to the original parent nucleus. In mitosis, both the parent and the daughter nuclei are at the same ploidy level—diploid for most plants and animals. Meiosis employs many of the same mechanisms as mitosis. However, the starting nucleus is always diploid and the nuclei that result at the end of a meiotic cell division are haploid. To achieve this reduction in chromosome number, meiosis consists of one round of chromosome duplication and two rounds of nuclear division. Because the events that occur during each of the division stages are analogous to the events of mitosis, the same stage names are assigned. However, because there are two rounds of division, the major process and the stages are designated with a “I” or a “II.” Thus, meiosis I is the first round of meiotic division and consists of prophase I, prometaphase I, and so on. Meiosis II, in which the second round of meiotic division takes place, includes prophase II, prometaphase II, and so on.

Meiosis I

Meiosis is preceded by an interphase consisting of the G_1, S, and G_2 phases, which are nearly identical to the phases preceding mitosis. The G_1 phase, which is also called the first gap phase, is the first phase of the interphase and is focused on cell growth. The S phase is the second phase of interphase, during which the DNA of the chromosomes is replicated. Finally, the G_2 phase, also called the second gap phase, is the third and final phase of interphase; in this phase, the cell undergoes the final preparations for meiosis.

During DNA duplication in the S phase, each chromosome is replicated to produce two identical copies, called sister chromatids, that are held together at the centromere by cohesin proteins. Cohesin holds the chromatids together until anaphase II. The centrosomes, which are the structures that organize the microtubules of the meiotic spindle, also replicate. This prepares the cell to enter prophase I, the first meiotic phase.

Prophase I

Early in prophase I, before the chromosomes can be seen clearly microscopically, the homologous chromosomes are attached at their tips to the nuclear envelope by proteins. As the nuclear envelope begins to break down, the proteins associated with homologous chromosomes bring the pair close to each other. Recall that, in mitosis, homologous chromosomes do not pair together. In mitosis, homologous chromosomes line up end-to-end so that when they divide, each daughter cell receives a sister chromatid from both members of the homologous pair. The synaptonemal complex, a lattice of proteins between the homologous chromosomes, first forms at specific locations and then spreads to cover the entire length of the chromosomes. The tight pairing of the homologous chromosomes is called synapsis. In synapsis, the genes on the chromatids of the homologous chromosomes are aligned precisely with each other. The synaptonemal complex supports the exchange of chromosomal segments between non-sister homologous chromatids, a process called crossing over. Crossing over can be observed visually after the exchange as chiasmata (singular = chiasma) (Figure 3.1.2.1).

In species such as humans, even though the X and Y sex chromosomes are not homologous (most of their genes differ), they have a small region of homology that allows the X and Y chromosomes to pair up during prophase I. A partial synaptonemal complex develops only between the regions of homology.

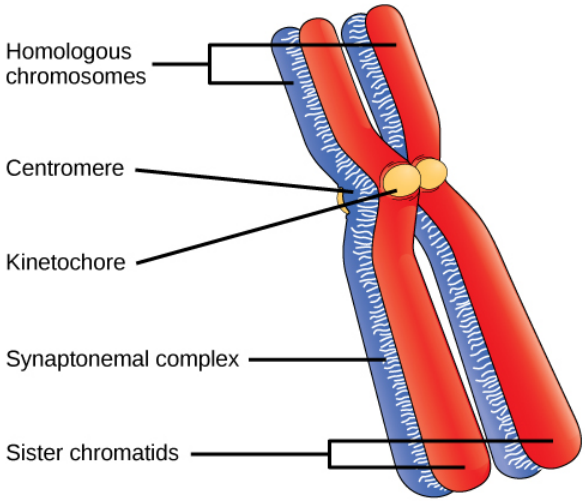


Figure 3.1.2.1: Early in prophase I, homologous chromosomes come together to form a synapse. The chromosomes are bound tightly together and in perfect alignment by a protein lattice called a synaptonemal complex and by cohesin proteins at the centromere.

Located at intervals along the synaptonemal complex are large protein assemblies called recombination nodules. These assemblies mark the points of later chiasmata and mediate the multistep process of crossover—or genetic recombination—between the non-sister chromatids. Near the recombination nodule on each chromatid, the double-stranded DNA is cleaved, the cut ends are modified, and a new connection is made between the non-sister chromatids. As prophase I progresses, the synaptonemal complex begins to break down and the chromosomes begin to condense. When the synaptonemal complex is gone, the homologous chromosomes remain attached to each other at the centromere and at chiasmata. The chiasmata remain until anaphase I. The number of chiasmata varies according to the species and the length of the chromosome. There must be at least one chiasma per

chromosome for proper separation of homologous chromosomes during meiosis I, but there may be as many as 25. Following crossover, the synaptonemal complex breaks down and the cohesin connection between homologous pairs is also removed. At the end of prophase I, the pairs are held together only at the chiasmata (Figure 3.1.2.2) and are called tetrads because the four sister chromatids of each pair of homologous chromosomes are now visible.

The crossover events are the first source of genetic variation in the nuclei produced by meiosis. A single crossover event between homologous non-sister chromatids leads to a reciprocal exchange of equivalent DNA between a maternal chromosome and a paternal chromosome. Now, when that sister chromatid is moved into a gamete cell it will carry some DNA from one parent of the individual and some DNA from the other parent. The sister recombinant chromatid has a combination of maternal and paternal genes that did not exist before the crossover. Multiple crossovers in an arm of the chromosome have the same effect, exchanging segments of DNA to create recombinant chromosomes.

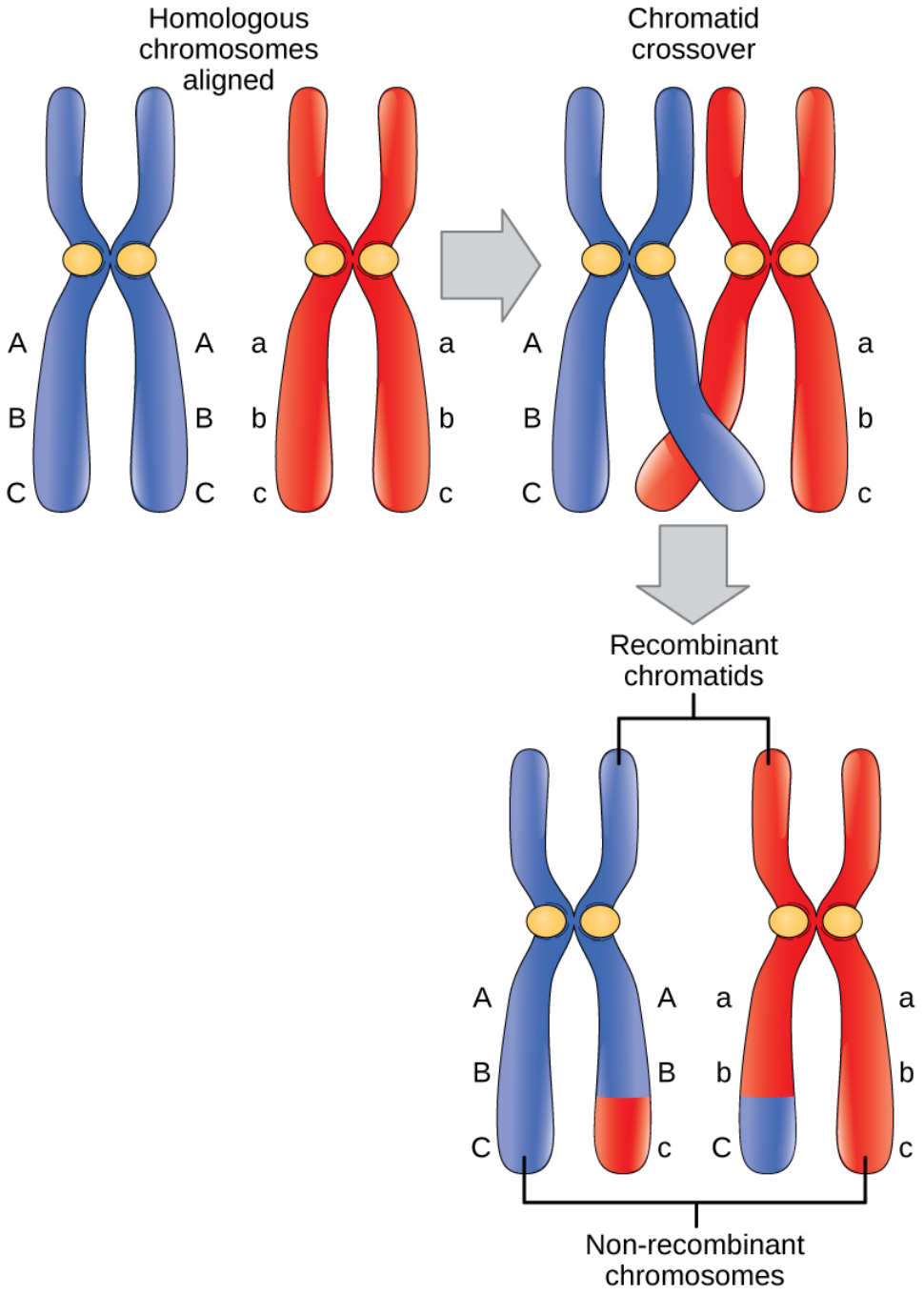


Figure 3.1.2.2: Crossover occurs between non-sister chromatids of homologous chromosomes. The result is an exchange of genetic material between homologous chromosomes.

Prometaphase I

The key event in prometaphase I is the attachment of the spindle fiber microtubules to the kinetochore proteins at the centromeres. Kinetochore proteins are multiprotein complexes that bind the centromeres of a chromosome to the microtubules of the mitotic spindle. Microtubules grow from centrosomes placed at opposite poles of the cell. The microtubules move toward the middle of the cell and attach to one of the two fused homologous chromosomes. The microtubules attach at each chromosomes' kinetochores. With each member of the homologous pair attached to opposite poles of the cell, in the next phase, the microtubules can pull the homologous pair apart. A spindle fiber that has attached to a kinetochore is called a kinetochore microtubule. At the end of prometaphase I, each tetrad is attached to microtubules from both poles, with one homologous chromosome facing each pole. The homologous chromosomes are still held together at chiasmata. In addition, the nuclear membrane has broken down entirely.

Metaphase I

During metaphase I, the homologous chromosomes are arranged in the center of the cell with the kinetochores facing opposite poles. The homologous pairs orient themselves randomly at the equator. For example, if the two homologous members of chromosome 1 are labeled a and b, then the chromosomes could line up a-b, or b-a. This is important in determining the genes carried by a gamete, as each will only receive one of the two homologous chromosomes. Recall that homologous chromosomes are not identical. They contain slight differences in their genetic information, causing each gamete to have a unique genetic makeup.

This randomness is the physical basis for the creation of the second form of genetic variation in offspring. Consider that the homologous chromosomes of a sexually reproducing organism are originally inherited as two separate sets, one from each parent. Using humans as an example, one set of 23 chromosomes is present in the egg donated by the mother. The father provides the other set of 23 chromosomes in the sperm that fertilizes the egg. Every cell of the multicellular offspring has copies of the original two sets of homologous chromosomes. In prophase I of meiosis, the homologous chromosomes form the tetrads. In metaphase I, these pairs line up at the midway point between the two poles of the cell to form the metaphase plate. Because there is an equal chance that a microtubule fiber will encounter a maternally or paternally inherited chromosome, the arrangement of the tetrads at the metaphase plate is random. Any maternally inherited chromosome may face either pole. Any paternally inherited chromosome may also face either pole. The orientation of each tetrad is independent of the orientation of the other 22 tetrads.

This event—the random (or independent) assortment of homologous chromosomes at the metaphase plate—is the second mechanism that introduces variation into the gametes or spores. In each cell that undergoes meiosis, the arrangement of the tetrads is different. The number of variations is dependent on the number of chromosomes making up a set. There are two possibilities for orientation at the metaphase plate; the possible number of alignments therefore equals 2^n, where n is the number of chromosomes per set. Humans have 23 chromosome pairs, which results in over eight million (2^{23}) possible genetically-distinct gametes. This number does not include the variability that was previously created in the sister chromatids by crossover. Given these two mechanisms, it is highly unlikely that any two haploid cells resulting from meiosis will have the same genetic composition (Figure 3.1.2.3).

To summarize the genetic consequences of meiosis I, the maternal and paternal genes are recombined by crossover events that occur between each homologous pair during prophase I. In addition, the random assortment of tetrads on the metaphase plate produces a unique combination of maternal and paternal chromosomes that will make their way into the gametes.

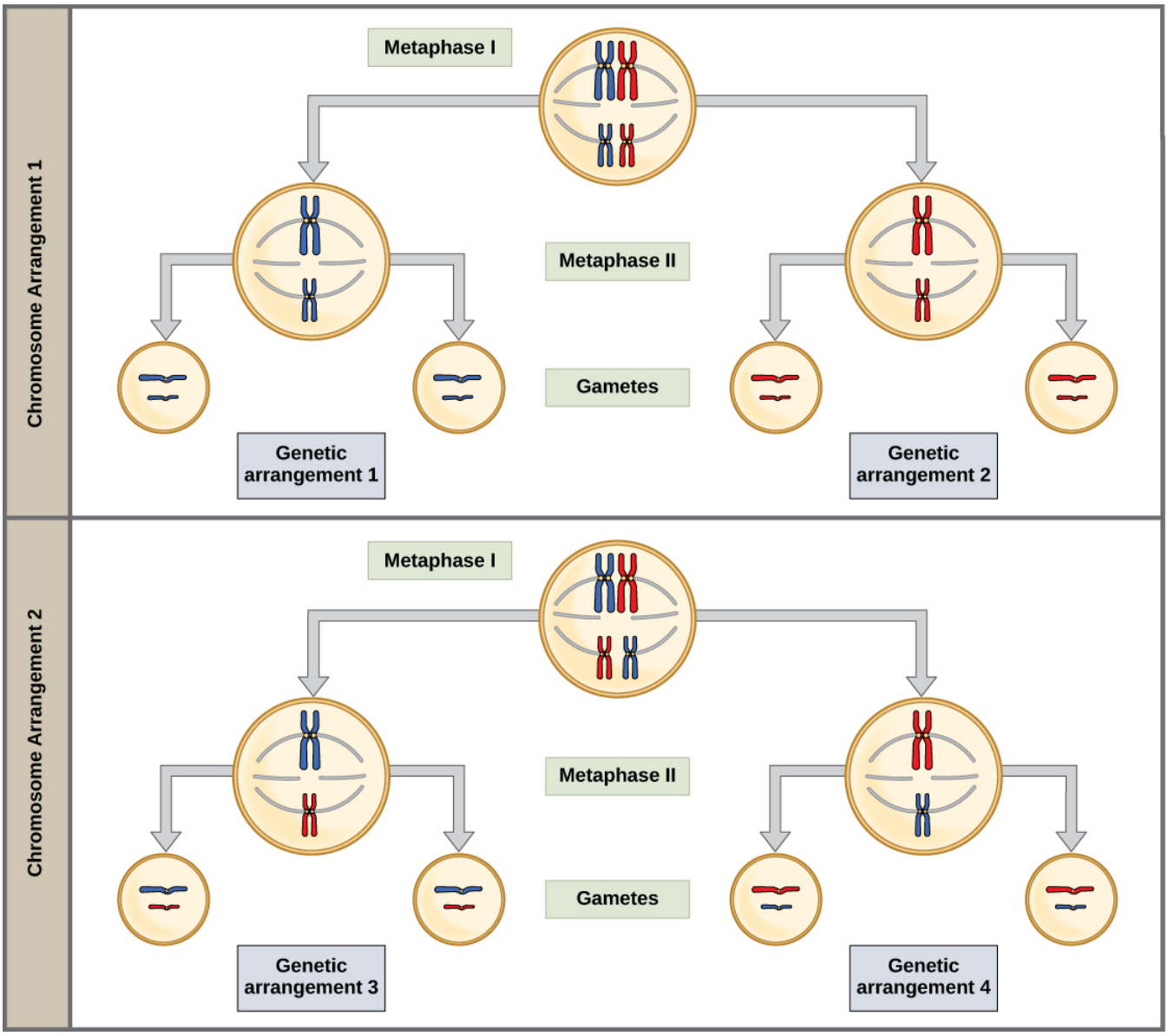


Figure 3.1.2.3: Random, independent assortment during metaphase I can be demonstrated by considering a cell with a set of two chromosomes (n = 2). In this case, there are two possible arrangements at the equatorial plane in metaphase I. The total possible number of different gametes is 2^n, where n equals the number of chromosomes in a set. In this example, there are four possible genetic combinations for the gametes. With n = 23 in human cells, there are over 8 million possible combinations of paternal and maternal chromosomes.

Anaphase I

In anaphase I, the microtubules pull the linked chromosomes apart. The sister chromatids remain tightly bound together at the centromere. The chiasmata are broken in anaphase I as the microtubules attached to the fused kinetochores pull the homologous chromosomes apart (Figure 3.1.2.4).

Telophase I and Cytokinesis

In telophase, the separated chromosomes arrive at opposite poles. The remainder of the typical telophase events may or may not occur, depending on the species. In some organisms, the chromosomes decondense and nuclear envelopes form around the chromatids in telophase I. In other organisms, cytokinesis—the physical separation of the cytoplasmic components into two daughter cells—occurs without reformation of the nuclei. In nearly all species of animals and some fungi, cytokinesis separates the cell contents via a cleavage furrow (constriction of the actin ring that leads to cytoplasmic division). In plants, a cell plate is formed

during cell cytokinesis by Golgi vesicles fusing at the metaphase plate. This cell plate will ultimately lead to the formation of cell walls that separate the two daughter cells.

Two haploid cells are the end result of the first meiotic division. The cells are haploid because at each pole, there is just one of each pair of the homologous chromosomes. Therefore, only one full set of the chromosomes is present. This is why the cells are considered haploid—there is only one chromosome set, even though each homolog still consists of two sister chromatids. Recall that sister chromatids are merely duplicates of one of the two homologous chromosomes (except for changes that occurred during crossing over). In meiosis II, these two sister chromatids will separate, creating four haploid daughter cells.

Meiosis II

In some species, cells enter a brief interphase, or interkinesis, before entering meiosis II. Interkinesis lacks an S phase, so chromosomes are not duplicated. The two cells produced in meiosis I go through the events of meiosis II in synchrony. During meiosis II, the sister chromatids within the two daughter cells separate, forming four new haploid gametes. The mechanics of meiosis II is similar to mitosis, except that each dividing cell has only one set of homologous chromosomes. Therefore, each cell has half the number of sister chromatids to separate out as a diploid cell undergoing mitosis.

Prophase II

If the chromosomes decondensed in telophase I, they condense again. If nuclear envelopes were formed, they fragment into vesicles. The centrosomes that were duplicated during interkinesis move away from each other toward opposite poles, and new spindles are formed.

Prometaphase II

The nuclear envelopes are completely broken down, and the spindle is fully formed. Each sister chromatid forms an individual kinetochore that attaches to microtubules from opposite poles.

Metaphase II

The sister chromatids are maximally condensed and aligned at the equator of the cell.

Anaphase II

The sister chromatids are pulled apart by the kinetochore microtubules and move toward opposite poles. Non-kinetochore microtubules elongate the cell.

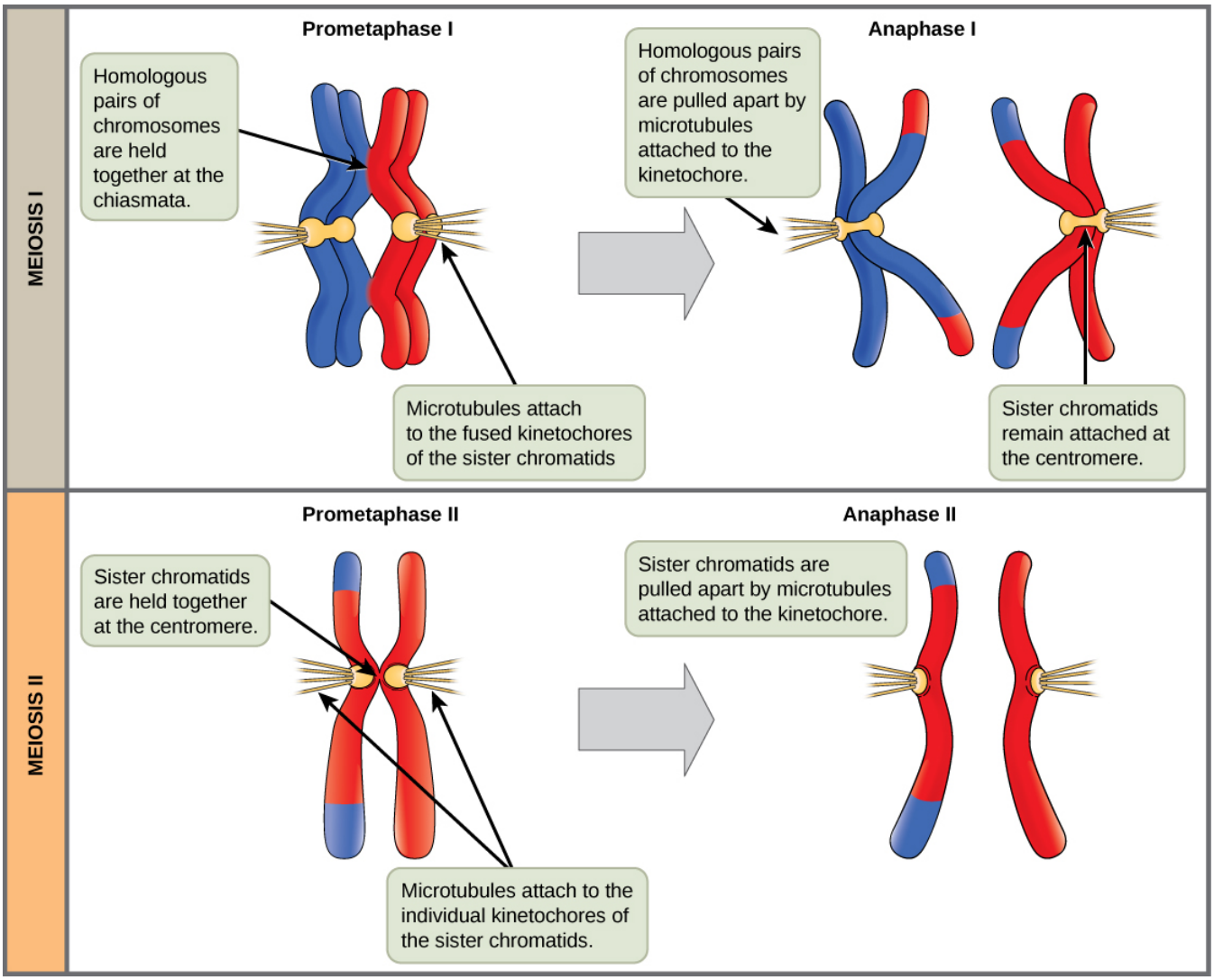
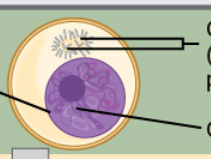
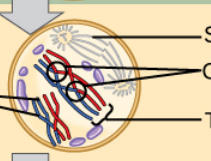
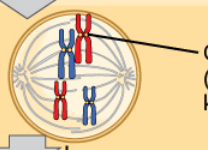
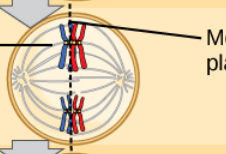
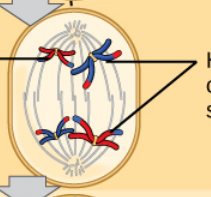
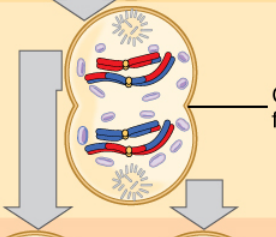
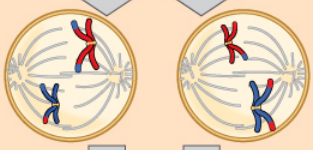
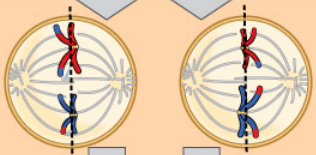
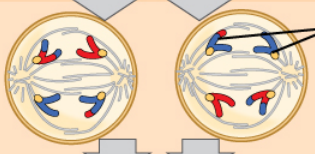


Figure 3.1.2.4: The process of chromosome alignment differs between meiosis I and meiosis II. In prometaphase I, microtubules attach to the fused kinetochores of homologous chromosomes, and the homologous chromosomes are arranged at the midpoint of the cell in metaphase I. In anaphase I, the homologous chromosomes are separated. In prometaphase II, microtubules attach to the kinetochores of sister chromatids, and the sister chromatids are arranged at the midpoint of the cells in metaphase II. In anaphase II, the sister chromatids are separated.

Telophase II and Cytokinesis

The chromosomes arrive at opposite poles and begin to decondense. Nuclear envelopes form around the chromosomes. Cytokinesis separates the two cells into four unique haploid cells. At this point, the newly formed nuclei are both haploid. The cells produced are genetically unique because of the random assortment of paternal and maternal homologs and because of the recombining of maternal and paternal segments of chromosomes (with their sets of genes) that occurs during crossover. The entire process of meiosis is outlined in Figure 3.1.2.5.

	Stage	Event	Outcome
INTERPHASE	S phase		Chromosomes are duplicated during interphase. The resulting sister chromatids are held together at the centromere. The centrosomes are also duplicated.
MEIOSIS I	Prophase I		Chromosomes condense, and the nuclear envelope fragments. Homologous chromosomes bind firmly together along their length, forming a tetrad. Chiasmata form between non-sister chromatids. Crossing over occurs at the chiasmata. Spindle fibers emerge from the centrosomes.
	Prometaphase I		Homologous chromosomes are attached to spindle microtubules at the fused kinetochore shared by the sister chromatids. Chromosomes continue to condense, and the nuclear envelope completely disappears.
	Metaphase I		Homologous chromosomes randomly assemble at the metaphase plate, where they have been maneuvered into place by the microtubules.
	Anaphase I		Spindle microtubules pull the homologous chromosomes apart. The sister chromatids are still attached at the centromere.
	Telophase I and Cytokinesis		Sister chromatids arrive at the poles of the cell and begin to decondense. A nuclear envelope forms around each nucleus and the cytoplasm is divided by a cleavage furrow. The result is two haploid cells. Each cell contains one duplicated copy of each homologous chromosome pair.
MEIOSIS II	Prophase II		Sister chromatids condense. A new spindle begins to form. The nuclear envelope starts to fragment.
	Prometaphase II		The nuclear envelope disappears, and the spindle fibers engage the individual kinetochores on the sister chromatids.
	Metaphase II		Sister chromatids line up at the metaphase plate.
	Anaphase II		Sister chromatids are pulled apart by the shortening of the kinetochore microtubules. Non-kinetochore microtubules lengthen the cell.
	Telophase II and		Chromosomes arrive at the poles of the cell and decondense. Nuclear envelopes surround the four

https://bio.libretexts.org/@go/page/82912

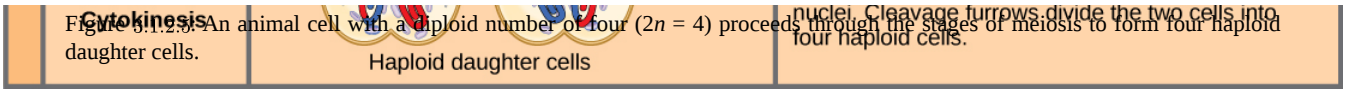


Figure 3.1.2.8: An animal cell with a diploid number of four ($2n = 4$) proceeds through the stages of meiosis to form four haploid daughter cells.

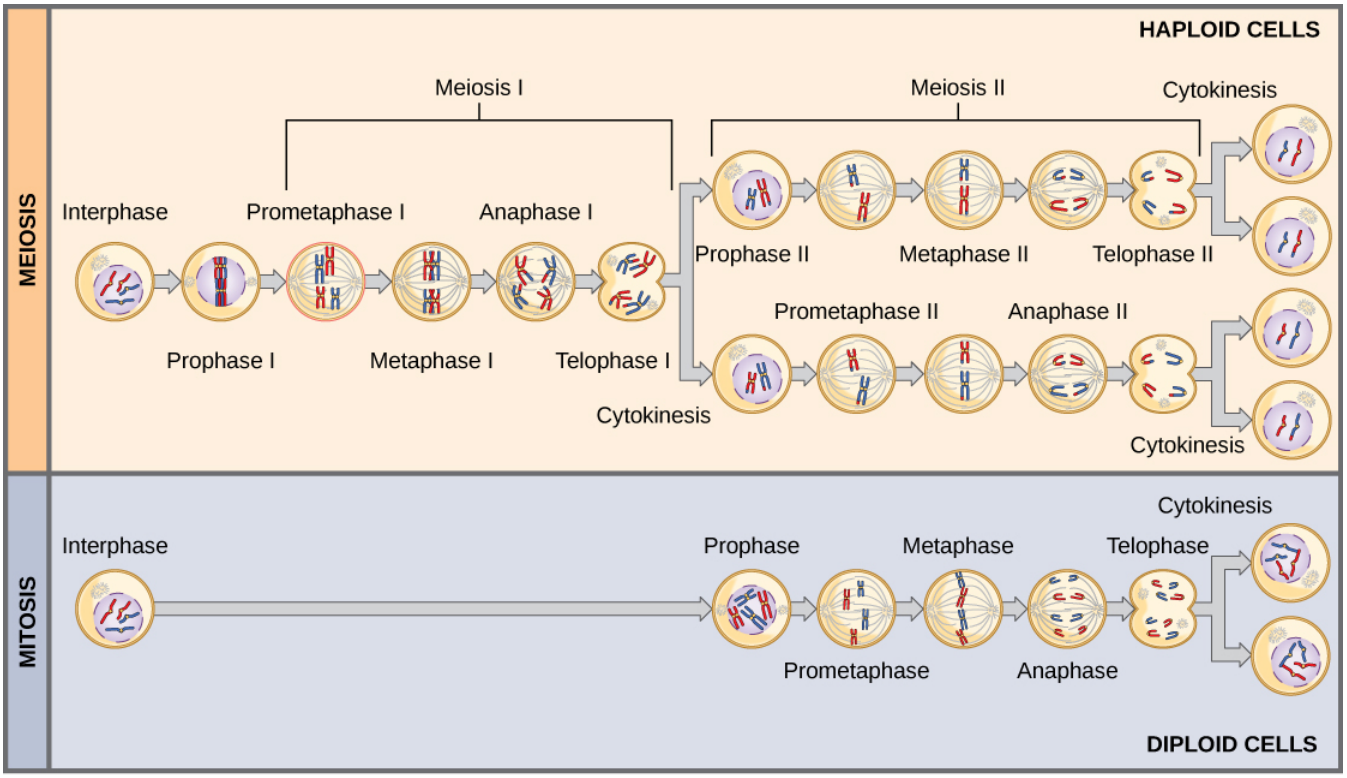
Comparing Meiosis and Mitosis

Mitosis and meiosis are both forms of division of the nucleus in eukaryotic cells. They share some similarities, but also exhibit distinct differences that lead to very different outcomes (Figure 3.1.2.6). Mitosis is a single nuclear division that results in two nuclei that are usually partitioned into two new cells. The nuclei resulting from a mitotic division are genetically identical to the original nucleus. They have the same number of sets of chromosomes, one set in the case of haploid cells and two sets in the case of diploid cells. In most plants and all animal species, it is typically diploid cells that undergo mitosis to form new diploid cells. In contrast, meiosis consists of two nuclear divisions resulting in four nuclei that are usually partitioned into four new cells. The nuclei resulting from meiosis are not genetically identical and they contain one chromosome set only. This is half the number of chromosome sets in the original cell, which is diploid.

The main differences between mitosis and meiosis occur in meiosis I, which is a very different nuclear division than mitosis. In meiosis I, the homologous chromosome pairs become associated with each other, are bound together with the synaptonemal complex, develop chiasmata and undergo crossover between sister chromatids, and line up along the metaphase plate in tetrads with kinetochore fibers from opposite spindle poles attached to each kinetochore of a homolog in a tetrad. All of these events occur only in meiosis I.

When the chiasmata resolve and the tetrad is broken up with the homologs moving to one pole or another, the ploidy level—the number of sets of chromosomes in each future nucleus—has been reduced from two to one. For this reason, meiosis I is referred to as a reduction division. There is no such reduction in ploidy level during mitosis.

Meiosis II is much more analogous to a mitotic division. In this case, the duplicated chromosomes (only one set of them) line up on the metaphase plate with divided kinetochores attached to kinetochore fibers from opposite poles. During anaphase II, as in mitotic anaphase, the kinetochores divide and one sister chromatid—now referred to as a chromosome—is pulled to one pole while the other sister chromatid is pulled to the other pole. If it were not for the fact that there had been crossover, the two products of each individual meiosis II division would be identical (like in mitosis). Instead, they are different because there has always been at least one crossover per chromosome. Meiosis II is not a reduction division because although there are fewer copies of the genome in the resulting cells, there is still one set of chromosomes, as there was at the end of meiosis I.



						OUTCOME
PROCESS	DNA synthesis	Synapsis of homologous chromosomes	Crossover	Homologous chromosomes line up at metaphase plate	Sister chromatids line up at metaphase plate	Number and genetic composition of daughter cells
MEIOSIS	Occurs in S phase of interphase	During prophase I	During prophase I	During metaphase I	During metaphase II	Four haploid cells at the end of meiosis II
MITOSIS	Occurs in S phase of interphase	Does not occur in mitosis	Does not occur in mitosis	Does not occur in mitosis	During metaphase	Two diploid cells at the end of mitosis

Figure 3.1.2.6: Meiosis and mitosis are both preceded by one round of DNA replication; however, meiosis includes two nuclear divisions. The four daughter cells resulting from meiosis are haploid and genetically distinct. The daughter cells resulting from mitosis are diploid and identical to the parent cell.

Evolution Connection: The Mystery of the Evolution of Meiosis

Some characteristics of organisms are so widespread and fundamental that it is sometimes difficult to remember that they evolved like other simpler traits. Meiosis is such an extraordinarily complex series of cellular events that biologists have had trouble hypothesizing and testing how it may have evolved. Although meiosis is inextricably entwined with sexual reproduction and its advantages and disadvantages, it is important to separate the questions of the evolution of meiosis and the evolution of sex, because early meiosis may have been advantageous for different reasons than it is now. Thinking outside the box and imagining what the early benefits from meiosis might have been is one approach to uncovering how it may have evolved.

Meiosis and mitosis share obvious cellular processes and it makes sense that meiosis evolved from mitosis. The difficulty lies in the clear differences between meiosis I and mitosis. Adam Wilkins and Robin Holliday[1] summarized the unique events that needed to occur for the evolution of meiosis from mitosis. These steps are homologous chromosome pairing, crossover

exchanges, sister chromatids remaining attached during anaphase, and suppression of DNA replication in interphase. They argue that the first step is the hardest and most important, and that understanding how it evolved would make the evolutionary process clearer. They suggest genetic experiments that might shed light on the evolution of synapsis.

There are other approaches to understanding the evolution of meiosis in progress. Different forms of meiosis exist in single-celled protists. Some appear to be simpler or more “primitive” forms of meiosis. Comparing the meiotic divisions of different protists may shed light on the evolution of meiosis. Marilee Ramesh and colleagues[2] compared the genes involved in meiosis in protists to understand when and where meiosis might have evolved. Although research is still ongoing, recent scholarship into meiosis in protists suggests that some aspects of meiosis may have evolved later than others. This kind of genetic comparison can tell us what aspects of meiosis are the oldest and what cellular processes they may have borrowed from in earlier cells.

Video



Summary

Sexual reproduction requires that diploid organisms produce haploid cells that can fuse during fertilization to form diploid offspring. As with mitosis, DNA replication occurs prior to meiosis during the S-phase of the cell cycle. Meiosis is a series of events that arrange and separate chromosomes and chromatids into daughter cells. During the interphases of meiosis, each chromosome is duplicated. In meiosis, there are two rounds of nuclear division resulting in four nuclei and usually four daughter cells, each with half the number of chromosomes as the parent cell. The first separates homologs, and the second—like mitosis—separates chromatids into individual chromosomes. During meiosis, variation in the daughter nuclei is introduced because of crossover in prophase I and random alignment of tetrads at metaphase I. The cells that are produced by meiosis are genetically unique.

Meiosis and mitosis share similarities, but have distinct outcomes. Mitotic divisions are single nuclear divisions that produce daughter nuclei that are genetically identical and have the same number of chromosome sets as the original cell. Meiotic divisions include two nuclear divisions that produce four daughter nuclei that are genetically different and have one chromosome set instead of the two sets of chromosomes in the parent cell. The main differences between the processes occur in the first division of meiosis, in which homologous chromosomes are paired and exchange non-sister chromatid segments. The homologous chromosomes separate into different nuclei during meiosis I, causing a reduction of ploidy level in the first division. The second division of meiosis is more similar to a mitotic division, except that the daughter cells do not contain identical genomes because of crossover.

Footnotes

1. 1 Adam S. Wilkins and Robin Holliday, “The Evolution of Meiosis from Mitosis,” *Genetics* 181 (2009): 3–12.
2. 2 Marilee A. Ramesh, Shehre-Banoo Malik and John M. Logsdon, Jr, “A Phylogenetic Inventory of Meiotic Genes: Evidence for Sex in *Giardia* and an Early Eukaryotic Origin of Meiosis,” *Current Biology* 15 (2005):185–91.

Glossary

chiasmata
(singular, *chiasma*) the structure that forms at the crossover points after genetic material is exchanged

cohesin
proteins that form a complex that seals sister chromatids together at their centromeres until anaphase II of meiosis

crossover
exchange of genetic material between non-sister chromatids resulting in chromosomes that incorporate genes from both parents of the organism

fertilization
union of two haploid cells from two individual organisms

interkinesis
(also, *interphase II*) brief period of rest between meiosis I and meiosis II

meiosis
a nuclear division process that results in four haploid cells

meiosis I
first round of meiotic cell division; referred to as reduction division because the ploidy level is reduced from diploid to haploid

meiosis II
second round of meiotic cell division following meiosis I; sister chromatids are separated into individual chromosomes, and the result is four unique haploid cells

recombination nodules
protein assemblies formed on the synaptonemal complex that mark the points of crossover events and mediate the multistep process of genetic recombination between non-sister chromatids

reduction division
nuclear division that produces daughter nuclei each having one-half as many chromosome sets as the parental nucleus; meiosis I is a reduction division

somatic cell
all the cells of a multicellular organism except the gametes or reproductive cells

spore
haploid cell that can produce a haploid multicellular organism or can fuse with another spore to form a diploid cell

synapsis
formation of a close association between homologous chromosomes during prophase I

synaptonemal complex

protein lattice that forms between homologous chromosomes during prophase I, supporting crossover

tetrad

two duplicated homologous chromosomes (four chromatids) bound together by chiasmata during prophase I

This page titled 3.1.2: The Process of Meiosis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **11.1: The Process of Meiosis** by OpenStax is licensed CC BY 4.0.

3.1.3: Sexual Reproduction

Learning Objectives

- Explain that meiosis and sexual reproduction are evolved traits
- Identify variation among offspring as a potential evolutionary advantage to sexual reproduction
- Describe the three different life-cycle types among sexual multicellular organisms and their commonalities

Sexual reproduction was an early evolutionary innovation after the appearance of eukaryotic cells. It appears to have been very successful because most eukaryotes are able to reproduce sexually, and in many animals, it is the only mode of reproduction. And yet, scientists recognize some real disadvantages to sexual reproduction. On the surface, creating offspring that are genetic clones of the parent appears to be a better system. If the parent organism is successfully occupying a habitat, offspring with the same traits would be similarly successful. There is also the obvious benefit to an organism that can produce offspring whenever circumstances are favorable by asexual budding, fragmentation, or asexual eggs. These methods of reproduction do not require another organism of the opposite sex. Indeed, some organisms that lead a solitary lifestyle have retained the ability to reproduce asexually. In addition, in asexual populations, every individual is capable of reproduction. In sexual populations, the males are not producing the offspring themselves, so in theory an asexual population could grow twice as fast.

However, multicellular organisms that exclusively depend on asexual reproduction are exceedingly rare. Why is sexuality (and meiosis) so common? This is one of the important unanswered questions in biology and has been the focus of much research beginning in the latter half of the twentieth century. There are several possible explanations, one of which is that the variation that sexual reproduction creates among offspring is very important to the survival and reproduction of the population. Thus, on average, a sexually reproducing population will leave more descendants than an otherwise similar asexually reproducing population. The only source of variation in asexual organisms is mutation. This is the ultimate source of variation in sexual organisms, but in addition, those different mutations are continually reshuffled from one generation to the next when different parents combine their unique genomes and the genes are mixed into different combinations by crossovers during prophase I and random assortment at metaphase I.

Evolution Connection: The Red Queen Hypothesis

It is not in dispute that sexual reproduction provides evolutionary advantages to organisms that employ this mechanism to produce offspring. But why, even in the face of fairly stable conditions, does sexual reproduction persist when it is more difficult and costly for individual organisms? Variation is the outcome of sexual reproduction, but why are ongoing variations necessary? Enter the Red Queen hypothesis, first proposed by Leigh Van Valen in 1973.[1] The concept was named in reference to the Red Queen's race in Lewis Carroll's book, *Through the Looking-Glass*.

All species co-evolve with other organisms; for example predators evolve with their prey, and parasites evolve with their hosts. Each tiny advantage gained by favorable variation gives a species an edge over close competitors, predators, parasites, or even prey. The only method that will allow a co-evolving species to maintain its own share of the resources is to also continually improve its fitness. As one species gains an advantage, this increases selection on the other species; they must also develop an advantage or they will be outcompeted. No single species progresses too far ahead because genetic variation among the progeny of sexual reproduction provides all species with a mechanism to improve rapidly. Species that cannot keep up become extinct. The Red Queen’s catchphrase was, “It takes all the running you can do to stay in the same place.” This is an apt description of co-evolution between competing species.

Life Cycles of Sexually Reproducing Organisms

Fertilization and meiosis alternate in sexual life cycles. What happens between these two events depends on the organism. The process of meiosis reduces the chromosome number by half. Fertilization, the joining of two haploid gametes, restores the diploid condition. There are three main categories of life cycles in multicellular organisms: diploid-dominant, in which the multicellular diploid stage is the most obvious life stage, such as with most animals including humans; haploid-dominant, in which the

multicellular haploid stage is the most obvious life stage, such as with all fungi and some algae; and alternation of generations, in which the two stages are apparent to different degrees depending on the group, as with plants and some algae.

Diploid-Dominant Life Cycle

Nearly all animals employ a diploid-dominant life-cycle strategy in which the only haploid cells produced by the organism are the gametes. Early in the development of the embryo, specialized diploid cells, called germ cells, are produced within the gonads, such as the testes and ovaries. Germ cells are capable of mitosis to perpetuate the cell line and meiosis to produce gametes. Once the haploid gametes are formed, they lose the ability to divide again. There is no multicellular haploid life stage. Fertilization occurs with the fusion of two gametes, usually from different individuals, restoring the diploid state (Figure 3.1.3.1).

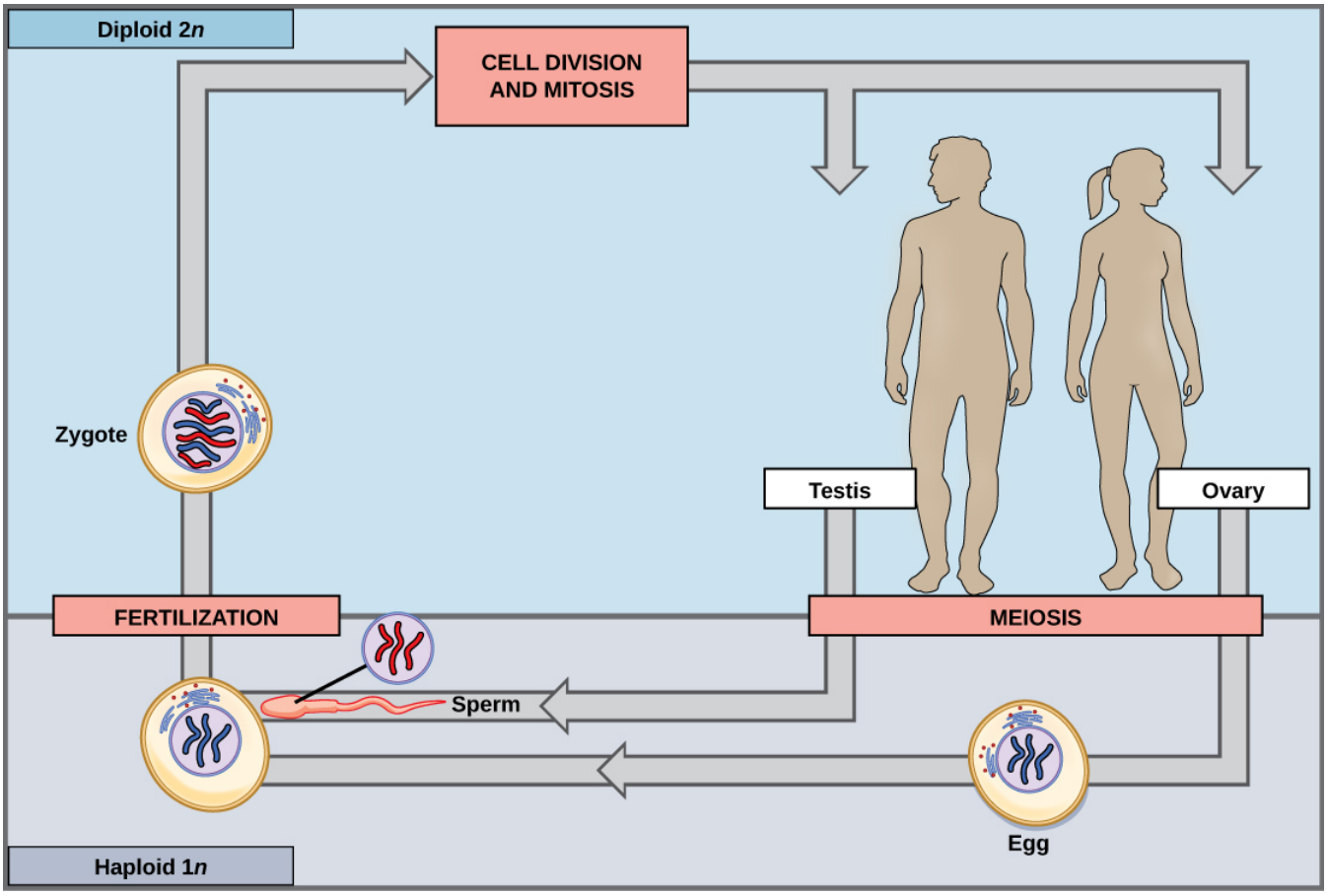


Figure 3.1.3.1: In animals, sexually reproducing adults form haploid gametes from diploid germ cells. Fusion of the gametes gives rise to a fertilized egg cell, or zygote. The zygote will undergo multiple rounds of mitosis to produce a multicellular offspring. The germ cells are generated early in the development of the zygote.

Haploid-Dominant Life Cycle

Most fungi and algae employ a life-cycle type in which the “body” of the organism—the ecologically important part of the life cycle—is haploid. The haploid cells that make up the tissues of the dominant multicellular stage are formed by mitosis. During sexual reproduction, specialized haploid cells from two individuals, designated the (+) and (−) mating types, join to form a diploid zygote. The zygote immediately undergoes meiosis to form four haploid cells called spores. Although haploid like the “parents,” these spores contain a new genetic combination from two parents. The spores can remain dormant for various time periods. Eventually, when conditions are conducive, the spores form multicellular haploid structures by many rounds of mitosis (Figure 3.1.3.2).

Art Connection

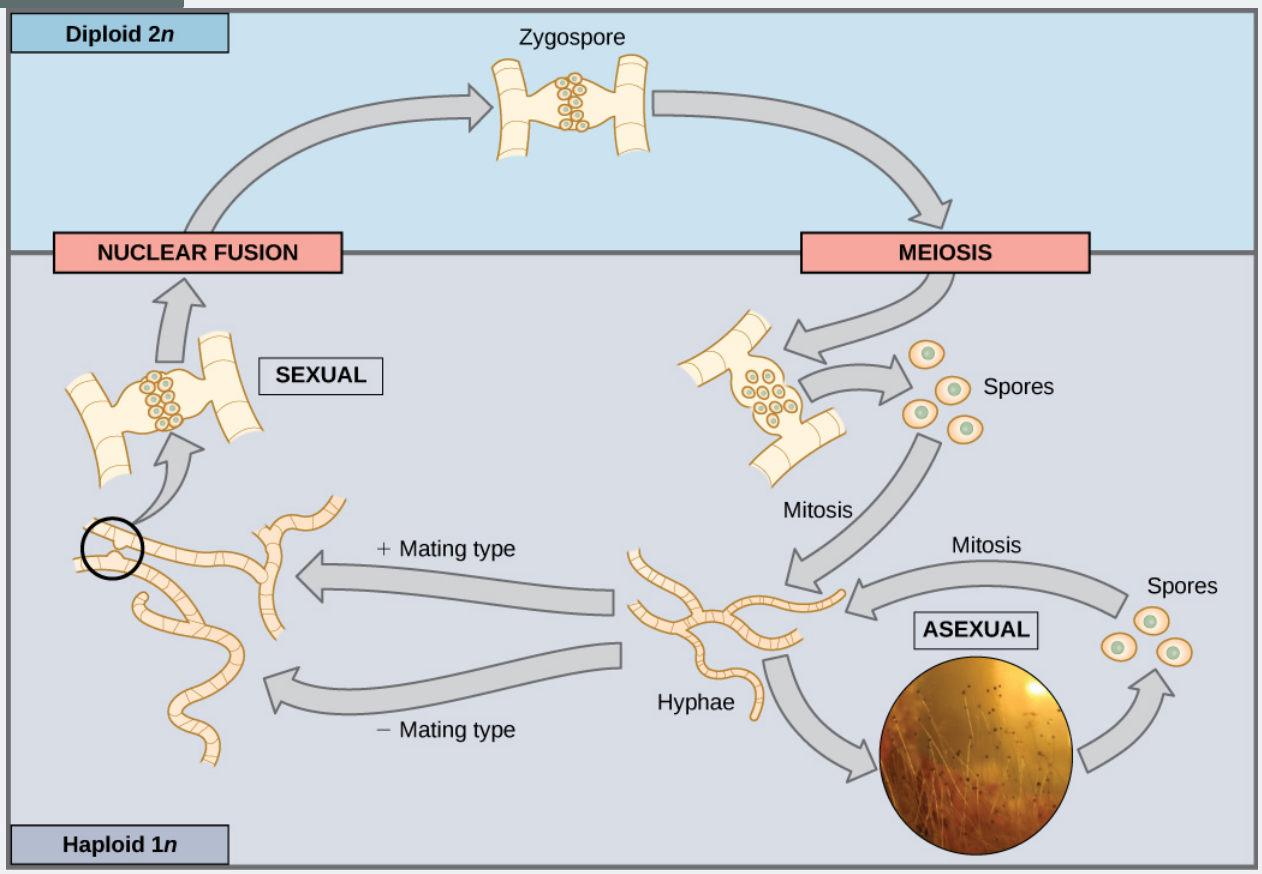


Figure 3.1.3.2: Fungi, such as black bread mold (*Rhizopus nigricans*), have haploid-dominant lifecycles. The haploid multicellular stage produces specialized haploid cells by mitosis that fuse to form a diploid zygote. The zygote undergoes meiosis to produce haploid spores. Each spore gives rise to a multicellular haploid organism by mitosis. (credit "zygomycota" micrograph: modification of work by "Fanaberka"/Wikimedia Commons)

If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Alternation of Generations

The third life-cycle type, employed by some algae and all plants, is a blend of the haploid-dominant and diploid-dominant extremes. Species with alternation of generations have both haploid and diploid multicellular organisms as part of their life cycle. The haploid multicellular plants are called gametophytes, because they produce gametes from specialized cells. Meiosis is not directly involved in the production of gametes in this case, because the organism that produces the gametes is already a haploid. Fertilization between the gametes forms a diploid zygote. The zygote will undergo many rounds of mitosis and give rise to a diploid multicellular plant called a sporophyte. Specialized cells of the sporophyte will undergo meiosis and produce haploid spores. The spores will subsequently develop into the gametophytes (Figure 3.1.3.3).

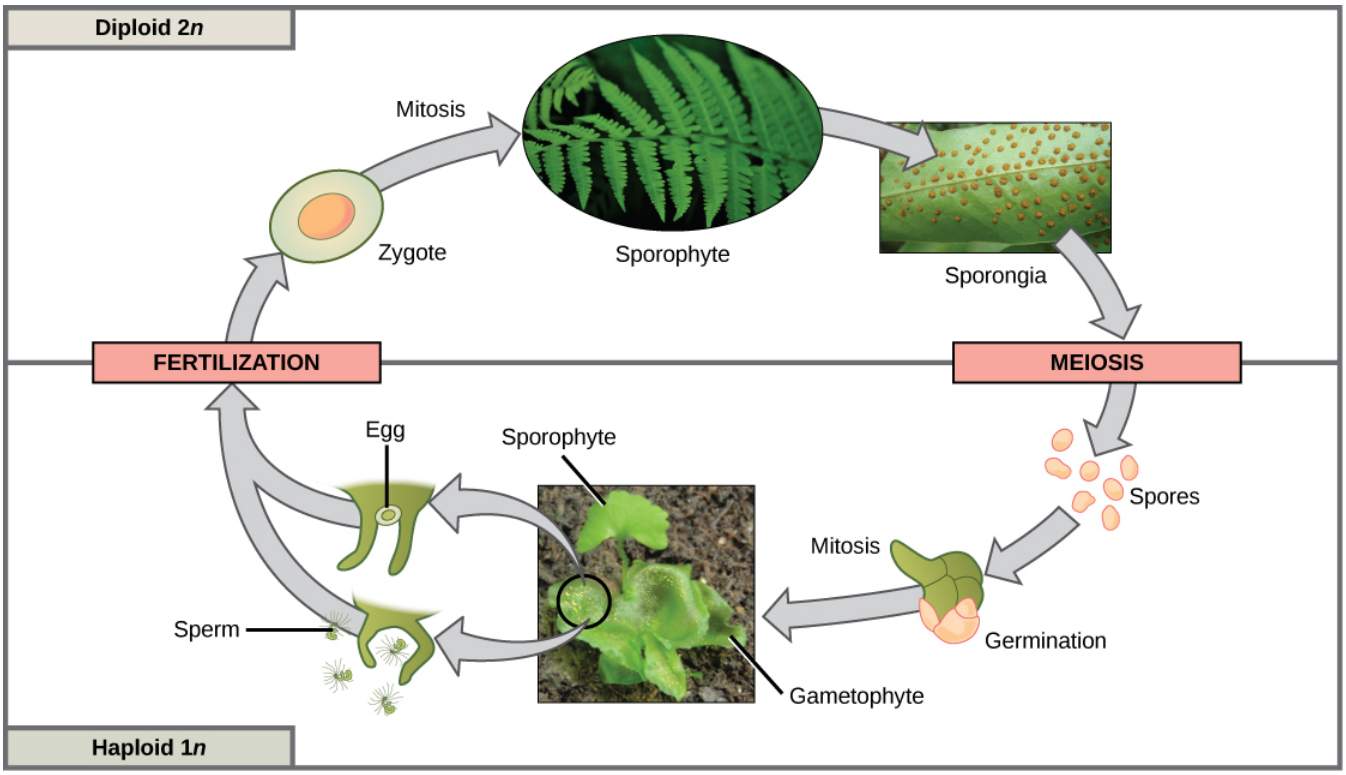


Figure 3.1.3.3: Plants have a life cycle that alternates between a multicellular haploid organism and a multicellular diploid organism. In some plants, such as ferns, both the haploid and diploid plant stages are free-living. The diploid plant is called a sporophyte because it produces haploid spores by meiosis. The spores develop into multicellular, haploid plants called gametophytes because they produce gametes. The gametes of two individuals will fuse to form a diploid zygote that becomes the sporophyte. (credit “fern”: modification of work by Cory Zanker; credit “sporangia”: modification of work by "Obsidian Soul"/Wikimedia Commons; credit “gametophyte and sporophyte”: modification of work by “Vlmastra”/Wikimedia Commons)

Although all plants utilize some version of the alternation of generations, the relative size of the sporophyte and the gametophyte and the relationship between them vary greatly. In plants such as moss, the gametophyte organism is the free-living plant, and the sporophyte is physically dependent on the gametophyte. In other plants, such as ferns, both the gametophyte and sporophyte plants are free-living; however, the sporophyte is much larger. In seed plants, such as magnolia trees and daisies, the gametophyte is composed of only a few cells and, in the case of the female gametophyte, is completely retained within the sporophyte.

Sexual reproduction takes many forms in multicellular organisms. However, at some point in each type of life cycle, meiosis produces haploid cells that will fuse with the haploid cell of another organism. The mechanisms of variation—crossover, random assortment of homologous chromosomes, and random fertilization—are present in all versions of sexual reproduction. The fact that nearly every multicellular organism on Earth employs sexual reproduction is strong evidence for the benefits of producing offspring with unique gene combinations, though there are other possible benefits as well.

Summary

Nearly all eukaryotes undergo sexual reproduction. The variation introduced into the reproductive cells by meiosis appears to be one of the advantages of sexual reproduction that has made it so successful. Meiosis and fertilization alternate in sexual life cycles. The process of meiosis produces unique reproductive cells called gametes, which have half the number of chromosomes as the parent cell. Fertilization, the fusion of haploid gametes from two individuals, restores the diploid condition. Thus, sexually reproducing organisms alternate between haploid and diploid stages. However, the ways in which reproductive cells are produced and the timing between meiosis and fertilization vary greatly. There are three main categories of life cycles: diploid-dominant, demonstrated by most animals; haploid-dominant, demonstrated by all fungi and some algae; and the alternation of generations, demonstrated by plants and some algae.

Art Connections

Figure 3.1.3.2: If a mutation occurs so that a fungus is no longer able to produce a minus mating type, will it still be able to reproduce?

Answer

Yes, it will be able to reproduce asexually.

Footnotes

1. 1 Leigh Van Valen, “A New Evolutionary Law,” *Evolutionary Theory* 1 (1973): 1–30

Glossary

alternation of generations
life-cycle type in which the diploid and haploid stages alternate

diploid-dominant
life-cycle type in which the multicellular diploid stage is prevalent

haploid-dominant
life-cycle type in which the multicellular haploid stage is prevalent

gametophyte
a multicellular haploid life-cycle stage that produces gametes

germ cells
specialized cell line that produces gametes, such as eggs or sperm

life cycle
the sequence of events in the development of an organism and the production of cells that produce offspring

sporophyte
a multicellular diploid life-cycle stage that produces haploid spores by meiosis

---

This page titled 3.1.3: Sexual Reproduction is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **11.2: Sexual Reproduction** by OpenStax is licensed CC BY 4.0.

3.1.E: Meiosis and Sexual Reproduction (Exercises)

11.1: The Process of Meiosis

Sexual reproduction requires fertilization, the union of two cells from two individual organisms. If those two cells each contain one set of chromosomes, then the resulting cell contains two sets of chromosomes. Haploid cells contain one set of chromosomes. Cells containing two sets of chromosomes are called diploid. The number of sets of chromosomes in a cell is called its ploidy level.

Review Questions

Meiosis produces _____ daughter cells.

A. two haploid
B. two diploid
C. four haploid
D. four diploid

Answer

C

What structure is most important in forming the tetrads?

A. centromere
B. synaptonemal complex
C. chiasma
D. kinetochore

Answer

B

At which stage of meiosis are sister chromatids separated from each other?

A. prophase I
B. prophase II
C. anaphase I
D. anaphase II

Answer

D

At metaphase I, homologous chromosomes are connected only at what structures?

A. chiasmata
B. recombination nodules
C. microtubules
D. kinetochores

Answer

A

Which of the following is *not* true in regard to crossover?

A. Spindle microtubules guide the transfer of DNA across the synaptonemal complex.

B. Non-sister chromatids exchange genetic material.
C. Chiasmata are formed.
D. Recombination nodules mark the crossover point.

Answer

C

What phase of mitotic interphase is missing from meiotic interkinesis?

A. G_0 phase
B. G_1 phase
C. S phase
D. G_2 phase

Answer

C

The part of meiosis that is similar to mitosis is _____.

A. meiosis I
B. anaphase I
C. meiosis II
D. interkinesis

Answer

C

If a muscle cell of a typical organism has 32 chromosomes, how many chromosomes will be in a gamete of that same organism?

A. 8
B. 16
C. 32
D. 64

Answer

B

Free Response

Describe the process that results in the formation of a tetrad.

Answer

During the meiotic interphase, each chromosome is duplicated. The sister chromatids that are formed during synthesis are held together at the centromere region by cohesin proteins. All chromosomes are attached to the nuclear envelope by their tips. As the cell enters prophase I, the nuclear envelope begins to fragment, and the proteins holding homologous chromosomes locate each other. The four sister chromatids align lengthwise, and a protein lattice called the synaptonemal complex is formed between them to bind them together. The synaptonemal complex facilitates crossover between non-sister chromatids, which is observed as chiasmata along the length of the chromosome. As prophase I progresses, the

synaptonemal complex breaks down and the sister chromatids become free, except where they are attached by chiasmata. At this stage, the four chromatids are visible in each homologous pairing and are called a tetrad.

Explain how the random alignment of homologous chromosomes during metaphase I contributes to the variation in gametes produced by meiosis.

Answer

Random alignment leads to new combinations of traits. The chromosomes that were originally inherited by the gamete-producing individual came equally from the egg and the sperm. In metaphase I, the duplicated copies of these maternal and paternal homologous chromosomes line up across the center of the cell. The orientation of each tetrad is random. There is an equal chance that the maternally derived chromosomes will be facing either pole. The same is true of the paternally derived chromosomes. The alignment should occur differently in almost every meiosis. As the homologous chromosomes are pulled apart in anaphase I, any combination of maternal and paternal chromosomes will move toward each pole. The gametes formed from these two groups of chromosomes will have a mixture of traits from the individual's parents. Each gamete is unique.

What is the function of the fused kinetochore found on sister chromatids in prometaphase I?

Answer

In metaphase I, the homologous chromosomes line up at the metaphase plate. In anaphase I, the homologous chromosomes are pulled apart and move to opposite poles. Sister chromatids are not separated until meiosis II. The fused kinetochore formed during meiosis I ensures that each spindle microtubule that binds to the tetrad will attach to both sister chromatids.

In a comparison of the stages of meiosis to the stages of mitosis, which stages are unique to meiosis and which stages have the same events in both meiosis and mitosis?

Answer

All of the stages of meiosis I, except possibly telophase I, are unique because homologous chromosomes are separated, not sister chromatids. In some species, the chromosomes do not decondense and the nuclear envelopes do not form in telophase I. All of the stages of meiosis II have the same events as the stages of mitosis, with the possible exception of prophase II. In some species, the chromosomes are still condensed and there is no nuclear envelope. Other than this, all processes are the same.

11.2: Sexual Reproduction

Sexual reproduction was an early evolutionary innovation after the appearance of eukaryotic cells. It appears to have been very successful because most eukaryotes are able to reproduce sexually, and in many animals, it is the only mode of reproduction. And yet, scientists recognize some real disadvantages to sexual reproduction. On the surface, creating offspring that are genetic clones of the parent appears to be a better system.

Review Questions

What is a likely evolutionary advantage of sexual reproduction over asexual reproduction?

A. Sexual reproduction involves fewer steps.
B. There is a lower chance of using up the resources in a given environment.
C. Sexual reproduction results in variation in the offspring.
D. Sexual reproduction is more cost-effective.

Answer

C

Which type of life cycle has both a haploid and diploid multicellular stage?

A. asexual
B. diploid-dominant
C. haploid-dominant
D. alternation of generations

Answer

D

Fungi typically display which type of life cycle?

A. diploid-dominant
B. haploid-dominant
C. alternation of generations
D. asexual

Answer

B

A diploid, multicellular life-cycle stage that gives rise to haploid cells by meiosis is called a _____.

A. sporophyte
B. gametophyte
C. spore
D. gamete

Answer

A

Free Response

List and briefly describe the three processes that lead to variation in offspring with the same parents.

Answer

a. Crossover occurs in prophase I between non-sister homologous chromosomes. Segments of DNA are exchanged between maternally derived and paternally derived chromosomes, and new gene combinations are formed. b. Random alignment during metaphase I leads to gametes that have a mixture of maternal and paternal chromosomes. c. Fertilization is random, in that any two gametes can fuse.

Compare the three main types of life cycles in multicellular organisms and give an example of an organism that employs each.

Answer

a. In the haploid-dominant life cycle, the multicellular stage is haploid. The diploid stage is a spore that undergoes meiosis to produce cells that will divide mitotically to produce new multicellular organisms. Fungi have a haploid-dominant life cycle. b. In the diploid-dominant life cycle, the most visible or largest multicellular stage is diploid. The haploid stage is usually reduced to a single cell type, such as a gamete or spore. Animals, such as humans, have a diploid-dominant life cycle. c. In the alternation of generations life cycle, there are both haploid and diploid multicellular stages, although the haploid stage may be completely retained by the diploid stage. Plants have a life cycle with alternation of generations.

This page titled 3.1.E: Meiosis and Sexual Reproduction (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **11.E: Meiosis and Sexual Reproduction (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

3.2: Mendel's Experiments and Heredity

Gregor Johann Mendel was a German-speaking Moravian scientist and Augustinian friar who gained posthumous fame as the founder of the modern science of genetics. Though farmers had known for centuries that crossbreeding of animals and plants could favor certain desirable traits, Mendel's experiments established many of the rules of heredity, now referred to as the laws of Mendelian inheritance.

3.2.1: Prelude to Mendel's Experiments and Heredity

3.2.2: Mendel’s Experiments and the Laws of Probability

3.2.3: Characteristics and Traits

3.2.4: Laws of Inheritance

3.2.E: Mendel's Experiments and Heredity (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.2: Mendel's Experiments and Heredity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.2.1: Prelude to Mendel's Experiments and Heredity



Figure 3.2.1.1: Experimenting with thousands of garden peas, Mendel uncovered the fundamentals of genetics. (credit: modification of work by Jerry Kirkhart)

Genetics is the study of heredity. Johann Gregor Mendel set the framework for genetics long before chromosomes or genes had been identified, at a time when meiosis was not well understood. Mendel selected a simple biological system and conducted methodical, quantitative analyses using large sample sizes. Because of Mendel's work, the fundamental principles of heredity were revealed. We now know that genes, carried on chromosomes, are the basic functional units of heredity with the capability to be replicated, expressed, or mutated. Today, the postulates put forth by Mendel form the basis of classical, or Mendelian, genetics. Not all genes are transmitted from parents to offspring according to Mendelian genetics, but Mendel's experiments serve as an excellent starting point for thinking about inheritance.

Video



This page titled 3.2.1: Prelude to Mendel's Experiments and Heredity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.0: Prelude to Mendel's Experiments and Heredity** by OpenStax is licensed CC BY 4.0.

3.2.2: Mendel's Experiments and the Laws of Probability

Learning Objectives

- Describe the scientific reasons for the success of Mendel's experimental work
- Describe the expected outcomes of monohybrid crosses involving dominant and recessive alleles
- Apply the sum and product rules to calculate probabilities

Johann Gregor Mendel (1822–1884) (Figure 3.2.2.1) was a lifelong learner, teacher, scientist, and man of faith. As a young adult, he joined the Augustinian Abbey of St. Thomas in Brno in what is now the Czech Republic. Supported by the monastery, he taught physics, botany, and natural science courses at the secondary and university levels. In 1856, he began a decade-long research pursuit involving inheritance patterns in honeybees and plants, ultimately settling on pea plants as his primary model system (a system with convenient characteristics used to study a specific biological phenomenon to be applied to other systems). In 1865, Mendel presented the results of his experiments with nearly 30,000 pea plants to the local Natural History Society. He demonstrated that traits are transmitted faithfully from parents to offspring independently of other traits and in dominant and recessive patterns. In 1866, he published his work, *Experiments in Plant Hybridization*,[1] in the proceedings of the Natural History Society of Brünn.



Figure 3.2.2.1: Johann Gregor Mendel is considered the father of genetics.

Mendel's work went virtually unnoticed by the scientific community that believed, incorrectly, that the process of inheritance involved a blending of parental traits that produced an intermediate physical appearance in offspring; this hypothetical process appeared to be correct because of what we know now as continuous variation. Continuous variation results from the action of many genes to determine a characteristic like human height. Offspring appear to be a "blend" of their parents' traits when we look at characteristics that exhibit continuous variation. The blending theory of inheritance asserted that the original parental traits were lost or absorbed by the blending in the offspring, but we now know that this is not the case. Mendel was the first researcher to see it. Instead of continuous characteristics, Mendel worked with traits that were inherited in distinct classes (specifically, violet versus white flowers); this is referred to as discontinuous variation. Mendel's choice of these kinds of traits allowed him to see experimentally that the traits were not blended in the offspring, nor were they absorbed, but rather that they kept their distinctness and could be passed on. In 1868, Mendel became abbot of the monastery and exchanged his scientific pursuits for his pastoral duties. He was not recognized for his extraordinary scientific contributions during his lifetime. In fact, it was not until 1900 that his work was rediscovered, reproduced, and revitalized by scientists on the brink of discovering the chromosomal basis of heredity.

Mendel's Model System

Mendel's seminal work was accomplished using the garden pea, *Pisum sativum*, to study inheritance. This species naturally self-fertilizes, such that pollen encounters ova within individual flowers. The flower petals remain sealed tightly until after pollination, preventing pollination from other plants. The result is highly inbred, or "true-breeding," pea plants. These are plants that always

produce offspring that look like the parent. By experimenting with true-breeding pea plants, Mendel avoided the appearance of unexpected traits in offspring that might occur if the plants were not true breeding. The garden pea also grows to maturity within one season, meaning that several generations could be evaluated over a relatively short time. Finally, large quantities of garden peas could be cultivated simultaneously, allowing Mendel to conclude that his results did not come about simply by chance.

Mendelian Crosses

Mendel performed hybridizations, which involve mating two true-breeding individuals that have different traits. In the pea, which is naturally self-pollinating, this is done by manually transferring pollen from the anther of a mature pea plant of one variety to the stigma of a separate mature pea plant of the second variety. In plants, pollen carries the male gametes (sperm) to the stigma, a sticky organ that traps pollen and allows the sperm to move down the pistil to the female gametes (ova) below. To prevent the pea plant that was receiving pollen from self-fertilizing and confounding his results, Mendel painstakingly removed all of the anthers from the plant's flowers before they had a chance to mature.

Plants used in first-generation crosses were called P_0, or parental generation one, plants (Figure 3.2.2.2). Mendel collected the seeds belonging to the P_0 plants that resulted from each cross and grew them the following season. These offspring were called the F_1, or the first filial (*filial* = offspring, daughter or son), generation. Once Mendel examined the characteristics in the F_1 generation of plants, he allowed them to self-fertilize naturally. He then collected and grew the seeds from the F_1 plants to produce the F_2, or second filial, generation. Mendel's experiments extended beyond the F_2 generation to the F_3 and F_4 generations, and so on, but it was the ratio of characteristics in the P_0–F_1–F_2 generations that were the most intriguing and became the basis for Mendel's postulates.

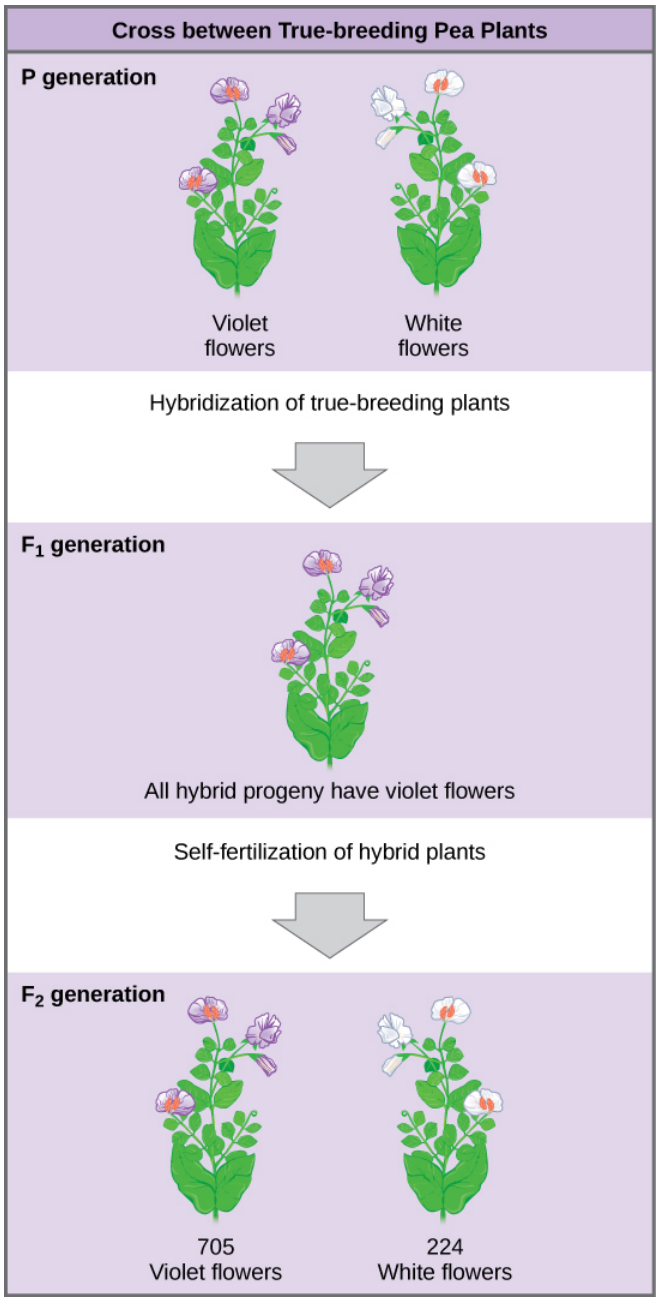


Figure 3.2.2.2: In one of his experiments on inheritance patterns, Mendel crossed plants that were true-breeding for violet flower color with plants true-breeding for white flower color (the P generation). The resulting hybrids in the F_1 generation all had violet flowers. In the F_2 generation, approximately three quarters of the plants had violet flowers, and one quarter had white flowers.

Garden Pea Characteristics Revealed the Basics of Heredity

In his 1865 publication, Mendel reported the results of his crosses involving seven different characteristics, each with two contrasting traits. A trait is defined as a variation in the physical appearance of a heritable characteristic. The characteristics included plant height, seed texture, seed color, flower color, pea pod size, pea pod color, and flower position. For the characteristic of flower color, for example, the two contrasting traits were white versus violet. To fully examine each characteristic, Mendel generated large numbers of F_1 and F_2 plants, reporting results from 19,959 F_2 plants alone. His findings were consistent.

What results did Mendel find in his crosses for flower color? First, Mendel confirmed that he had plants that bred true for white or violet flower color. Regardless of how many generations Mendel examined, all self-crossed offspring of parents with white flowers had white flowers, and all self-crossed offspring of parents with violet flowers had violet flowers. In addition, Mendel confirmed that, other than flower color, the pea plants were physically identical.

Once these validations were complete, Mendel applied the pollen from a plant with violet flowers to the stigma of a plant with white flowers. After gathering and sowing the seeds that resulted from this cross, Mendel found that 100 percent of the F_1 hybrid generation had violet flowers. Conventional wisdom at that time would have predicted the hybrid flowers to be pale violet or for hybrid plants to have equal numbers of white and violet flowers. In other words, the contrasting parental traits were expected to blend in the offspring. Instead, Mendel's results demonstrated that the white flower trait in the F_1 generation had completely disappeared.

Importantly, Mendel did not stop his experimentation there. He allowed the F_1 plants to self-fertilize and found that, of F_2-generation plants, 705 had violet flowers and 224 had white flowers. This was a ratio of 3.15 violet flowers per one white flower, or approximately 3:1. When Mendel transferred pollen from a plant with violet flowers to the stigma of a plant with white flowers and vice versa, he obtained about the same ratio regardless of which parent, male or female, contributed which trait. This is called a reciprocal cross—a paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross. For the other six characteristics Mendel examined, the F_1 and F_2 generations behaved in the same way as they had for flower color. One of the two traits would disappear completely from the F_1 generation only to reappear in the F_2 generation at a ratio of approximately 3:1 (Table 3.2.2.1).

Table 3.2.2.1: The Results of Mendel's Garden Pea Hybridizations

Characteristic	Contrasting P_0 Traits	F_1 Offspring Traits	F_2 Offspring Traits	F_2 Trait Ratios
Flower color	Violet vs. white	100 percent violet	• 705 violet • 224 white	3.15:1
Flower position	Axial vs. terminal	100 percent axial	• 651 axial • 207 terminal	3.14:1
Plant height	Tall vs. dwarf	100 percent tall	• 787 tall • 277 dwarf	2.84:1
Seed texture	Round vs. wrinkled	100 percent round	• 5,474 round • 1,850 wrinkled	2.96:1
Seed color	Yellow vs. green	100 percent yellow	• 6,022 yellow • 2,001 green	3.01:1
Pea pod texture	Inflated vs. constricted	100 percent inflated	• 882 inflated • 299 constricted	2.95:1
Pea pod color	Green vs. yellow	100 percent green	• 428 green • 152 yellow	2.82:1

Upon compiling his results for many thousands of plants, Mendel concluded that the characteristics could be divided into expressed and latent traits. He called these, respectively, *dominant* and *recessive traits*. Dominant traits are those that are inherited unchanged in a hybridization. Recessive traits become latent, or disappear, in the offspring of a hybridization. The recessive trait does, however, reappear in the progeny of the hybrid offspring. An example of a dominant trait is the violet-flower trait. For this same characteristic (flower color), white-colored flowers are a recessive trait. The fact that the recessive trait reappeared in the F_2 generation meant that the traits remained separate (not blended) in the plants of the F_1 generation. Mendel also proposed that plants possessed two copies of the trait for the flower-color characteristic, and that each parent transmitted one of its two copies to its offspring, where they came together. Moreover, the physical observation of a dominant trait could mean that the genetic composition of the organism included two dominant versions of the characteristic or that it included one dominant and one recessive version. Conversely, the observation of a recessive trait meant that the organism lacked any dominant versions of this characteristic.

So why did Mendel repeatedly obtain 3:1 ratios in his crosses? To understand how Mendel deduced the basic mechanisms of inheritance that lead to such ratios, we must first review the laws of probability.

Video



Probability Basics

Probabilities are mathematical measures of likelihood. The empirical probability of an event is calculated by dividing the number of times the event occurs by the total number of opportunities for the event to occur. It is also possible to calculate theoretical probabilities by dividing the number of times that an event is expected to occur by the number of times that it could occur. Empirical probabilities come from observations, like those of Mendel. Theoretical probabilities come from knowing how the events are produced and assuming that the probabilities of individual outcomes are equal. A probability of one for some event indicates that it is guaranteed to occur, whereas a probability of zero indicates that it is guaranteed not to occur. An example of a genetic event is a round seed produced by a pea plant. In his experiment, Mendel demonstrated that the probability of the event "round seed" occurring was one in the F_1 offspring of true-breeding parents, one of which has round seeds and one of which has wrinkled seeds. When the F_1 plants were subsequently self-crossed, the probability of any given F_2 offspring having round seeds was now three out of four. In other words, in a large population of F_2 offspring chosen at random, 75 percent were expected to have round seeds, whereas 25 percent were expected to have wrinkled seeds. Using large numbers of crosses, Mendel was able to calculate probabilities and use these to predict the outcomes of other crosses.

The Product Rule and Sum Rule

Mendel demonstrated that the pea-plant characteristics he studied were transmitted as discrete units from parent to offspring. As will be discussed, Mendel also determined that different characteristics, like seed color and seed texture, were transmitted independently of one another and could be considered in separate probability analyses. For instance, performing a cross between a plant with green, wrinkled seeds and a plant with yellow, round seeds still produced offspring that had a 3:1 ratio of green:yellow seeds (ignoring seed texture) and a 3:1 ratio of round:wrinkled seeds (ignoring seed color). The characteristics of color and texture did not influence each other.

The product rule of probability can be applied to this phenomenon of the independent transmission of characteristics. The product rule states that the probability of two independent events occurring together can be calculated by multiplying the individual probabilities of each event occurring alone. To demonstrate the product rule, imagine that you are rolling a six-sided die (D) and flipping a penny (P) at the same time. The die may roll any number from 1–6 ($D_{\#}$), whereas the penny may turn up heads (P_H) or tails (P_T). The outcome of rolling the die has no effect on the outcome of flipping the penny and vice versa. There are 12 possible outcomes of this action (Table 3.2.2.2), and each event is expected to occur with equal probability.

Table 3.2.2.2: Twelve Equally Likely Outcomes of Rolling a Die and Flipping a Penny

Rolling Die	Flipping Penny
D_1	P_H
D_1	P_T
D_2	P_H
D_2	P_T
D_3	P_H
D_3	P_T
D_4	P_H
D_4	P_T
D_5	P_H
D_5	P_T
D_6	P_H
D_6	P_T

Of the 12 possible outcomes, the die has a 2/12 (or 1/6) probability of rolling a two, and the penny has a 6/12 (or 1/2) probability of coming up heads. By the product rule, the probability that you will obtain the combined outcome 2 and heads is: (D_2) x (P_H) = (1/6) x (1/2) or 1/12 (table above). Notice the word “and” in the description of the probability. The “and” is a signal to apply the product rule. For example, consider how the product rule is applied to the dihybrid cross: the probability of having both dominant traits in the F_2 progeny is the product of the probabilities of having the dominant trait for each characteristic, as shown here:

$$\frac{3}{4} * \frac{3}{4} = \frac{9}{16}$$

On the other hand, the sum rule of probability is applied when considering two mutually exclusive outcomes that can come about by more than one pathway. The sum rule states that the probability of the occurrence of one event or the other event, of two mutually exclusive events, is the sum of their individual probabilities. Notice the word “or” in the description of the probability. The “or” indicates that you should apply the sum rule. In this case, let’s imagine you are flipping a penny (P) and a quarter (Q). What is the probability of one coin coming up heads and one coin coming up tails? This outcome can be achieved by two cases: the penny may be heads (P_H) and the quarter may be tails (Q_T), or the quarter may be heads (Q_H) and the penny may be tails (P_T). Either case fulfills the outcome. By the sum rule, we calculate the probability of obtaining one head and one tail as

$$[(P_H) \times (Q_T)] + [(Q_H) \times (P_T)] = [(1/2) \times (1/2)] + [(1/2) \times (1/2)] = 1/2.$$

You should also notice that we used the product rule to calculate the probability of P_H and Q_T, and also the probability of P_T and Q_H, before we summed them. Again, the sum rule can be applied to show the probability of having just one dominant trait in the F_2 generation of a dihybrid cross:

$$\frac{3}{16} + \frac{3}{4} = \frac{15}{16}$$

Table 3.2.2.3: The Product rule and the Sum rule

Product Rule	Sum Rule
For independent events A and B, the probability (P) of them both occurring (A *and* B) is ($P_A \times P_B$)	For mutually exclusive events A and B, the probability (P) that at least one occurs (A *or* B) is ($P_A + P_B$)

To use probability laws in practice, it is necessary to work with large sample sizes because small sample sizes are prone to deviations caused by chance. The large quantities of pea plants that Mendel examined allowed him calculate the probabilities of the

traits appearing in his F_2 generation. As you will learn, this discovery meant that when parental traits were known, the offspring's traits could be predicted accurately even before fertilization.

Summary

Working with garden pea plants, Mendel found that crosses between parents that differed by one trait produced F_1 offspring that all expressed the traits of one parent. Observable traits are referred to as dominant, and non-expressed traits are described as recessive. When the offspring in Mendel's experiment were self-crossed, the F_2 offspring exhibited the dominant trait or the recessive trait in a 3:1 ratio, confirming that the recessive trait had been transmitted faithfully from the original P_0 parent. Reciprocal crosses generated identical F_1 and F_2 offspring ratios. By examining sample sizes, Mendel showed that his crosses behaved reproducibly according to the laws of probability, and that the traits were inherited as independent events.

Two rules in probability can be used to find the expected proportions of offspring of different traits from different crosses. To find the probability of two or more independent events occurring together, apply the product rule and multiply the probabilities of the individual events. The use of the word "and" suggests the appropriate application of the product rule. To find the probability of two or more events occurring in combination, apply the sum rule and add their individual probabilities together. The use of the word "or" suggests the appropriate application of the sum rule.

Footnotes

1. 1 Johann Gregor Mendel, *Versuche über Pflanzenhybriden Verhandlungen des naturforschenden Vereines in Brünn, Bd. IV für das Jahr*, 1865 Abhandlungen, 3–47. [for English translation see www.mendelweb.org/Mendel.plain.html]

Glossary

blending theory of inheritance

hypothetical inheritance pattern in which parental traits are blended together in the offspring to produce an intermediate physical appearance

continuous variation

inheritance pattern in which a character shows a range of trait values with small gradations rather than large gaps between them

discontinuous variation

inheritance pattern in which traits are distinct and are transmitted independently of one another

dominant

trait which confers the same physical appearance whether an individual has two copies of the trait or one copy of the dominant trait and one copy of the recessive trait

F_1

first filial generation in a cross; the offspring of the parental generation

F_2

second filial generation produced when F_1 individuals are self-crossed or fertilized with each other

hybridization

process of mating two individuals that differ with the goal of achieving a certain characteristic in their offspring

model system

species or biological system used to study a specific biological phenomenon to be applied to other different species

P_0

parental generation in a cross

product rule

probability of two independent events occurring simultaneously can be calculated by multiplying the individual probabilities of each event occurring alone

recessive
trait that appears “latent” or non-expressed when the individual also carries a dominant trait for that same characteristic; when present as two identical copies, the recessive trait is expressed

reciprocal cross
paired cross in which the respective traits of the male and female in one cross become the respective traits of the female and male in the other cross

sum rule
probability of the occurrence of at least one of two mutually exclusive events is the sum of their individual probabilities

trait
variation in the physical appearance of a heritable characteristic

---

This page titled 3.2.2: Mendel’s Experiments and the Laws of Probability is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.1: Mendel’s Experiments and the Laws of Probability** by OpenStax is licensed CC BY 4.0.

3.2.3: Characteristics and Traits

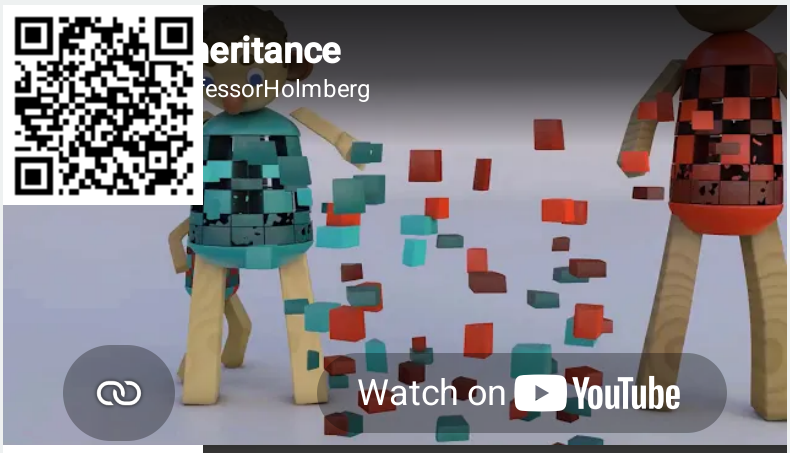
Learning Objectives

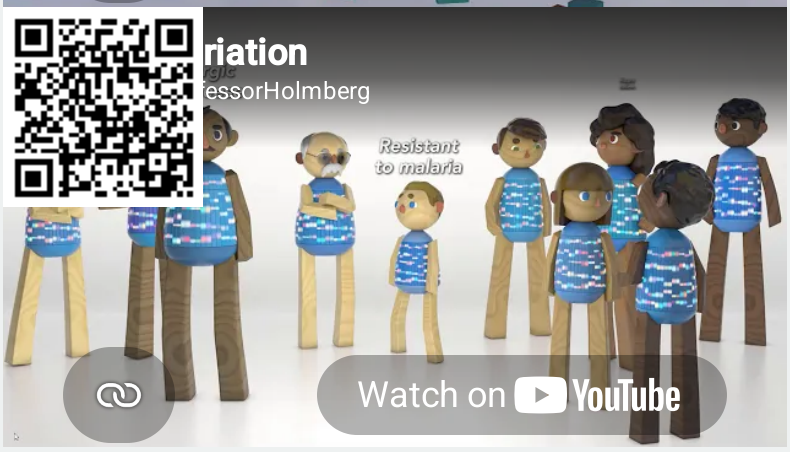
- Explain the relationship between genotypes and phenotypes in dominant and recessive gene systems
- Develop a Punnett square to calculate the expected proportions of genotypes and phenotypes in a monohybrid cross
- Explain the purpose and methods of a test cross
- Identify non-Mendelian inheritance patterns such as incomplete dominance, codominance, recessive lethals, multiple alleles, and sex linkage

The seven characteristics that Mendel evaluated in his pea plants were each expressed as one of two versions, or traits. The physical expression of characteristics is accomplished through the expression of genes carried on chromosomes. The genetic makeup of peas consists of two similar or homologous copies of each chromosome, one from each parent. Each pair of homologous chromosomes has the same linear order of genes. In other words, peas are diploid organisms in that they have two copies of each chromosome. The same is true for many other plants and for virtually all animals. Diploid organisms utilize meiosis to produce haploid gametes, which contain one copy of each homologous chromosome that unite at fertilization to create a diploid zygote.

For cases in which a single gene controls a single characteristic, a diploid organism has two genetic copies that may or may not encode the same version of that characteristic. Gene variants that arise by mutation and exist at the same relative locations on homologous chromosomes are called alleles. Mendel examined the inheritance of genes with just two allele forms, but it is common to encounter more than two alleles for any given gene in a natural population.

Videos







Phenotypes and Genotypes

Two alleles for a given gene in a diploid organism are expressed and interact to produce physical characteristics. The observable traits expressed by an organism are referred to as its phenotype. An organism's underlying genetic makeup, consisting of both physically visible and non-expressed alleles, is called its genotype. Mendel's hybridization experiments demonstrate the difference between phenotype and genotype. When true-breeding plants in which one parent had yellow pods and one had green pods were cross-fertilized, all of the F_1 hybrid offspring had yellow pods. That is, the hybrid offspring were phenotypically identical to the true-breeding parent with yellow pods. However, we know that the allele donated by the parent with green pods was not simply lost because it reappeared in some of the F_2 offspring. Therefore, the F_1 plants must have been genotypically different from the parent with yellow pods.

The P_1 plants that Mendel used in his experiments were each homozygous for the trait he was studying. Diploid organisms that are homozygous at a given gene, or locus, have two identical alleles for that gene on their homologous chromosomes. Mendel's parental pea plants always bred true because both of the gametes produced carried the same trait. When P_1 plants with contrasting traits were cross-fertilized, all of the offspring were heterozygous for the contrasting trait, meaning that their genotype reflected that they had different alleles for the gene being examined.

Dominant and Recessive Alleles

Our discussion of homozygous and heterozygous organisms brings us to why the F_1 heterozygous offspring were identical to one of the parents, rather than expressing both alleles. In all seven pea-plant characteristics, one of the two contrasting alleles was dominant, and the other was recessive. Mendel called the dominant allele the expressed unit factor; the recessive allele was referred to as the latent unit factor. We now know that these so-called unit factors are actually genes on homologous chromosome pairs. For a gene that is expressed in a dominant and recessive pattern, homozygous dominant and heterozygous organisms will look identical (that is, they will have different genotypes but the same phenotype). The recessive allele will only be observed in homozygous recessive individuals (Table 3.2.3.1).

Table 3.2.3.1: Human Inheritance in Dominant and Recessive Patterns

Dominant Traits	Recessive Traits
Achondroplasia	Albinism
Brachydactyly	Cystic fibrosis
Huntington's disease	Duchenne muscular dystrophy
Marfan syndrome	Galactosemia
Neurofibromatosis	Phenylketonuria
Widow's peak	Sickle-cell anemia
Wooly hair	Tay-Sachs disease

Several conventions exist for referring to genes and alleles. For the purposes of this chapter, we will abbreviate genes using the first letter of the gene's corresponding dominant trait. For example, violet is the dominant trait for a pea plant's flower color, so the flower-color gene would be abbreviated as *V* (note that it is customary to italicize gene designations). Furthermore, we will use uppercase and lowercase letters to represent dominant and recessive alleles, respectively. Therefore, we would refer to the genotype of a homozygous dominant pea plant with violet flowers as *VV*, a homozygous recessive pea plant with white flowers as *vv*, and a heterozygous pea plant with violet flowers as *Vv*.

The Punnett Square Approach for a Monohybrid Cross

When fertilization occurs between two true-breeding parents that differ in only one characteristic, the process is called a monohybrid cross, and the resulting offspring are monohybrids. Mendel performed seven monohybrid crosses involving contrasting traits for each characteristic. On the basis of his results in F_1 and F_2 generations, Mendel postulated that each parent in the monohybrid cross contributed one of two paired unit factors to each offspring, and every possible combination of unit factors was equally likely.

To demonstrate a monohybrid cross, consider the case of true-breeding pea plants with yellow versus green pea seeds. The dominant seed color is yellow; therefore, the parental genotypes were *YY* for the plants with yellow seeds and *yy* for the plants with green seeds, respectively. A Punnett square, devised by the British geneticist Reginald Punnett, can be drawn that applies the rules of probability to predict the possible outcomes of a genetic cross or mating and their expected frequencies. To prepare a Punnett square, all possible combinations of the parental alleles are listed along the top (for one parent) and side (for the other parent) of a grid, representing their meiotic segregation into haploid gametes. Then the combinations of egg and sperm are made in the boxes in the table to show which alleles are combining. Each box then represents the diploid genotype of a zygote, or fertilized egg, that could result from this mating. Because each possibility is equally likely, genotypic ratios can be determined from a Punnett square. If the pattern of inheritance (dominant or recessive) is known, the phenotypic ratios can be inferred as well. For a monohybrid cross of two true-breeding parents, each parent contributes one type of allele. In this case, only one genotype is possible. All offspring are *Yy* and have yellow seeds (Figure 3.2.3.1).

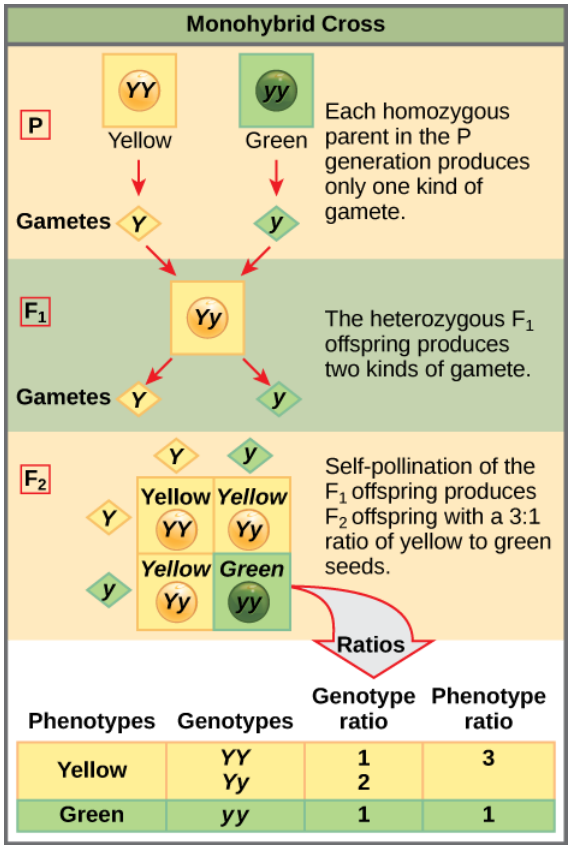


Figure 3.2.3.1: In the P generation, pea plants that are true-breeding for the dominant yellow phenotype are crossed with plants with the recessive green phenotype. This cross produces F_1 heterozygotes with a yellow phenotype. Punnett square analysis can be used to predict the genotypes of the F_2 generation.

A self-cross of one of the *Yy* heterozygous offspring can be represented in a 2 × 2 Punnett square because each parent can donate one of two different alleles. Therefore, the offspring can potentially have one of four allele combinations: *YY*, *Yy*, *yY*, or *yy* (Figure 3.2.3.1). Notice that there are two ways to obtain the *Yy* genotype: a *Y* from the egg and a *y* from the sperm, or a *y* from the egg and a *Y* from the sperm. Both of these possibilities must be counted. Recall that Mendel's pea-plant characteristics behaved in the same way in reciprocal crosses. Therefore, the two possible heterozygous combinations produce offspring that are genotypically and phenotypically identical despite their dominant and recessive alleles deriving from different parents. They are grouped together. Because fertilization is a random event, we expect each combination to be equally likely and for the offspring to exhibit a ratio of *YY*:*Yy*:*yy* genotypes of 1:2:1 (Figure 3.2.3.1). Furthermore, because the *YY* and *Yy* offspring have yellow seeds and are phenotypically identical, applying the sum rule of probability, we expect the offspring to exhibit a phenotypic ratio of 3 yellow:1 green. Indeed, working with large sample sizes, Mendel observed approximately this ratio in every F_2 generation resulting from crosses for individual traits.

Mendel validated these results by performing an F_3 cross in which he self-crossed the dominant- and recessive-expressing F_2 plants. When he self-crossed the plants expressing green seeds, all of the offspring had green seeds, confirming that all green seeds had homozygous genotypes of *yy*. When he self-crossed the F_2 plants expressing yellow seeds, he found that one-third of the plants bred true, and two-thirds of the plants segregated at a 3:1 ratio of yellow:green seeds. In this case, the true-breeding plants had homozygous (*YY*) genotypes, whereas the segregating plants corresponded to the heterozygous (*Yy*) genotype. When these plants self-fertilized, the outcome was just like the F_1 self-fertilizing cross.

The Test Cross Distinguishes the Dominant Phenotype

Beyond predicting the offspring of a cross between known homozygous or heterozygous parents, Mendel also developed a way to determine whether an organism that expressed a dominant trait was a heterozygote or a homozygote. Called the test cross, this technique is still used by plant and animal breeders. In a test cross, the dominant-expressing organism is crossed with an organism that is homozygous recessive for the same characteristic. If the dominant-expressing organism is a homozygote, then all F_1

offspring will be heterozygotes expressing the dominant trait (Figure 3.2.3.2). Alternatively, if the dominant expressing organism is a heterozygote, the F_1 offspring will exhibit a 1:1 ratio of heterozygotes and recessive homozygotes (Figure 3.2.3.2). The test cross further validates Mendel's postulate that pairs of unit factors segregate equally.

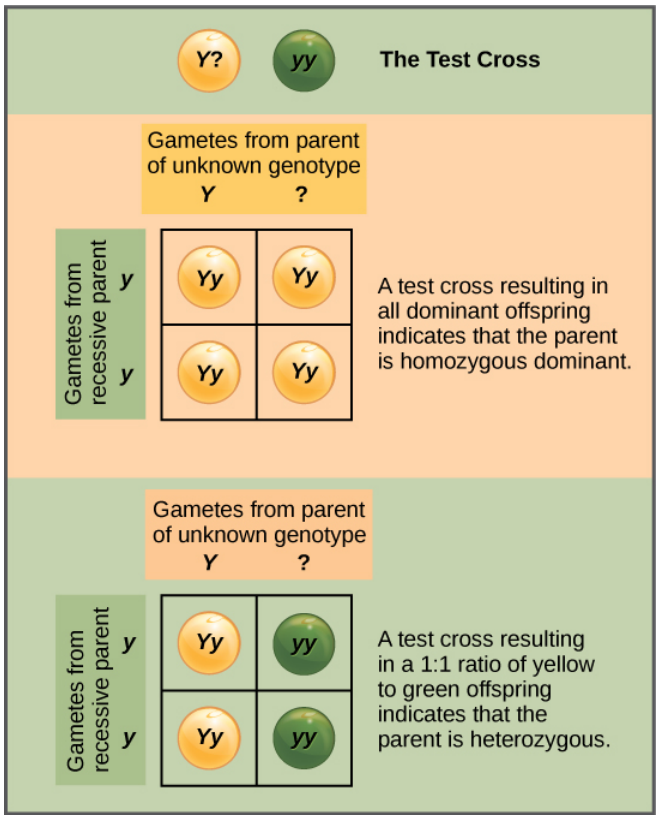


Figure 3.2.3.2: A test cross can be performed to determine whether an organism expressing a dominant trait is a homozygote or a heterozygote.

? Exercise

In pea plants, round peas (*R*) are dominant to wrinkled peas (*r*). You do a test cross between a pea plant with wrinkled peas (genotype *rr*) and a plant of unknown genotype that has round peas. You end up with three plants, all which have round peas. From this data, can you tell if the round pea parent plant is homozygous dominant or heterozygous? If the round pea parent plant is heterozygous, what is the probability that a random sample of 3 progeny peas will all be round?

Answer

You cannot be sure if the plant is homozygous or heterozygous as the data set is too small: by random chance, all three plants might have acquired only the dominant gene even if the recessive one is present. If the round pea parent is heterozygous, there is a one-eighth probability that a random sample of three progeny peas will all be round.

Many human diseases are genetically inherited. A healthy person in a family in which some members suffer from a recessive genetic disorder may want to know if he or she has the disease-causing gene and what risk exists of passing the disorder on to his or her offspring. Of course, doing a test cross in humans is unethical and impractical. Instead, geneticists use pedigree analysis to study the inheritance pattern of human genetic diseases (Figure 3.2.3.3).

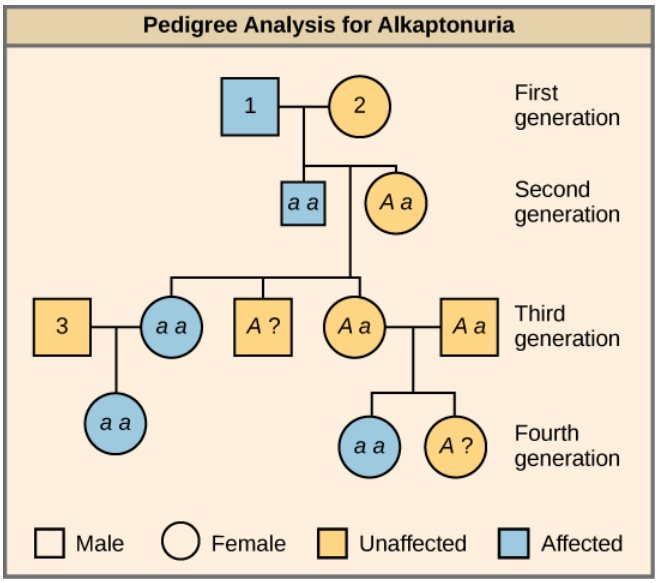


Figure 3.2.3.3: Alkaptonuria is a recessive genetic disorder in which two amino acids, phenylalanine and tyrosine, are not properly metabolized. Affected individuals may have darkened skin and brown urine, and may suffer joint damage and other complications. In this pedigree, individuals with the disorder are indicated in blue and have the genotype *aa*. Unaffected individuals are indicated in yellow and have the genotype *AA* or *Aa*. Note that it is often possible to determine a person's genotype from the genotype of their offspring. For example, if neither parent has the disorder but their child does, they must be heterozygous. Two individuals on the pedigree have an unaffected phenotype but unknown genotype. Because they do not have the disorder, they must have at least one normal allele, so their genotype gets the "*A*?" designation.

? Exercise

What are the genotypes of the individuals labeled 1, 2 and 3?

Answer

Individual 1 has the genotype *aa*. Individual 2 has the genotype *Aa*. Individual 3 has the genotype *Aa*.

Alternatives to Dominance and Recessiveness

Mendel's experiments with pea plants suggested that: (1) two "units" or alleles exist for every gene; (2) alleles maintain their integrity in each generation (no blending); and (3) in the presence of the dominant allele, the recessive allele is hidden and makes no contribution to the phenotype. Therefore, recessive alleles can be "carried" and not expressed by individuals. Such heterozygous individuals are sometimes referred to as "carriers." Further genetic studies in other plants and animals have shown that much more complexity exists, but that the fundamental principles of Mendelian genetics still hold true. In the sections to follow, we consider some of the extensions of Mendelism. If Mendel had chosen an experimental system that exhibited these genetic complexities, it's possible that he would not have understood what his results meant.

Incomplete Dominance

Mendel's results, that traits are inherited as dominant and recessive pairs, contradicted the view at that time that offspring exhibited a blend of their parents' traits. However, the heterozygote phenotype occasionally does appear to be intermediate between the two parents. For example, in the snapdragon, *Antirrhinum majus* (Figure 3.2.3.4), a cross between a homozygous parent with white flowers (C^WC^W) and a homozygous parent with red flowers (C^RC^R) will produce offspring with pink flowers (C^RC^W). (Note that different genotypic abbreviations are used for Mendelian extensions to distinguish these patterns from simple dominance and recessiveness.) This pattern of inheritance is described as incomplete dominance, denoting the expression of two contrasting alleles such that the individual displays an intermediate phenotype. The allele for red flowers is incompletely dominant over the allele for white flowers. However, the results of a heterozygote self-cross can still be predicted, just as with Mendelian dominant and recessive crosses. In this case, the genotypic ratio would be 1 C^RC^R:2 C^RC^W:1 C^WC^W, and the phenotypic ratio would be 1:2:1 for red:pink:white.



Figure 3.2.3.4: These pink flowers of a heterozygote snapdragon result from incomplete dominance. (credit: "storebukkebruse"/Flickr)

Codominance

A variation on incomplete dominance is codominance, in which both alleles for the same characteristic are simultaneously expressed in the heterozygote. An example of codominance is the MN blood groups of humans. The M and N alleles are expressed in the form of an M or N antigen present on the surface of red blood cells. Homozygotes (L^ML^M and L^NL^N) express either the M or the N allele, and heterozygotes (L^ML^N) express both alleles equally. In a self-cross between heterozygotes expressing a codominant trait, the three possible offspring genotypes are phenotypically distinct. However, the 1:2:1 genotypic ratio characteristic of a Mendelian monohybrid cross still applies.

Multiple Alleles

Mendel implied that only two alleles, one dominant and one recessive, could exist for a given gene. We now know that this is an oversimplification. Although individual humans (and all diploid organisms) can only have two alleles for a given gene, multiple alleles may exist at the population level such that many combinations of two alleles are observed. Note that when many alleles exist for the same gene, the convention is to denote the most common phenotype or genotype among wild animals as the wild type (often abbreviated "+"); this is considered the standard or norm. All other phenotypes or genotypes are considered variants of this standard, meaning that they deviate from the wild type. The variant may be recessive or dominant to the wild-type allele.

An example of multiple alleles is coat color in rabbits (Figure 3.2.3.5). Here, four alleles exist for the *c* gene. The wild-type version, C^+C^+, is expressed as brown fur. The chinchilla phenotype, $c^{ch}c^{ch}$, is expressed as black-tipped white fur. The Himalayan phenotype, c^hc^h, has black fur on the extremities and white fur elsewhere. Finally, the albino, or "colorless" phenotype, *cc*, is expressed as white fur. In cases of multiple alleles, dominance hierarchies can exist. In this case, the wild-type allele is dominant over all the others, chinchilla is incompletely dominant over Himalayan and albino, and Himalayan is dominant over albino. This hierarchy, or allelic series, was revealed by observing the phenotypes of each possible heterozygote offspring.

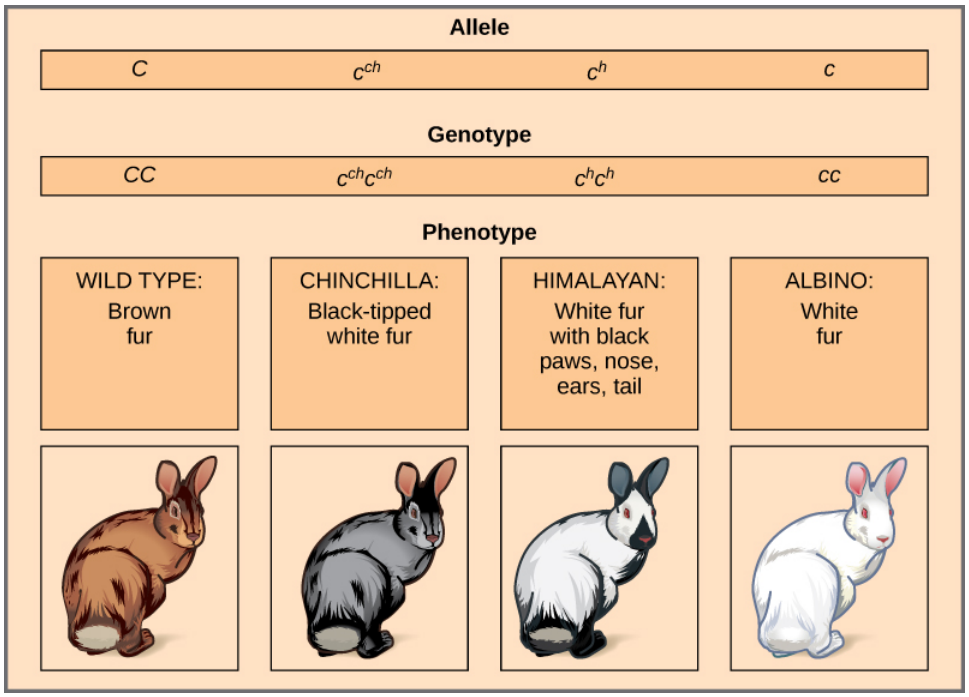


Figure 3.2.3.5: Four different alleles exist for the rabbit coat color (*C*) gene.

The complete dominance of a wild-type phenotype over all other mutants often occurs as an effect of "dosage" of a specific gene product, such that the wild-type allele supplies the correct amount of gene product whereas the mutant alleles cannot. For the allelic series in rabbits, the wild-type allele may supply a given dosage of fur pigment, whereas the mutants supply a lesser dosage or none at all. Interestingly, the Himalayan phenotype is the result of an allele that produces a temperature-sensitive gene product that only produces pigment in the cooler extremities of the rabbit's body.

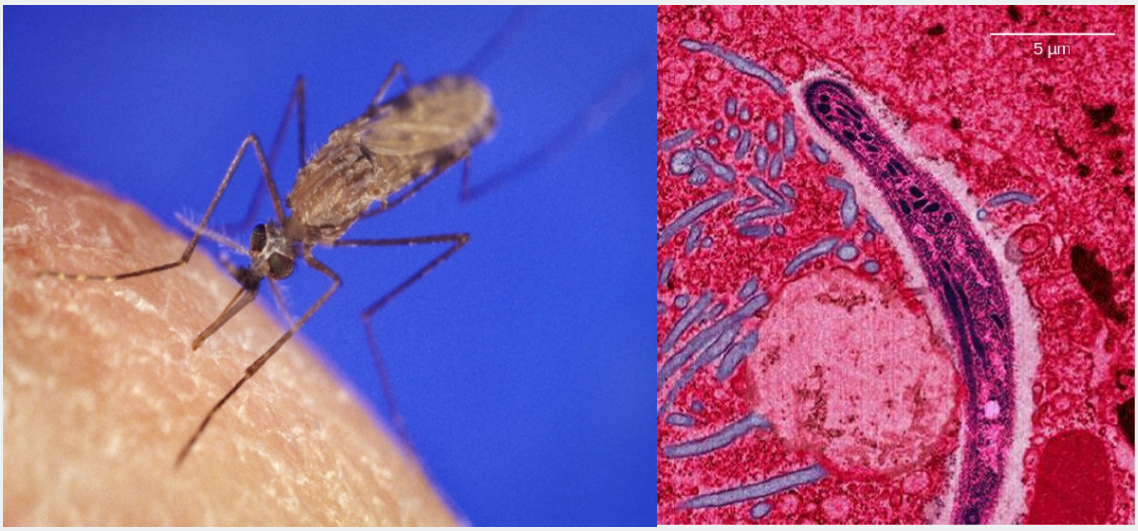
Alternatively, one mutant allele can be dominant over all other phenotypes, including the wild type. This may occur when the mutant allele somehow interferes with the genetic message so that even a heterozygote with one wild-type allele copy expresses the mutant phenotype. One way in which the mutant allele can interfere is by enhancing the function of the wild-type gene product or changing its distribution in the body. One example of this is the *Antennapedia* mutation in *Drosophila* (Figure 3.2.3.6). In this case, the mutant allele expands the distribution of the gene product, and as a result, the *Antennapedia* heterozygote develops legs on its head where its antennae should be.



Figure 3.2.3.6: As seen in comparing the wild-type *Drosophila* (left) and the *Antennapedia* mutant (right), the *Antennapedia* mutant has legs on its head in place of antennae.

Evolution Connection: Multiple Alleles Confer Drug Resistance in the Malaria Parasite

Malaria is a parasitic disease in humans that is transmitted by infected female mosquitoes, including *Anopheles gambiae* (Figure 3.2.3.7a), and is characterized by cyclic high fevers, chills, flu-like symptoms, and severe anemia. *Plasmodium falciparum* and *P. vivax* are the most common causative agents of malaria, and *P. falciparum* is the most deadly (Figure 3.2.3.7 b). When promptly and correctly treated, *P. falciparum* malaria has a mortality rate of 0.1 percent. However, in some parts of the world, the parasite has evolved resistance to commonly used malaria treatments, so the most effective malarial treatments can vary by geographic region.



(a) (b)

Figure 3.2.3.7: The (a) *Anopheles gambiae*, or African malaria mosquito, acts as a vector in the transmission to humans of the malaria-causing parasite (b) *Plasmodium falciparum*, here visualized using false-color transmission electron microscopy. (credit a: James D. Gathany; credit b: Ute Frevert; false color by Margaret Shear; scale-bar data from Matt Russell)

In Southeast Asia, Africa, and South America, *P. falciparum* has developed resistance to the anti-malarial drugs chloroquine, mefloquine, and sulfadoxine-pyrimethamine. *P. falciparum*, which is haploid during the life stage in which it is infectious to

humans, has evolved multiple drug-resistant mutant alleles of the *dhps* gene. Varying degrees of sulfadoxine resistance are associated with each of these alleles. Being haploid, *P. falciparum* needs only one drug-resistant allele to express this trait.

In Southeast Asia, different sulfadoxine-resistant alleles of the *dhps* gene are localized to different geographic regions. This is a common evolutionary phenomenon that occurs because drug-resistant mutants arise in a population and interbreed with other *P. falciparum* isolates in close proximity. Sulfadoxine-resistant parasites cause considerable human hardship in regions where this drug is widely used as an over-the-counter malaria remedy. As is common with pathogens that multiply to large numbers within an infection cycle, *P. falciparum* evolves relatively rapidly (over a decade or so) in response to the selective pressure of commonly used anti-malarial drugs. For this reason, scientists must constantly work to develop new drugs or drug combinations to combat the worldwide malaria burden.[1]

X-Linked Traits

In humans, as well as in many other animals and some plants, the sex of the individual is determined by sex chromosomes. The sex chromosomes are one pair of non-homologous chromosomes. Until now, we have only considered inheritance patterns among non-sex chromosomes, or autosomes. In addition to 22 homologous pairs of autosomes, human females have a homologous pair of X chromosomes, whereas human males have an XY chromosome pair. Although the Y chromosome contains a small region of similarity to the X chromosome so that they can pair during meiosis, the Y chromosome is much shorter and contains many fewer genes. When a gene being examined is present on the X chromosome, but not on the Y chromosome, it is said to be X-linked.

Eye color in *Drosophila* was one of the first X-linked traits to be identified. Thomas Hunt Morgan mapped this trait to the X chromosome in 1910. Like humans, *Drosophila* males have an XY chromosome pair, and females are XX. In flies, the wild-type eye color is red (X^W) and it is dominant to white eye color (X^w) (Figure 3.2.3.8). Because of the location of the eye-color gene, reciprocal crosses do not produce the same offspring ratios. Males are said to be hemizygous, because they have only one allele for any X-linked characteristic. Hemizygosity makes the descriptions of dominance and recessiveness irrelevant for XY males. *Drosophila* males lack a second allele copy on the Y chromosome; that is, their genotype can only be X^WY or X^wY. In contrast, females have two allele copies of this gene and can be X^WX^W, X^WX^w, or X^wX^w.



Figure 3.2.3.8: In *Drosophila*, the gene for eye color is located on the X chromosome. Clockwise from top left are brown, cinnabar, sepia, vermilion, white, and red. Red eye color is wild-type and is dominant to white eye color.

In an X-linked cross, the genotypes of F_1 and F_2 offspring depend on whether the recessive trait was expressed by the male or the female in the P_1 generation. With regard to *Drosophila* eye color, when the P_1 male expresses the white-eye phenotype and the female is homozygous red-eyed, all members of the F_1 generation exhibit red eyes (Figure 3.2.3.9). The F_1 females are heterozygous (X^WX^w), and the males are all X^WY, having received their X chromosome from the homozygous dominant P_1 female and their Y chromosome from the P_1 male. A subsequent cross between the X^WX^w female and the X^WY male would produce only red-eyed females (with X^WX^W or X^WX^w genotypes) and both red- and white-eyed males (with X^WY or X^wY genotypes). Now, consider a cross between a homozygous white-eyed female and a male with red eyes. The F_1 generation would exhibit only heterozygous red-eyed females (X^WX^w) and only white-eyed males (X^wY). Half of the F_2 females would be red-eyed (X^WX^w) and half would be white-eyed (X^wX^w). Similarly, half of the F_2 males would be red-eyed (X^WY) and half would be white-eyed (X^wY).

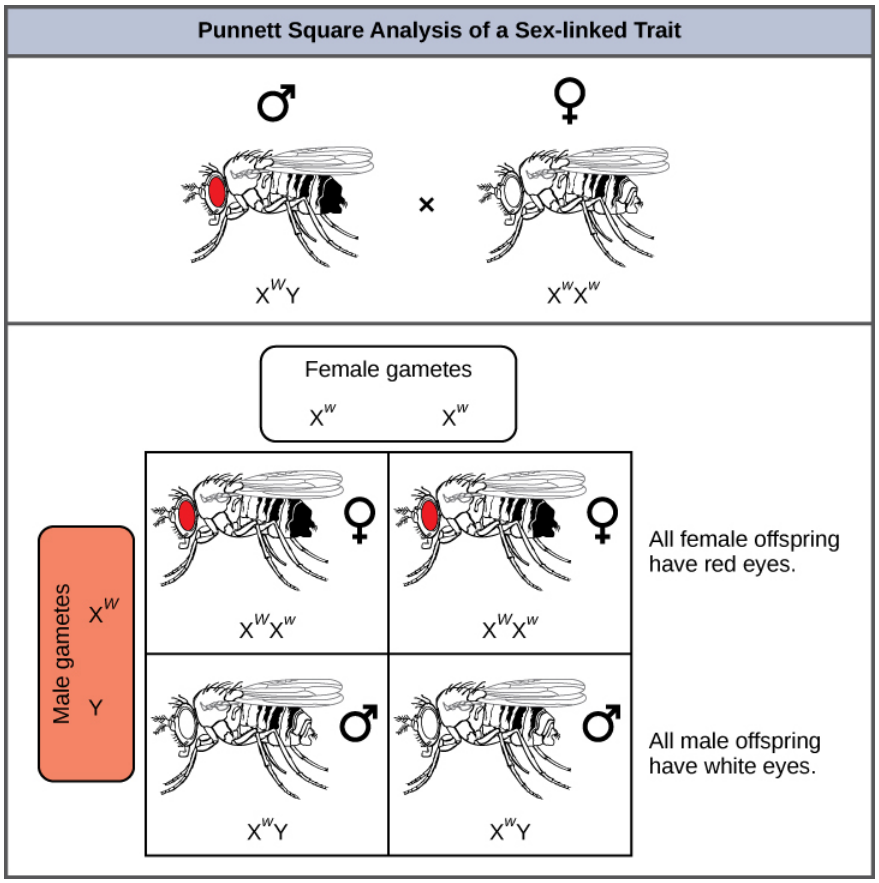


Figure 3.2.3.9: Punnett square analysis is used to determine the ratio of offspring from a cross between a red-eyed male fruit fly and a white-eyed female fruit fly.

? Exercise

What ratio of offspring would result from a cross between a white-eyed male and a female that is heterozygous for red eye color?

Answer

Half of the female offspring would be heterozygous (X^WX^w) with red eyes, and half would be homozygous recessive (X^wX^w) with white eyes. Half of the male offspring would be hemizygous dominant (X^WY) withe red yes, and half would be hemizygous recessive (X^wY) with white eyes.

Discoveries in fruit fly genetics can be applied to human genetics. When a female parent is homozygous for a recessive X-linked trait, she will pass the trait on to 100 percent of her offspring. Her male offspring are, therefore, destined to express the trait, as they will inherit their father's Y chromosome. In humans, the alleles for certain conditions (some forms of color blindness, hemophilia,

and muscular dystrophy) are X-linked. Females who are heterozygous for these diseases are said to be carriers and may not exhibit any phenotypic effects. These females will pass the disease to half of their sons and will pass carrier status to half of their daughters; therefore, recessive X-linked traits appear more frequently in males than females.

In some groups of organisms with sex chromosomes, the gender with the non-homologous sex chromosomes is the female rather than the male. This is the case for all birds. In this case, sex-linked traits will be more likely to appear in the female, in which they are hemizygous.

Video



Human Sex-linked Disorders

Sex-linkage studies in Morgan's laboratory provided the fundamentals for understanding X-linked recessive disorders in humans, which include red-green color blindness, and Types A and B hemophilia. Because human males need to inherit only one recessive mutant X allele to be affected, X-linked disorders are disproportionately observed in males. Females must inherit recessive X-linked alleles from both of their parents in order to express the trait. When they inherit one recessive X-linked mutant allele and one dominant X-linked wild-type allele, they are carriers of the trait and are typically unaffected. Carrier females can manifest mild forms of the trait due to the inactivation of the dominant allele located on one of the X chromosomes. However, female carriers can contribute the trait to their sons, resulting in the son exhibiting the trait, or they can contribute the recessive allele to their daughters, resulting in the daughters being carriers of the trait (Figure 3.2.3.10). Although some Y-linked recessive disorders exist, typically they are associated with infertility in males and are therefore not transmitted to subsequent generations.

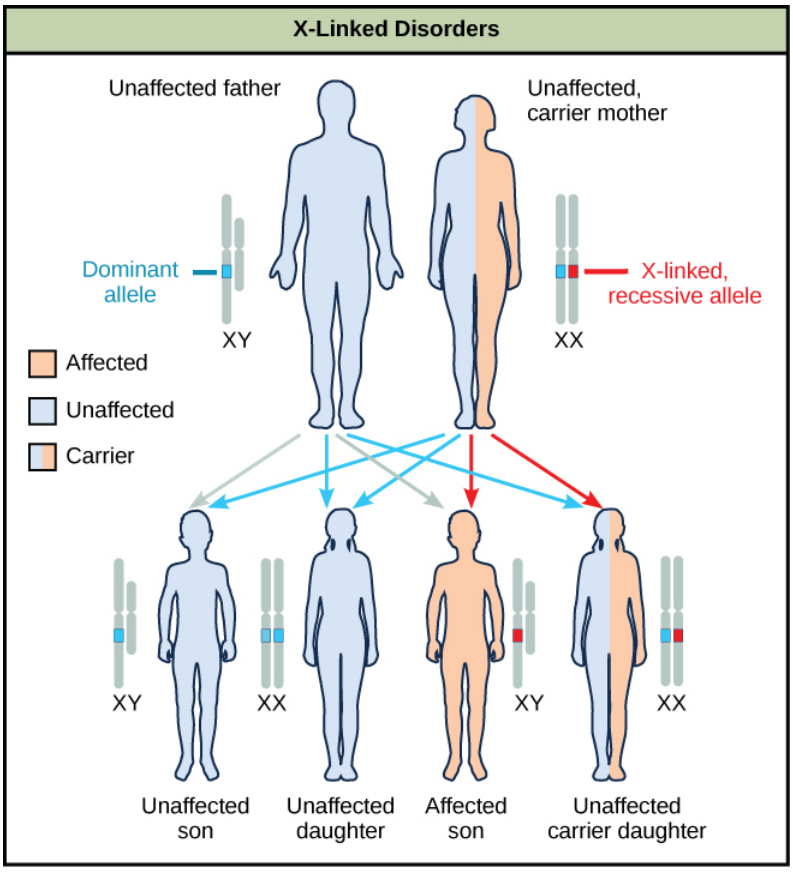


Figure 3.2.3.10: The son of a woman who is a carrier of a recessive X-linked disorder will have a 50 percent chance of being affected. A daughter will not be affected, but she will have a 50 percent chance of being a carrier like her mother.

Lethality

A large proportion of genes in an individual's genome are essential for survival. Occasionally, a nonfunctional allele for an essential gene can arise by mutation and be transmitted in a population as long as individuals with this allele also have a wild-type, functional copy. The wild-type allele functions at a capacity sufficient to sustain life and is therefore considered to be dominant over the nonfunctional allele. However, consider two heterozygous parents that have a genotype of wild-type/nonfunctional mutant for a hypothetical essential gene. In one quarter of their offspring, we would expect to observe individuals that are homozygous recessive for the nonfunctional allele. Because the gene is essential, these individuals might fail to develop past fertilization, die in utero, or die later in life, depending on what life stage requires this gene. An inheritance pattern in which an allele is only lethal in the homozygous form and in which the heterozygote may be normal or have some altered non-lethal phenotype is referred to as recessive lethal.

For crosses between heterozygous individuals with a recessive lethal allele that causes death before birth when homozygous, only wild-type homozygotes and heterozygotes would be observed. The genotypic ratio would therefore be 2:1. In other instances, the recessive lethal allele might also exhibit a dominant (but not lethal) phenotype in the heterozygote. For instance, the recessive lethal Curly allele in Drosophila affects wing shape in the heterozygote form but is lethal in the homozygote.

A single copy of the wild-type allele is not always sufficient for normal functioning or even survival. The dominant lethal inheritance pattern is one in which an allele is lethal both in the homozygote and the heterozygote; this allele can only be transmitted if the lethality phenotype occurs after reproductive age. Individuals with mutations that result in dominant lethal alleles fail to survive even in the heterozygote form. Dominant lethal alleles are very rare because, as you might expect, the allele only lasts one generation and is not transmitted. However, just as the recessive lethal allele might not immediately manifest the phenotype of death, dominant lethal alleles also might not be expressed until adulthood. Once the individual reaches reproductive age, the allele may be unknowingly passed on, resulting in a delayed death in both generations. An example of this in humans is Huntington's disease, in which the nervous system gradually wastes away (Figure 3.2.3.11). People who are heterozygous for the

dominant Huntington allele (Hh) will inevitably develop the fatal disease. However, the onset of Huntington's disease may not occur until age 40, at which point the afflicted persons may have already passed the allele to 50 percent of their offspring.

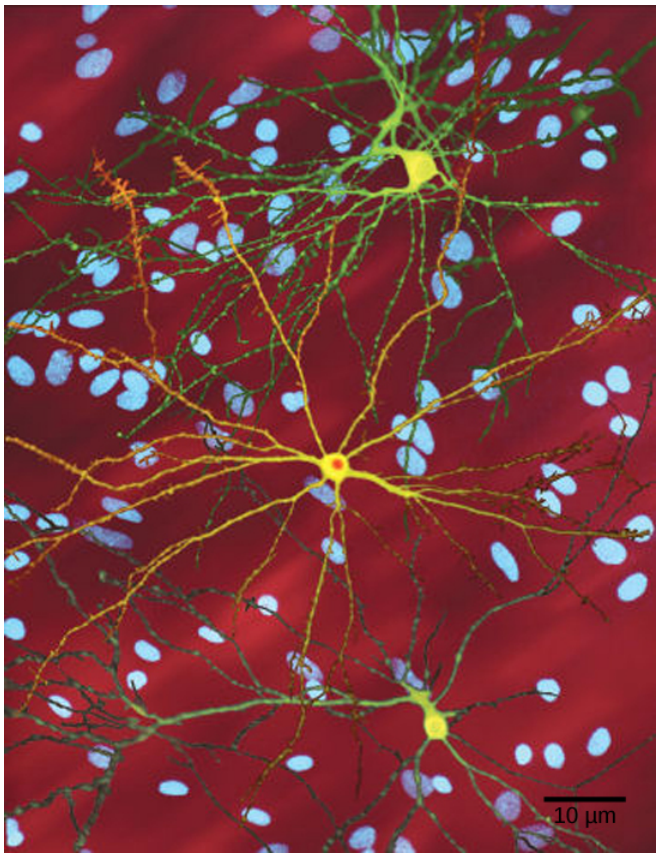


Figure 3.2.3.11: The neuron in the center of this micrograph (yellow) has nuclear inclusions characteristic of Huntington's disease (orange area in the center of the neuron). Huntington's disease occurs when an abnormal dominant allele for the Huntington gene is present. (credit: Dr. Steven Finkbeiner, Gladstone Institute of Neurological Disease, The Taube-Koret Center for Huntington's Disease Research, and the University of California San Francisco/Wikimedia)

Summary

When true-breeding or homozygous individuals that differ for a certain trait are crossed, all of the offspring will be heterozygotes for that trait. If the traits are inherited as dominant and recessive, the F_1 offspring will all exhibit the same phenotype as the parent homozygous for the dominant trait. If these heterozygous offspring are self-crossed, the resulting F_2 offspring will be equally likely to inherit gametes carrying the dominant or recessive trait, giving rise to offspring of which one quarter are homozygous dominant, half are heterozygous, and one quarter are homozygous recessive. Because homozygous dominant and heterozygous individuals are phenotypically identical, the observed traits in the F_2 offspring will exhibit a ratio of three dominant to one recessive.

Alleles do not always behave in dominant and recessive patterns. Incomplete dominance describes situations in which the heterozygote exhibits a phenotype that is intermediate between the homozygous phenotypes. Codominance describes the simultaneous expression of both of the alleles in the heterozygote. Although diploid organisms can only have two alleles for any given gene, it is common for more than two alleles of a gene to exist in a population. In humans, as in many animals and some plants, females have two X chromosomes and males have one X and one Y chromosome. Genes that are present on the X but not the Y chromosome are said to be X-linked, such that males only inherit one allele for the gene, and females inherit two. Finally, some alleles can be lethal. Recessive lethal alleles are only lethal in homozygotes, but dominant lethal alleles are fatal in heterozygotes as well.

Footnotes

1. 1 Sumiti Vinayak, et al., "Origin and Evolution of Sulfadoxine Resistant Plasmodium falciparum," Public Library of Science Pathogens 6, no. 3 (2010): e1000830, doi:10.1371/journal.ppat.1000830.

Glossary

allele
gene variations that arise by mutation and exist at the same relative locations on homologous chromosomes

autosomes
any of the non-sex chromosomes

codominance
in a heterozygote, complete and simultaneous expression of both alleles for the same characteristic

dominant lethal
inheritance pattern in which an allele is lethal both in the homozygote and the heterozygote; this allele can only be transmitted if the lethality phenotype occurs after reproductive age

genotype
underlying genetic makeup, consisting of both physically visible and non-expressed alleles, of an organism

hemizygous
presence of only one allele for a characteristic, as in X-linkage; hemizygosity makes descriptions of dominance and recessiveness irrelevant

heterozygous
having two different alleles for a given gene on the homologous chromosome

homozygous
having two identical alleles for a given gene on the homologous chromosome

incomplete dominance
in a heterozygote, expression of two contrasting alleles such that the individual displays an intermediate phenotype

monohybrid
result of a cross between two true-breeding parents that express different traits for only one characteristic

phenotype
observable traits expressed by an organism

Punnett square
visual representation of a cross between two individuals in which the gametes of each individual are denoted along the top and side of a grid, respectively, and the possible zygotic genotypes are recombined at each box in the grid

recessive lethal
inheritance pattern in which an allele is only lethal in the homozygous form; the heterozygote may be normal or have some altered, non-lethal phenotype

sex-linked
any gene on a sex chromosome

test cross
cross between a dominant expressing individual with an unknown genotype and a homozygous recessive individual; the offspring phenotypes indicate whether the unknown parent is heterozygous or homozygous for the dominant trait

X-linked
gene present on the X, but not the Y chromosome

This page titled 3.2.3: Characteristics and Traits is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.2: Characteristics and Traits** by OpenStax is licensed CC BY 4.0.

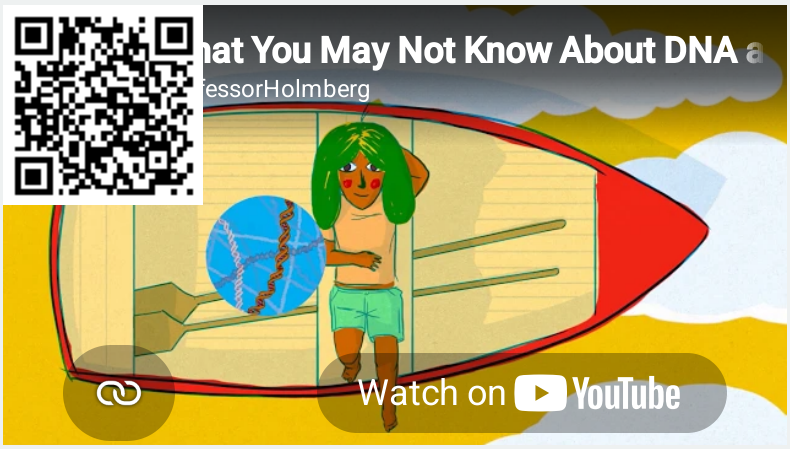
3.2.4: Laws of Inheritance

Learning Objectives

- Explain Mendel's law of segregation and independent assortment in terms of genetics and the events of meiosis
- Use the forked-line method and the probability rules to calculate the probability of genotypes and phenotypes from multiple gene crosses
- Explain the effect of linkage and recombination on gamete genotypes
- Explain the phenotypic outcomes of epistatic effects between genes

Mendel generalized the results of his pea-plant experiments into four postulates, some of which are sometimes called "laws," that describe the basis of dominant and recessive inheritance in diploid organisms. As you have learned, more complex extensions of Mendelism exist that do not exhibit the same F_2 phenotypic ratios (3:1). Nevertheless, these laws summarize the basics of classical genetics.

Video



Pairs of Unit Factors, or Genes

Mendel proposed first that paired unit factors of heredity were transmitted faithfully from generation to generation by the dissociation and reassociation of paired factors during gametogenesis and fertilization, respectively. After he crossed peas with contrasting traits and found that the recessive trait resurfaced in the F_2 generation, Mendel deduced that hereditary factors must be inherited as discrete units. This finding contradicted the belief at that time that parental traits were blended in the offspring.

Alleles Can Be Dominant or Recessive

Mendel's law of dominance states that in a heterozygote, one trait will conceal the presence of another trait for the same characteristic. Rather than both alleles contributing to a phenotype, the dominant allele will be expressed exclusively. The recessive allele will remain "latent" but will be transmitted to offspring by the same manner in which the dominant allele is transmitted. The recessive trait will only be expressed by offspring that have two copies of this allele (Figure 3.2.4.1), and these offspring will breed true when self-crossed.

Since Mendel's experiments with pea plants, other researchers have found that the law of dominance does not always hold true. Instead, several different patterns of inheritance have been found to exist.



Figure 3.2.4.1: The child in the photo expresses albinism, a recessive trait.

Equal Segregation of Alleles

Observing that true-breeding pea plants with contrasting traits gave rise to F_1 generations that all expressed the dominant trait and F_2 generations that expressed the dominant and recessive traits in a 3:1 ratio, Mendel proposed the law of segregation. This law states that paired unit factors (genes) must segregate equally into gametes such that offspring have an equal likelihood of inheriting either factor. For the F_2 generation of a monohybrid cross, the following three possible combinations of genotypes could result: homozygous dominant, heterozygous, or homozygous recessive. Because heterozygotes could arise from two different pathways (receiving one dominant and one recessive allele from either parent), and because heterozygotes and homozygous dominant individuals are phenotypically identical, the law supports Mendel's observed 3:1 phenotypic ratio. The equal segregation of alleles is the reason we can apply the Punnett square to accurately predict the offspring of parents with known genotypes. The physical basis of Mendel's law of segregation is the first division of meiosis, in which the homologous chromosomes with their different versions of each gene are segregated into daughter nuclei. The role of the meiotic segregation of chromosomes in sexual reproduction was not understood by the scientific community during Mendel's lifetime.

Independent Assortment

Mendel's law of independent assortment states that genes do not influence each other with regard to the sorting of alleles into gametes, and every possible combination of alleles for every gene is equally likely to occur. The independent assortment of genes can be illustrated by the dihybrid cross, a cross between two true-breeding parents that express different traits for two characteristics. Consider the characteristics of seed color and seed texture for two pea plants, one that has green, wrinkled seeds (*yyrr*) and another that has yellow, round seeds (*YYRR*). Because each parent is homozygous, the law of segregation indicates that the gametes for the green/wrinkled plant all are *yr*, and the gametes for the yellow/round plant are all *YR*. Therefore, the F_1 generation of offspring all are *YyRr* (Figure 3.2.4.2).

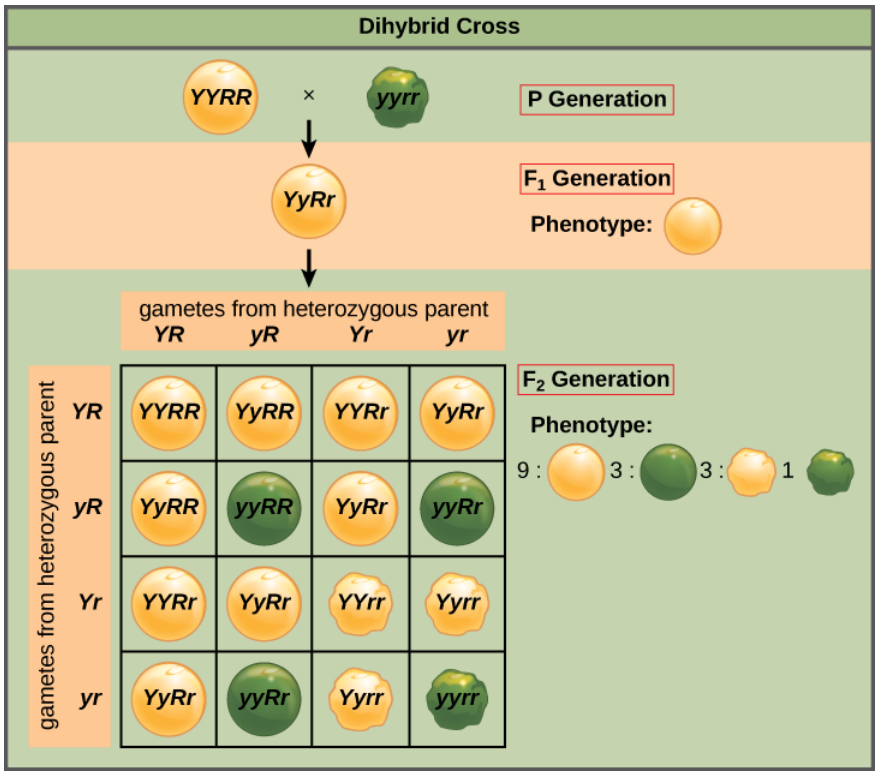


Figure 3.2.4.2: This dihybrid cross of pea plants involves the genes for seed color and texture.

? Exercise

In pea plants, purple flowers (*P*) are dominant to white flowers (*p*) and yellow peas (*Y*) are dominant to green peas (*y*). What are the possible genotypes and phenotypes for a cross between *PpYY* and *ppYy* pea plants? How many squares do you need to do a Punnett square analysis of this cross?

Answer

The possible genotypes are *PpYY*, *PpYy*, *ppYY*, and *ppYy*. The former two genotypes would result in plants with purple flowers and yellow peas, while the latter two genotypes would result in plants with white flowers with yellow peas, for a 1:1 ratio of each phenotype. You only need a 2 × 2 Punnett square (four squares total) to do this analysis because two of the alleles are homozygous.

For the F_2 generation, the law of segregation requires that each gamete receive either an *R* allele or an *r* allele along with either a *Y* allele or a *y* allele. The law of independent assortment states that a gamete into which an *r* allele sorted would be equally likely to contain either a *Y* allele or a *y* allele. Thus, there are four equally likely gametes that can be formed when the *YyRr* heterozygote is self-crossed, as follows: *YR*, *Yr*, *yR*, and *yr*. Arranging these gametes along the top and left of a 4 × 4 Punnett square (Figure 3.2.4.2) gives us 16 equally likely genotypic combinations. From these genotypes, we infer a phenotypic ratio of 9 round/yellow:3 round/green:3 wrinkled/yellow:1 wrinkled/green (Figure 3.2.4.2). These are the offspring ratios we would expect, assuming we performed the crosses with a large enough sample size.

Because of independent assortment and dominance, the 9:3:3:1 dihybrid phenotypic ratio can be collapsed into two 3:1 ratios, characteristic of any monohybrid cross that follows a dominant and recessive pattern. Ignoring seed color and considering only seed texture in the above dihybrid cross, we would expect that three quarters of the F_2 generation offspring would be round, and one quarter would be wrinkled. Similarly, isolating only seed color, we would assume that three quarters of the F_2 offspring would be yellow and one quarter would be green. The sorting of alleles for texture and color are independent events, so we can apply the product rule. Therefore, the proportion of round and yellow F_2 offspring is expected to be (3/4) × (3/4) = 9/16, and the proportion of wrinkled and green offspring is expected to be (1/4) × (1/4) = 1/16. These proportions are identical to those obtained using a

Punnett square. Round, green and wrinkled, yellow offspring can also be calculated using the product rule, as each of these genotypes includes one dominant and one recessive phenotype. Therefore, the proportion of each is calculated as (3/4) × (1/4) = 3/16.

The law of independent assortment also indicates that a cross between yellow, wrinkled (*YYrr*) and green, round (*yyRR*) parents would yield the same F_1 and F_2 offspring as in the *YYRR* x *yyrr* cross.

The physical basis for the law of independent assortment also lies in meiosis I, in which the different homologous pairs line up in random orientations. Each gamete can contain any combination of paternal and maternal chromosomes (and therefore the genes on them) because the orientation of tetrads on the metaphase plane is random.

Linked Genes Violate the Law of Independent Assortment

Although all of Mendel's pea characteristics behaved according to the law of independent assortment, we now know that some allele combinations are not inherited independently of each other. Genes that are located on separate non-homologous chromosomes will always sort independently. However, each chromosome contains hundreds or thousands of genes, organized linearly on chromosomes like beads on a string. The segregation of alleles into gametes can be influenced by linkage, in which genes that are located physically close to each other on the same chromosome are more likely to be inherited as a pair. However, because of the process of recombination, or "crossover," it is possible for two genes on the same chromosome to behave independently, or as if they are not linked. To understand this, let's consider the biological basis of gene linkage and recombination.

Homologous chromosomes possess the same genes in the same linear order. The alleles may differ on homologous chromosome pairs, but the genes to which they correspond do not. In preparation for the first division of meiosis, homologous chromosomes replicate and synapse. Like genes on the homologs align with each other. At this stage, segments of homologous chromosomes exchange linear segments of genetic material (Figure 3.2.4.4). This process is called recombination, or crossover, and it is a common genetic process. Because the genes are aligned during recombination, the gene order is not altered. Instead, the result of recombination is that maternal and paternal alleles are combined onto the same chromosome. Across a given chromosome, several recombination events may occur, causing extensive shuffling of alleles.

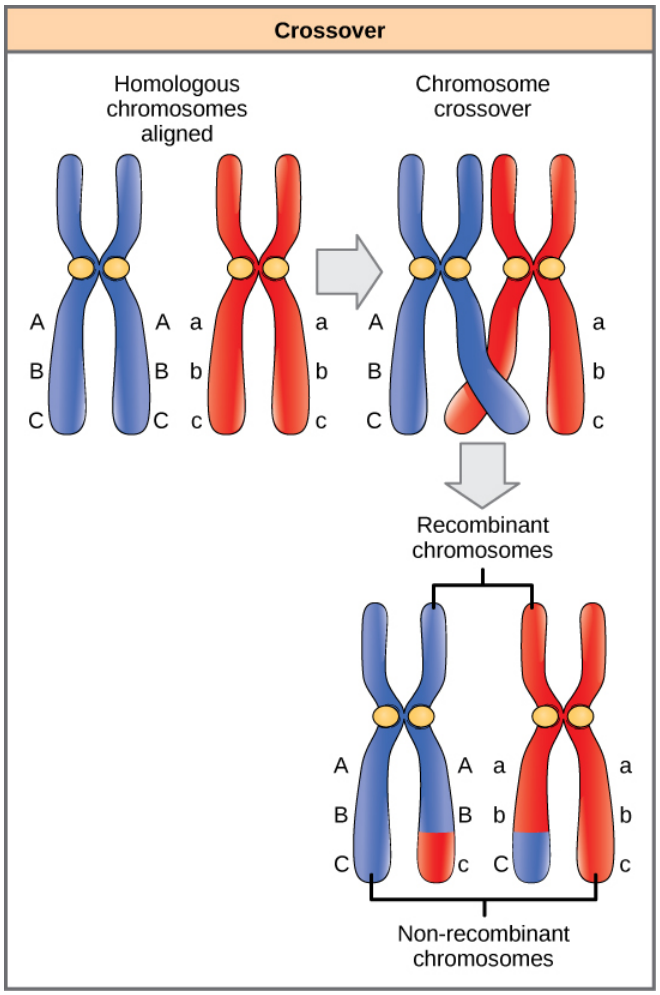


Figure 3.2.4.4: The process of crossover, or recombination, occurs when two homologous chromosomes align during meiosis and exchange a segment of genetic material. Here, the alleles for gene C were exchanged. The result is two recombinant and two non-recombinant chromosomes.

When two genes are located in close proximity on the same chromosome, they are considered linked, and their alleles tend to be transmitted through meiosis together. To exemplify this, imagine a dihybrid cross involving flower color and plant height in which the genes are next to each other on the chromosome. If one homologous chromosome has alleles for tall plants and red flowers, and the other chromosome has genes for short plants and yellow flowers, then when the gametes are formed, the tall and red alleles will go together into a gamete and the short and yellow alleles will go into other gametes. These are called the parental genotypes because they have been inherited intact from the parents of the individual producing gametes. But unlike if the genes were on different chromosomes, there will be no gametes with tall and yellow alleles and no gametes with short and red alleles. If you create the Punnett square with these gametes, you will see that the classical Mendelian prediction of a 9:3:3:1 outcome of a dihybrid cross would not apply. As the distance between two genes increases, the probability of one or more crossovers between them increases, and the genes behave more like they are on separate chromosomes. Geneticists have used the proportion of recombinant gametes (the ones not like the parents) as a measure of how far apart genes are on a chromosome. Using this information, they have constructed elaborate maps of genes on chromosomes for well-studied organisms, including humans.

Mendel's seminal publication makes no mention of linkage, and many researchers have questioned whether he encountered linkage but chose not to publish those crosses out of concern that they would invalidate his independent assortment postulate. The garden pea has seven chromosomes, and some have suggested that his choice of seven characteristics was not a coincidence. However, even if the genes he examined were not located on separate chromosomes, it is possible that he simply did not observe linkage because of the extensive shuffling effects of recombination.

Scientific Method Connection: Testing the Hypothesis of Independent Assortment

To better appreciate the amount of labor and ingenuity that went into Mendel's experiments, proceed through one of Mendel's dihybrid crosses.

Question: What will be the offspring of a dihybrid cross?

Background: Consider that pea plants mature in one growing season, and you have access to a large garden in which you can cultivate thousands of pea plants. There are several true-breeding plants with the following pairs of traits: tall plants with inflated pods, and dwarf plants with constricted pods. Before the plants have matured, you remove the pollen-producing organs from the tall/inflated plants in your crosses to prevent self-fertilization. Upon plant maturation, the plants are manually crossed by transferring pollen from the dwarf/constricted plants to the stigmata of the tall/inflated plants.

Hypothesis: Both trait pairs will sort independently according to Mendelian laws. When the true-breeding parents are crossed, all of the F_1 offspring are tall and have inflated pods, which indicates that the tall and inflated traits are dominant over the dwarf and constricted traits, respectively. A self-cross of the F_1 heterozygotes results in 2,000 F_2 progeny.

Test the hypothesis: Because each trait pair sorts independently, the ratios of tall:dwarf and inflated:constricted are each expected to be 3:1. The tall/dwarf trait pair is called *T/t*, and the inflated/constricted trait pair is designated *I/i*. Each member of the F_1 generation therefore has a genotype of *TtIi*. Construct a grid analogous to Figure 3.2.4.2, in which you cross two *TtIi* individuals. Each individual can donate four combinations of two traits: *TI*, *Ti*, *tI*, or *ti*, meaning that there are 16 possibilities of offspring genotypes. Because the *T* and *I* alleles are dominant, any individual having one or two of those alleles will express the tall or inflated phenotypes, respectively, regardless if they also have a *t* or *i* allele. Only individuals that are *tt* or *ii* will express the dwarf and constricted alleles, respectively. As shown in Figure 3.2.4.5, you predict that you will observe the following offspring proportions: tall/inflated:tall/constricted:dwarf/inflated:dwarf/constricted in a 9:3:3:1 ratio. Notice from the grid that when considering the tall/dwarf and inflated/constricted trait pairs in isolation, they are each inherited in 3:1 ratios.

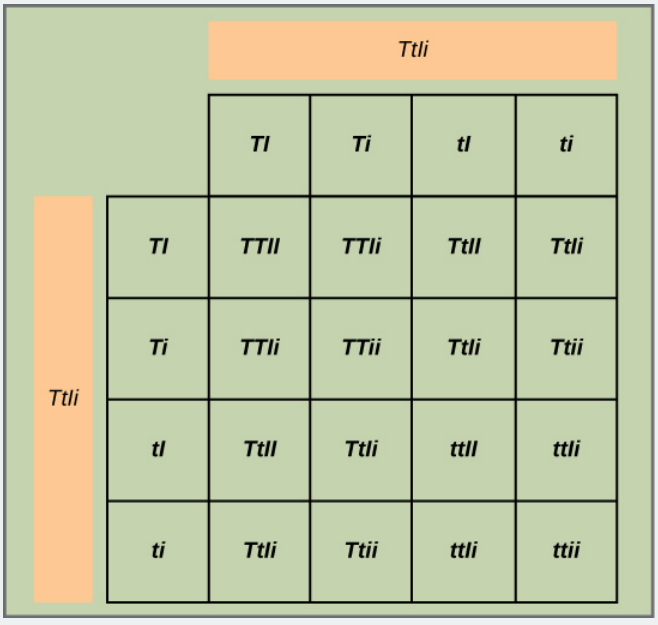


Figure 3.2.4.5: This figure shows all possible combinations of offspring resulting from a dihybrid cross of pea plants that are heterozygous for the tall/dwarf and inflated/constricted alleles.

Test the hypothesis: You cross the dwarf and tall plants and then self-cross the offspring. For best results, this is repeated with hundreds or even thousands of pea plants. What special precautions should be taken in the crosses and in growing the plants?

Analyze your data: You observe the following plant phenotypes in the F_2 generation: 2706 tall/inflated, 930 tall/constricted, 888 dwarf/inflated, and 300 dwarf/constricted. Reduce these findings to a ratio and determine if they are consistent with Mendelian laws.

> **Form a conclusion**: Were the results close to the expected 9:3:3:1 phenotypic ratio? Do the results support the prediction? What might be observed if far fewer plants were used, given that alleles segregate randomly into gametes? Try to imagine growing that many pea plants, and consider the potential for experimental error. For instance, what would happen if it was extremely windy one day?

Epistasis

Mendel's studies in pea plants implied that the sum of an individual's phenotype was controlled by genes (or as he called them, unit factors), such that every characteristic was distinctly and completely controlled by a single gene. In fact, single observable characteristics are almost always under the influence of multiple genes (each with two or more alleles) acting in unison. For example, at least eight genes contribute to eye color in humans.

In some cases, several genes can contribute to aspects of a common phenotype without their gene products ever directly interacting. In the case of organ development, for instance, genes may be expressed sequentially, with each gene adding to the complexity and specificity of the organ. Genes may function in complementary or synergistic fashions, such that two or more genes need to be expressed simultaneously to affect a phenotype. Genes may also oppose each other, with one gene modifying the expression of another.

In epistasis, the interaction between genes is antagonistic, such that one gene masks or interferes with the expression of another. "Epistasis" is a word composed of Greek roots that mean "standing upon." The alleles that are being masked or silenced are said to be hypostatic to the epistatic alleles that are doing the masking. Often the biochemical basis of epistasis is a gene pathway in which the expression of one gene is dependent on the function of a gene that precedes or follows it in the pathway.

An example of epistasis is pigmentation in mice. The wild-type coat color, agouti (*AA*), is dominant to solid-colored fur (*aa*). However, a separate gene (*C*) is necessary for pigment production. A mouse with a recessive *c* allele at this locus is unable to produce pigment and is albino regardless of the allele present at locus *A* (Figure 3.2.4.6). Therefore, the genotypes *AAcc*, *Aacc*, and *aacc* all produce the same albino phenotype. A cross between heterozygotes for both genes (*AaCc* x *AaCc*) would generate offspring with a phenotypic ratio of 9 agouti:3 solid color:4 albino (Figure 3.2.4.6). In this case, the *C* gene is epistatic to the *A* gene.

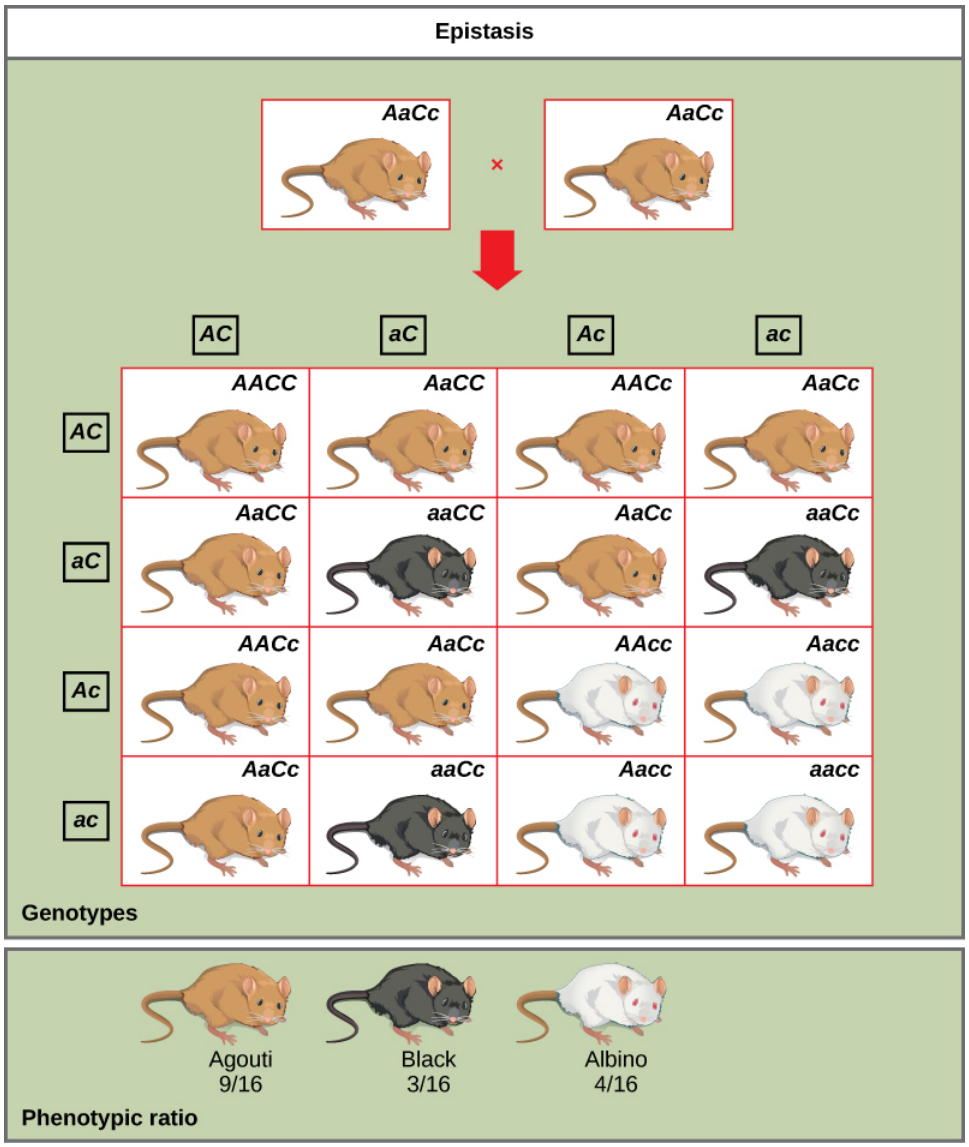


Figure 3.2.4.6: In mice, the mottled agouti coat color (*A*) is dominant to a solid coloration, such as black or gray. A gene at a separate locus (*C*) is responsible for pigment production. The recessive *c* allele does not produce pigment, and a mouse with the homozygous recessive *cc* genotype is albino regardless of the allele present at the *A* locus. Thus, the *C* gene is epistatic to the *A* gene.

Epistasis can also occur when a dominant allele masks expression at a separate gene. Fruit color in summer squash is expressed in this way. Homozygous recessive expression of the *W* gene (*ww*) coupled with homozygous dominant or heterozygous expression of the *Y* gene (*YY* or *Yy*) generates yellow fruit, and the *wwyy* genotype produces green fruit. However, if a dominant copy of the *W* gene is present in the homozygous or heterozygous form, the summer squash will produce white fruit regardless of the *Y* alleles. A cross between white heterozygotes for both genes (*WwYy* × *WwYy*) would produce offspring with a phenotypic ratio of 12 white:3 yellow:1 green.

Finally, epistasis can be reciprocal such that either gene, when present in the dominant (or recessive) form, expresses the same phenotype. In the shepherd's purse plant (*Capsella bursa-pastoris*), the characteristic of seed shape is controlled by two genes in a dominant epistatic relationship. When the genes *A* and *B* are both homozygous recessive (*aabb*), the seeds are ovoid. If the dominant allele for either of these genes is present, the result is triangular seeds. That is, every possible genotype other than *aabb* results in triangular seeds, and a cross between heterozygotes for both genes (*AaBb* x *AaBb*) would yield offspring with a phenotypic ratio of 15 triangular:1 ovoid.

As you work through genetics problems, keep in mind that any single characteristic that results in a phenotypic ratio that totals 16 is typical of a two-gene interaction. Recall the phenotypic inheritance pattern for Mendel's dihybrid cross, which considered two

non-interacting genes—9:3:3:1. Similarly, we would expect interacting gene pairs to also exhibit ratios expressed as 16 parts. Note that we are assuming the interacting genes are not linked; they are still assorting independently into gametes.

Epigenetics

Video



Summary

Mendel postulated that genes (characteristics) are inherited as pairs of alleles (traits) that behave in a dominant and recessive pattern. Alleles segregate into gametes such that each gamete is equally likely to receive either one of the two alleles present in a diploid individual. In addition, genes are assorted into gametes independently of one another. That is, alleles are generally not more likely to segregate into a gamete with a particular allele of another gene. A dihybrid cross demonstrates independent assortment when the genes in question are on different chromosomes or distant from each other on the same chromosome. For crosses involving more than two genes, use the forked line or probability methods to predict offspring genotypes and phenotypes rather than a Punnett square.

Although chromosomes sort independently into gametes during meiosis, Mendel's law of independent assortment refers to genes, not chromosomes, and a single chromosome may carry more than 1,000 genes. When genes are located in close proximity on the same chromosome, their alleles tend to be inherited together. This results in offspring ratios that violate Mendel's law of independent assortment. However, recombination serves to exchange genetic material on homologous chromosomes such that maternal and paternal alleles may be recombined on the same chromosome. This is why alleles on a given chromosome are not always inherited together. Recombination is a random event occurring anywhere on a chromosome. Therefore, genes that are far apart on the same chromosome are likely to still assort independently because of recombination events that occurred in the intervening chromosomal space.

Whether or not they are sorting independently, genes may interact at the level of gene products such that the expression of an allele for one gene masks or modifies the expression of an allele for a different gene. This is called epistasis.

Glossary

dihybrid
: result of a cross between two true-breeding parents that express different traits for two characteristics

epistasis
: antagonistic interaction between genes such that one gene masks or interferes with the expression of another

law of dominance
: in a heterozygote, one trait will conceal the presence of another trait for the same characteristic

law of independent assortment

genes do not influence each other with regard to sorting of alleles into gametes; every possible combination of alleles is equally likely to occur

law of segregation

paired unit factors (i.e., genes) segregate equally into gametes such that offspring have an equal likelihood of inheriting any combination of factors

linkage

phenomenon in which alleles that are located in close proximity to each other on the same chromosome are more likely to be inherited together

---

This page titled 3.2.4: Laws of Inheritance is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.3: Laws of Inheritance** by OpenStax is licensed CC BY 4.0.

3.2.E: Mendel's Experiments and Heredity (Exercises)

12.1: Mendel’s Experiments and the Laws of Probability

In 1865, Mendel presented the results of his experiments with nearly 30,000 pea plants to the local Natural History Society. He demonstrated that traits are transmitted faithfully from parents to offspring independently of other traits and in dominant and recessive patterns.

Review Questions

Mendel performed hybridizations by transferring pollen from the _____ of the male plant to the female ova.

A. anther
B. pistil
C. stigma
D. seed

Answer

A

Which is one of the seven characteristics that Mendel observed in pea plants?

A. flower size
B. seed texture
C. leaf shape
D. stem color

Answer

B

Imagine you are performing a cross involving seed color in garden pea plants. What F_1 offspring would you expect if you cross true-breeding parents with green seeds and yellow seeds? Yellow seed color is dominant over green.

A. 100 percent yellow-green seeds
B. 100 percent yellow seeds
C. 50 percent yellow, 50 percent green seeds
D. 25 percent green, 75 percent yellow seeds

Answer

B

Consider a cross to investigate the pea pod texture trait, involving constricted or inflated pods. Mendel found that the traits behave according to a dominant/recessive pattern in which inflated pods were dominant. If you performed this cross and obtained 650 inflated-pod plants in the F_2 generation, approximately how many constricted-pod plants would you expect to have?

A. 600
B. 165
C. 217
D. 468

Answer

C

Free Response

Describe one of the reasons why the garden pea was an excellent choice of model system for studying inheritance.

Answer

The garden pea is sessile and has flowers that close tightly during self-pollination. These features help to prevent accidental or unintentional fertilizations that could have diminished the accuracy of Mendel's data.

How would you perform a reciprocal cross for the characteristic of stem height in the garden pea?

Answer

Two sets of P_0 parents would be used. In the first cross, pollen would be transferred from a true-breeding tall plant to the stigma of a true-breeding dwarf plant. In the second cross, pollen would be transferred from a true-breeding dwarf plant to the stigma of a true-breeding tall plant. For each cross, F_1 and F_2 offspring would be analyzed to determine if offspring traits were affected according to which parent donated each trait.

12.2: Characteristics and Traits

The genetic makeup of peas consists of two similar or homologous copies of each chromosome, one from each parent. Each pair of homologous chromosomes has the same linear order of genes; hence peas are diploid organisms. The same is true for many other plants and for virtually all animals. Diploid organisms utilize meiosis to produce haploid gametes, which contain one copy of each homologous chromosome that unite at fertilization to create a diploid zygote.

Review Questions

The observable traits expressed by an organism are described as its _____.

A. phenotype
B. genotype
C. alleles
D. zygote

Answer

A

A recessive trait will be observed in individuals that are _____ for that trait.

A. heterozygous
B. homozygous or heterozygous
C. homozygous
D. diploid

Answer

C

If black and white true-breeding mice are mated and the result is all gray offspring, what inheritance pattern would this be indicative of?

A. dominance
B. codominance
C. multiple alleles

D. incomplete dominance

Answer

D

The ABO blood groups in humans are expressed as the I^A, I^B, and i alleles. The I^A allele encodes the A blood group antigen, I^B encodes B, and i encodes O. Both A and B are dominant to O. If a heterozygous blood type A parent (I^Ai) and a heterozygous blood type B parent (I^Bi) mate, one quarter of their offspring will have AB blood type (I^AI^B) in which both antigens are expressed equally. Therefore, ABO blood groups are an example of:

A. multiple alleles and incomplete dominance
B. codominance and incomplete dominance
C. incomplete dominance only
D. multiple alleles and codominance

Answer

D

In a mating between two individuals that are heterozygous for a recessive lethal allele that is expressed in utero, what genotypic ratio (homozygous dominant:heterozygous:homozygous recessive) would you expect to observe in the offspring?

A. 1:2:1
B. 3:1:1
C. 1:2:0
D. 0:2:1

Answer

C

Free Response

The gene for flower position in pea plants exists as axial or terminal alleles. Given that axial is dominant to terminal, list all of the possible F_1 and F_2 genotypes and phenotypes from a cross involving parents that are homozygous for each trait. Express genotypes with conventional genetic abbreviations.

Answer

Because axial is dominant, the gene would be designated as A. F_1 would be all heterozygous Aa with axial phenotype. F_2 would have possible genotypes of AA, Aa, and aa; these would correspond to axial, axial, and terminal phenotypes, respectively.

Use a Punnett square to predict the offspring in a cross between a dwarf pea plant (homozygous recessive) and a tall pea plant (heterozygous). What is the phenotypic ratio of the offspring?

Answer

The Punnett square would be 2 × 2 and will have T and T along the top, and T and t along the left side. Clockwise from the top left, the genotypes listed within the boxes will be Tt, Tt, tt, and tt. The phenotypic ratio will be 1 tall:1 dwarf.

Can a human male be a carrier of red-green color blindness?

Answer

No, males can only express color blindness. They cannot carry it because an individual needs two X chromosomes to be a carrier.

12.3: Laws of Inheritance

Mendel generalized the results of his pea-plant experiments into four postulates, some of which are sometimes called “laws,” that describe the basis of dominant and recessive inheritance in diploid organisms. As you have learned, more complex extensions of Mendelism exist that do not exhibit the same F2 phenotypic ratios (3:1). Nevertheless, these laws summarize the basics of classical genetics.

Multiple Choice

Assuming no gene linkage, in a dihybrid cross of *AABB* x *aabb* with *AaBb* F_1 heterozygotes, what is the ratio of the F_1 gametes (*AB*, *aB*, *Ab*, *ab*) that will give rise to the F_2 offspring?

A. 1:1:1:1
B. 1:3:3:1
C. 1:2:2:1
D. 4:3:2:1

Answer

A

The forked line and probability methods make use of what probability rule?

A. test cross
B. product rule
C. monohybrid rule
D. sum rule

Answer

B

How many different offspring genotypes are expected in a trihybrid cross between parents heterozygous for all three traits when the traits behave in a dominant and recessive pattern? How many phenotypes?

A. 64 genotypes; 16 phenotypes
B. 16 genotypes; 64 phenotypes
C. 8 genotypes; 27 phenotypes
D. 27 genotypes; 8 phenotypes

Answer

D

Free Response

Use the probability method to calculate the genotypes and genotypic proportions of a cross between *AABBCc* and *Aabbcc* parents.

Answer

Considering each gene separately, the cross at *A* will produce offspring of which half are *AA* and half are *Aa*; *B* will produce all *Bb*; *C* will produce half *Cc* and half *cc*. Proportions then are (1/2) × (1) × (1/2), or 1/4 *AABbCc*; continuing for the other possibilities yields 1/4 *AABbcc*, 1/4 *AaBbCc*, and 1/4 *AaBbcc*. The proportions therefore are 1:1:1:1.

Explain epistatis in terms of its Greek-language roots “standing upon.”

Answer

Epistasis describes an antagonistic interaction between genes wherein one gene masks or interferes with the expression of another. The gene that is interfering is referred to as epistatic, as if it is “standing upon” the other (hypostatic) gene to block its expression.

In Section 12.3, “Laws of Inheritance,” an example of epistasis was given for the summer squash. Cross white *WwYy* heterozygotes to prove the phenotypic ratio of 12 white:3 yellow:1 green that was given in the text.

Answer

The cross can be represented as a 4 × 4 Punnett square, with the following gametes for each parent: *WY*, *Wy*, *wY*, and *wy*. For all 12 of the offspring that express a dominant *W* gene, the offspring will be white. The three offspring that are homozygous recessive for *w* but express a dominant *Y* gene will be yellow. The remaining *wwyy* offspring will be green.

This page titled 3.2.E: Mendel's Experiments and Heredity (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.E: Mendel's Experiments and Heredity (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

3.3: Modern Understandings of Inheritance

The gene is the physical unit of inheritance, and genes are arranged in a linear order on chromosomes. The behaviors and interactions of chromosomes during meiosis explain, at a cellular level, the patterns of inheritance that we observe in populations. Genetic disorders involving alterations in chromosome number or structure may have dramatic effects and can prevent a fertilized egg from developing altogether.

3.3.1: Prelude to Modern Understandings of Inheritance

3.3.2: Chromosomal Theory and Genetic Linkage

3.3.3: Chromosomal Basis of Inherited Disorders

3.3.E: Modern Understandings of Inheritance (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.3: Modern Understandings of Inheritance is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.3.1: Prelude to Modern Understandings of Inheritance

The gene is the physical unit of inheritance, and genes are arranged in a linear order on chromosomes. The behaviors and interactions of chromosomes during meiosis explain, at a cellular level, the patterns of inheritance that we observe in populations. Genetic disorders involving alterations in chromosome number or structure may have dramatic effects and can prevent a fertilized egg from developing altogether.

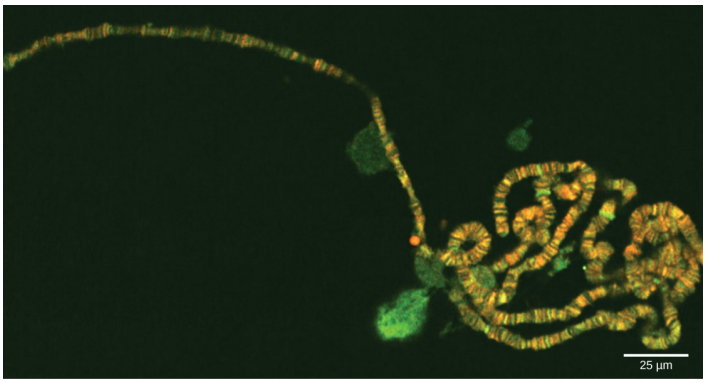


Figure 3.3.1.1: Chromosomes are threadlike nuclear structures consisting of DNA and proteins that serve as the repositories for genetic information. The chromosomes depicted here were isolated from a fruit fly's salivary gland, stained with dye, and visualized under a microscope. Akin to miniature bar codes, chromosomes absorb different dyes to produce characteristic banding patterns, which allows for their routine identification. (credit: modification of work by "LPLT"/Wikimedia Commons; scale-bar data from Matt Russell)

Video



This page titled 3.3.1: Prelude to Modern Understandings of Inheritance is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **13.0: Prelude to Modern Understandings of Inheritance** by OpenStax is licensed CC BY 4.0.

3.3.2: Chromosomal Theory and Genetic Linkage

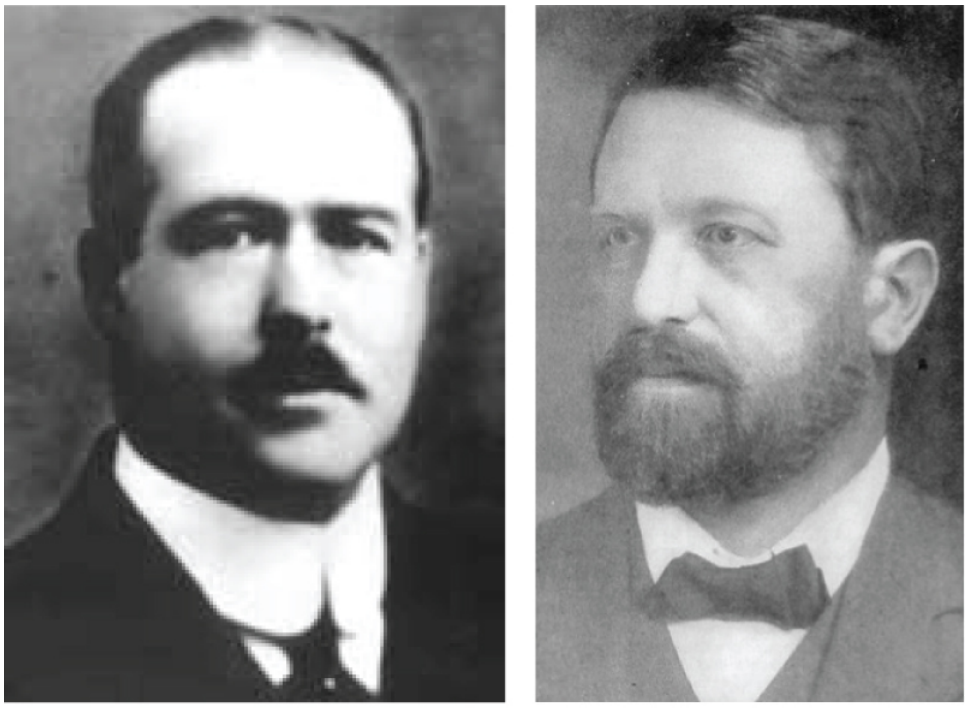
Skills to Develop

- Discuss Sutton's Chromosomal Theory of Inheritance
- Describe genetic linkage
- Explain the process of homologous recombination, or crossing over
- Describe how chromosome maps are created
- Calculate the distances between three genes on a chromosome using a three-point test cross

Long before chromosomes were visualized under a microscope, the father of modern genetics, Gregor Mendel, began studying heredity in 1843. With the improvement of microscopic techniques during the late 1800s, cell biologists could stain and visualize subcellular structures with dyes and observe their actions during cell division and meiosis. With each mitotic division, chromosomes replicated, condensed from an amorphous (no constant shape) nuclear mass into distinct X-shaped bodies (pairs of identical sister chromatids), and migrated to separate cellular poles.

Chromosomal Theory of Inheritance

The speculation that chromosomes might be the key to understanding heredity led several scientists to examine Mendel's publications and re-evaluate his model in terms of the behavior of chromosomes during mitosis and meiosis. In 1902, Theodor Boveri observed that proper embryonic development of sea urchins does not occur unless chromosomes are present. That same year, Walter Sutton observed the separation of chromosomes into daughter cells during meiosis (Figure 3.3.2.1). Together, these observations led to the development of the Chromosomal Theory of Inheritance, which identified chromosomes as the genetic material responsible for Mendelian inheritance.



(a) (b)

Figure 3.3.2.1: (a) Walter Sutton and (b) Theodor Boveri are credited with developing the Chromosomal Theory of Inheritance, which states that chromosomes carry the unit of heredity (genes).

The Chromosomal Theory of Inheritance was consistent with Mendel's laws and was supported by the following observations:

- During meiosis, homologous chromosome pairs migrate as discrete structures that are independent of other chromosome pairs.
- The sorting of chromosomes from each homologous pair into pre-gametes appears to be random.

- Each parent synthesizes gametes that contain only half of their chromosomal complement.
- Even though male and female gametes (sperm and egg) differ in size and morphology, they have the same number of chromosomes, suggesting equal genetic contributions from each parent.
- The gametic chromosomes combine during fertilization to produce offspring with the same chromosome number as their parents.

Despite compelling correlations between the behavior of chromosomes during meiosis and Mendel's abstract laws, the Chromosomal Theory of Inheritance was proposed long before there was any direct evidence that traits were carried on chromosomes. Critics pointed out that individuals had far more independently segregating traits than they had chromosomes. It was only after several years of carrying out crosses with the fruit fly, *Drosophila melanogaster*, that Thomas Hunt Morgan provided experimental evidence to support the Chromosomal Theory of Inheritance.

Genetic Linkage and Distances

Mendel's work suggested that traits are inherited independently of each other. Morgan identified a 1:1 correspondence between a segregating trait and the X chromosome, suggesting that the random segregation of chromosomes was the physical basis of Mendel's model. This also demonstrated that linked genes disrupt Mendel's predicted outcomes. The fact that each chromosome can carry many linked genes explains how individuals can have many more traits than they have chromosomes. However, observations by researchers in Morgan's laboratory suggested that alleles positioned on the same chromosome were not always inherited together. During meiosis, linked genes somehow became unlinked.

Homologous Recombination

In 1909, Frans Janssen observed chiasmata—the point at which chromatids are in contact with each other and may exchange segments—prior to the first division of meiosis. He suggested that alleles become unlinked and chromosomes physically exchange segments. As chromosomes condensed and paired with their homologs, they appeared to interact at distinct points. Janssen suggested that these points corresponded to regions in which chromosome segments were exchanged. It is now known that the pairing and interaction between homologous chromosomes, known as synapsis, does more than simply organize the homologs for migration to separate daughter cells. When synapsed, homologous chromosomes undergo reciprocal physical exchanges at their arms in a process called homologous recombination, or more simply, "crossing over."

To better understand the type of experimental results that researchers were obtaining at this time, consider a heterozygous individual that inherited dominant maternal alleles for two genes on the same chromosome (such as *AB*) and two recessive paternal alleles for those same genes (such as *ab*). If the genes are linked, one would expect this individual to produce gametes that are either *AB* or *ab* with a 1:1 ratio. If the genes are unlinked, the individual should produce *AB*, *Ab*, *aB*, and *ab* gametes with equal frequencies, according to the Mendelian concept of independent assortment. Because they correspond to new allele combinations, the genotypes Ab and aB are nonparental types that result from homologous recombination during meiosis. Parental types are progeny that exhibit the same allelic combination as their parents. Morgan and his colleagues, however, found that when such heterozygous individuals were test crossed to a homozygous recessive parent (*AaBb* × *aabb*), both parental and nonparental cases occurred. For example, 950 offspring might be recovered that were either *AaBb* or *aabb*, but 50 offspring would also be obtained that were either *Aabb* or *aaBb*. These results suggested that linkage occurred most often, but a significant minority of offspring were the products of recombination.

Art Connection

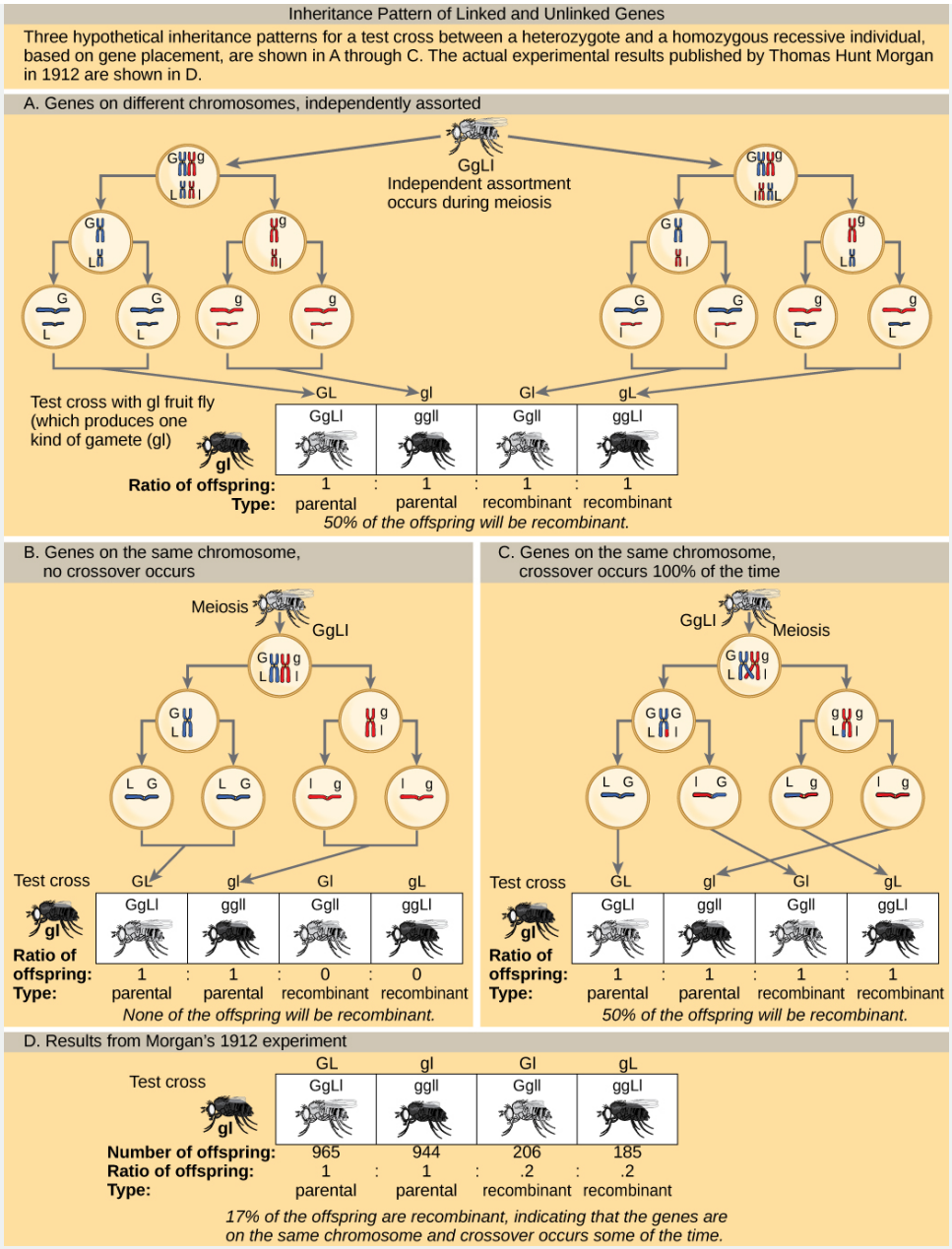


Figure 3.3.2.2: Inheritance patterns of unlinked and linked genes are shown. In (a), two genes are located on different chromosomes so independent assortment occurs during meiosis. The offspring have an equal chance of being the parental type (inheriting the same combination of traits as the parents) or a nonparental type (inheriting a different combination of traits than the parents). In (b), two genes are very close together on the same chromosome so that no crossing over occurs between them. The genes are therefore always inherited together and all of the offspring are the parental type. In (c), two genes are far apart on the chromosome such that crossing over occurs during every meiotic event. The recombination frequency will be the same as if the genes were on separate chromosomes. (d) The actual recombination frequency of fruit fly wing length and body color that Thomas Morgan observed in 1912 was 17 percent. A crossover frequency between 0 percent and 50 percent indicates that the genes are on the same chromosome and crossover occurs some of the time.

In a test cross for two characteristics such as the one shown here, can the predicted frequency of recombinant offspring be 60 percent? Why or why not?

Genetic Maps

Janssen did not have the technology to demonstrate crossing over so it remained an abstract idea that was not widely accepted. Scientists thought chiasmata were a variation on synapsis and could not understand how chromosomes could break and rejoin. Yet,

the data were clear that linkage did not always occur. Ultimately, it took a young undergraduate student and an “all-nighter” to mathematically elucidate the problem of linkage and recombination.

In 1913, Alfred Sturtevant, a student in Morgan’s laboratory, gathered results from researchers in the laboratory, and took them home one night to mull them over. By the next morning, he had created the first “chromosome map,” a linear representation of gene order and relative distance on a chromosome (Figure 13.1.3).

Art Connection

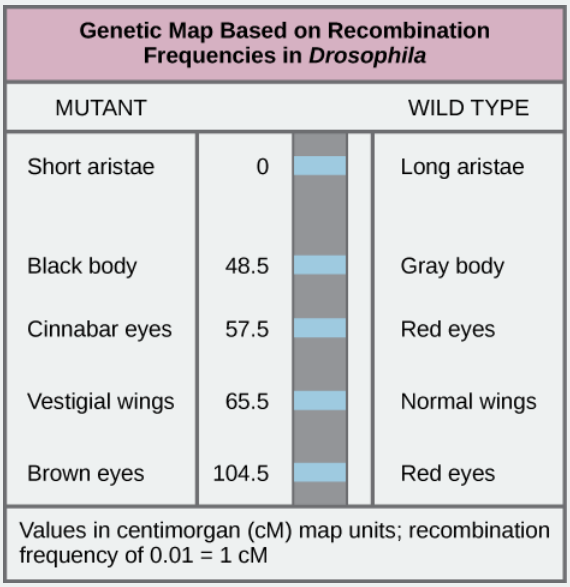


Figure 3.3.2.3: This genetic map orders *Drosophila* genes on the basis of recombination frequency.

Which of the following statements is true?

A. Recombination of the body color and red/cinnabar eye alleles will occur more frequently than recombination of the alleles for wing length and aristae length.
B. Recombination of the body color and aristae length alleles will occur more frequently than recombination of red/brown eye alleles and the aristae length alleles.
C. Recombination of the gray/black body color and long/short aristae alleles will not occur.
D. Recombination of the red/brown eye and long/short aristae alleles will occur more frequently than recombination of the alleles for wing length and body color.

As shown in Figure 3.3.2.3, by using recombination frequency to predict genetic distance, the relative order of genes on chromosome 2 could be inferred. The values shown represent map distances in centimorgans (cM), which correspond to recombination frequencies (in percent). Therefore, the genes for body color and wing size were 65.5 − 48.5 = 17 cM apart, indicating that the maternal and paternal alleles for these genes recombine in 17 percent of offspring, on average.

To construct a chromosome map, Sturtevant assumed that genes were ordered serially on threadlike chromosomes. He also assumed that the incidence of recombination between two homologous chromosomes could occur with equal likelihood anywhere along the length of the chromosome. Operating under these assumptions, Sturtevant postulated that alleles that were far apart on a chromosome were more likely to dissociate during meiosis simply because there was a larger region over which recombination could occur. Conversely, alleles that were close to each other on the chromosome were likely to be inherited together. The average number of crossovers between two alleles—that is, their recombination frequency—correlated with their genetic distance from each other, relative to the locations of other genes on that chromosome. Considering the example cross between *AaBb* and *aabb* above, the frequency of recombination could be calculated as 50/1000 = 0.05. That is, the likelihood of a crossover between genes *A/a* and *B/b* was 0.05, or 5 percent. Such a result would indicate that the genes were definitively linked, but that they were far enough apart for crossovers to occasionally occur. Sturtevant divided his genetic map into map units, or centimorgans (cM), in which a recombination frequency of 0.01 corresponds to 1 cM.

By representing alleles in a linear map, Sturtevant suggested that genes can range from being perfectly linked (recombination frequency = 0) to being perfectly unlinked (recombination frequency = 0.5) when genes are on different chromosomes or genes are separated very far apart on the same chromosome. Perfectly unlinked genes correspond to the frequencies predicted by Mendel to assort independently in a dihybrid cross. A recombination frequency of 0.5 indicates that 50 percent of offspring are recombinants and the other 50 percent are parental types. That is, every type of allele combination is represented with equal frequency. This representation allowed Sturtevant to additively calculate distances between several genes on the same chromosome. However, as the genetic distances approached 0.50, his predictions became less accurate because it was not clear whether the genes were very far apart on the same chromosome or on different chromosomes.

In 1931, Barbara McClintock and Harriet Creighton demonstrated the crossover of homologous chromosomes in corn plants. Weeks later, homologous recombination in *Drosophila* was demonstrated microscopically by Curt Stern. Stern observed several X-linked phenotypes that were associated with a structurally unusual and dissimilar X chromosome pair in which one X was missing a small terminal segment, and the other X was fused to a piece of the Y chromosome. By crossing flies, observing their offspring, and then visualizing the offspring's chromosomes, Stern demonstrated that every time the offspring allele combination deviated from either of the parental combinations, there was a corresponding exchange of an X chromosome segment. Using mutant flies with structurally distinct X chromosomes was the key to observing the products of recombination because DNA sequencing and other molecular tools were not yet available. It is now known that homologous chromosomes regularly exchange segments in meiosis by reciprocally breaking and rejoining their DNA at precise locations.

Link to Learning

Review Sturtevant's process to create a genetic map on the basis of recombination frequencies here.

Mendel's Mapped Traits

Homologous recombination is a common genetic process, yet Mendel never observed it. Had he investigated both linked and unlinked genes, it would have been much more difficult for him to create a unified model of his data on the basis of probabilistic calculations. Researchers who have since mapped the seven traits investigated by Mendel onto the seven chromosomes of the pea plant genome have confirmed that all of the genes he examined are either on separate chromosomes or are sufficiently far apart as to be statistically unlinked. Some have suggested that Mendel was enormously lucky to select only unlinked genes, whereas others question whether Mendel discarded any data suggesting linkage. In any case, Mendel consistently observed independent assortment because he examined genes that were effectively unlinked.

Summary

The Chromosomal Theory of inheritance, proposed by Sutton and Boveri, states that chromosomes are the vehicles of genetic heredity. Neither Mendelian genetics nor gene linkage is perfectly accurate; instead, chromosome behavior involves segregation, independent assortment, and occasionally, linkage. Sturtevant devised a method to assess recombination frequency and infer the relative positions and distances of linked genes on a chromosome on the basis of the average number of crossovers in the intervening region between the genes. Sturtevant correctly presumed that genes are arranged in serial order on chromosomes and that recombination between homologs can occur anywhere on a chromosome with equal likelihood. Whereas linkage causes alleles on the same chromosome to be inherited together, homologous recombination biases alleles toward an inheritance pattern of independent assortment.

Art Connections

Figure 3.3.2.2: In a test cross for two characteristics such as the one shown here, can the predicted frequency of recombinant offspring be 60 percent? Why or why not?

Answer

No. The predicted frequency of recombinant offspring ranges from 0% (for linked traits) to 50% (for unlinked traits).

Figure 3.3.2.3: Which of the following statements is true?

A. Recombination of the body color and red/cinnabar eye alleles will occur more frequently than recombination of the alleles for wing length and aristae length.
B. Recombination of the body color and aristae length alleles will occur more frequently than recombination of red/brown eye alleles and the aristae length alleles.
C. Recombination of the gray/black body color and long/short aristae alleles will not occur.
D. Recombination of the red/brown eye and long/short aristae alleles will occur more frequently than recombination of the alleles for wing length and body color.

Answer

D

Glossary

centimorgan (cM)
(also, map unit) relative distance that corresponds to a recombination frequency of 0.01

Chromosomal Theory of Inheritance
theory proposing that chromosomes are the vehicles of genes and that their behavior during meiosis is the physical basis of the inheritance patterns that Mendel observed

homologous recombination
process by which homologous chromosomes undergo reciprocal physical exchanges at their arms, also known as crossing over

nonparental (recombinant) type
progeny resulting from homologous recombination that exhibits a different allele combination compared with its parents

parental types
progeny that exhibits the same allelic combination as its parents

recombination frequency
average number of crossovers between two alleles; observed as the number of nonparental types in a population of progeny

This page titled 3.3.2: Chromosomal Theory and Genetic Linkage is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **13.1: Chromosomal Theory and Genetic Linkage** by OpenStax is licensed CC BY 4.0.

3.3.3: Chromosomal Basis of Inherited Disorders

Skills to Develop

- Describe how a karyogram is created
- Explain how nondisjunction leads to disorders in chromosome number
- Compare disorders caused by aneuploidy
- Describe how errors in chromosome structure occur through inversions and translocations

Inherited disorders can arise when chromosomes behave abnormally during meiosis. Chromosome disorders can be divided into two categories: abnormalities in chromosome number and chromosomal structural rearrangements. Because even small segments of chromosomes can span many genes, chromosomal disorders are characteristically dramatic and often fatal.

Identification of Chromosomes

The isolation and microscopic observation of chromosomes forms the basis of cytogenetics and is the primary method by which clinicians detect chromosomal abnormalities in humans. A karyotype is the number and appearance of chromosomes, and includes their length, banding pattern, and centromere position. To obtain a view of an individual's karyotype, cytologists photograph the chromosomes and then cut and paste each chromosome into a chart, or karyogram, also known as an ideogram (Figure 3.3.3.1).

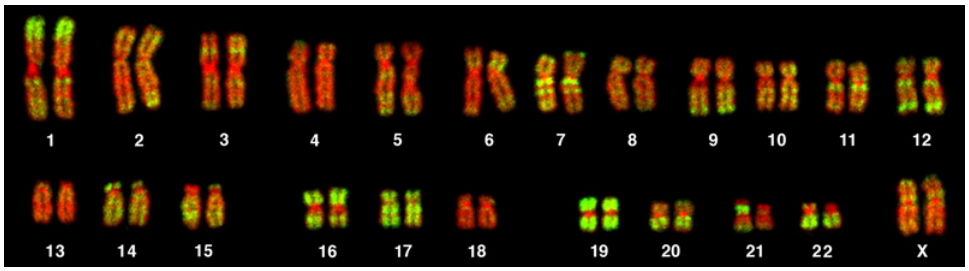


Figure 3.3.3.1: This karyotype is of a female human. Notice that homologous chromosomes are the same size, and have the same centromere positions and banding patterns. A human male would have an XY chromosome pair instead of the XX pair shown. (credit: Andreas Blozer et al)

In a given species, chromosomes can be identified by their number, size, centromere position, and banding pattern. In a human karyotype, autosomes or "body chromosomes" (all of the non–sex chromosomes) are generally organized in approximate order of size from largest (chromosome 1) to smallest (chromosome 22). The X and Y chromosomes are not autosomes. However, chromosome 21 is actually shorter than chromosome 22. This was discovered after the naming of Down syndrome as trisomy 21, reflecting how this disease results from possessing one extra chromosome 21 (three total). Not wanting to change the name of this important disease, chromosome 21 retained its numbering, despite describing the shortest set of chromosomes. The chromosome "arms" projecting from either end of the centromere may be designated as short or long, depending on their relative lengths. The short arm is abbreviated *p* (for "petite"), whereas the long arm is abbreviated *q* (because it follows "p" alphabetically). Each arm is further subdivided and denoted by a number. Using this naming system, locations on chromosomes can be described consistently in the scientific literature.

Career Connection: Geneticists Use Karyograms to Identify Chromosomal Aberrations

Although Mendel is referred to as the "father of modern genetics," he performed his experiments with none of the tools that the geneticists of today routinely employ. One such powerful cytological technique is karyotyping, a method in which traits characterized by chromosomal abnormalities can be identified from a single cell. To observe an individual's karyotype, a person's cells (like white blood cells) are first collected from a blood sample or other tissue. In the laboratory, the isolated cells are stimulated to begin actively dividing. A chemical called colchicine is then applied to cells to arrest condensed chromosomes in metaphase. Cells are then made to swell using a hypotonic solution so the chromosomes spread apart. Finally, the sample is preserved in a fixative and applied to a slide.

The geneticist then stains chromosomes with one of several dyes to better visualize the distinct and reproducible banding patterns of each chromosome pair. Following staining, the chromosomes are viewed using bright-field microscopy. A common

stain choice is the Giemsa stain. Giemsa staining results in approximately 400–800 bands (of tightly coiled DNA and condensed proteins) arranged along all of the 23 chromosome pairs; an experienced geneticist can identify each band. In addition to the banding patterns, chromosomes are further identified on the basis of size and centromere location. To obtain the classic depiction of the karyotype in which homologous pairs of chromosomes are aligned in numerical order from longest to shortest, the geneticist obtains a digital image, identifies each chromosome, and manually arranges the chromosomes into this pattern (Figure 3.3.3.1).

At its most basic, the karyogram may reveal genetic abnormalities in which an individual has too many or too few chromosomes per cell. Examples of this are Down Syndrome, which is identified by a third copy of chromosome 21, and Turner Syndrome, which is characterized by the presence of only one X chromosome in women instead of the normal two. Geneticists can also identify large deletions or insertions of DNA. For instance, Jacobsen Syndrome—which involves distinctive facial features as well as heart and bleeding defects—is identified by a deletion on chromosome 11. Finally, the karyotype can pinpoint translocations, which occur when a segment of genetic material breaks from one chromosome and reattaches to another chromosome or to a different part of the same chromosome. Translocations are implicated in certain cancers, including chronic myelogenous leukemia.

During Mendel's lifetime, inheritance was an abstract concept that could only be inferred by performing crosses and observing the traits expressed by offspring. By observing a karyogram, today's geneticists can actually visualize the chromosomal composition of an individual to confirm or predict genetic abnormalities in offspring, even before birth.

Disorders in Chromosome Number

Of all of the chromosomal disorders, abnormalities in chromosome number are the most obviously identifiable from a karyogram. Disorders of chromosome number include the duplication or loss of entire chromosomes, as well as changes in the number of complete sets of chromosomes. They are caused by nondisjunction, which occurs when pairs of homologous chromosomes or sister chromatids fail to separate during meiosis. Misaligned or incomplete synapsis, or a dysfunction of the spindle apparatus that facilitates chromosome migration, can cause nondisjunction. The risk of nondisjunction occurring increases with the age of the parents.

Nondisjunction can occur during either meiosis I or II, with differing results (Figure 3.3.3.2). If homologous chromosomes fail to separate during meiosis I, the result is two gametes that lack that particular chromosome and two gametes with two copies of the chromosome. If sister chromatids fail to separate during meiosis II, the result is one gamete that lacks that chromosome, two normal gametes with one copy of the chromosome, and one gamete with two copies of the chromosome.

Art Connection

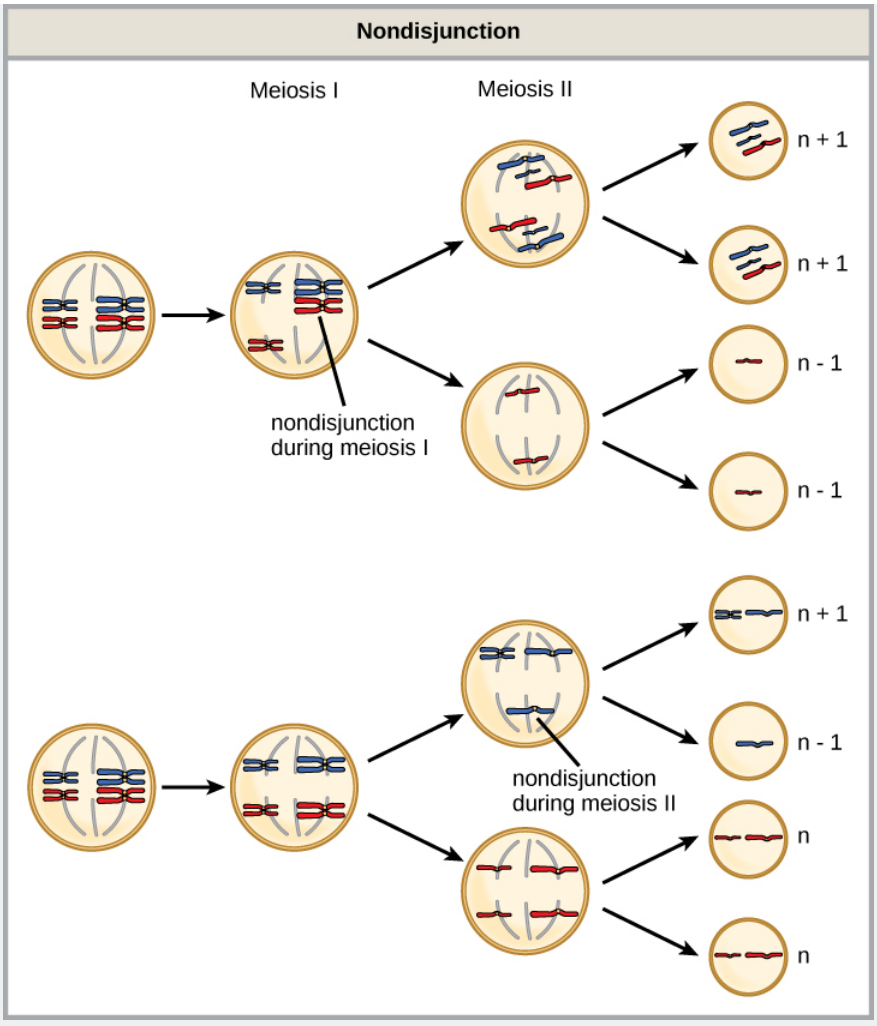


Figure 3.3.3.2: Nondisjunction occurs when homologous chromosomes or sister chromatids fail to separate during meiosis, resulting in an abnormal chromosome number. Nondisjunction may occur during meiosis I or meiosis II.

Which of the following statements about nondisjunction is true?

A. Nondisjunction only results in gametes with n+1 or n–1 chromosomes.
B. Nondisjunction occurring during meiosis II results in 50 percent normal gametes.
C. Nondisjunction during meiosis I results in 50 percent normal gametes.
D. Nondisjunction always results in four different kinds of gametes.

Aneuploidy

An individual with the appropriate number of chromosomes for their species is called euploid; in humans, euploidy corresponds to 22 pairs of autosomes and one pair of sex chromosomes. An individual with an error in chromosome number is described as aneuploid, a term that includes monosomy (loss of one chromosome) or trisomy (gain of an extraneous chromosome). Monosomic human zygotes missing any one copy of an autosome invariably fail to develop to birth because they lack essential genes. This underscores the importance of “gene dosage” in humans. Most autosomal trisomies also fail to develop to birth; however, duplications of some of the smaller chromosomes (13, 15, 18, 21, or 22) can result in offspring that survive for several weeks to many years. Trisomic individuals suffer from a different type of genetic imbalance: an excess in gene dose. Individuals with an extra chromosome may synthesize an abundance of the gene products encoded by that chromosome. This extra dose (150 percent) of specific genes can lead to a number of functional challenges and often precludes development. The most common trisomy among viable births is that of chromosome 21, which corresponds to Down Syndrome. Individuals with this inherited disorder are characterized by short stature and stunted digits, facial distinctions that include a broad skull and large tongue, and significant

developmental delays. The incidence of Down syndrome is correlated with maternal age; older women are more likely to become pregnant with fetuses carrying the trisomy 21 genotype (Figure 3.3.3.3).

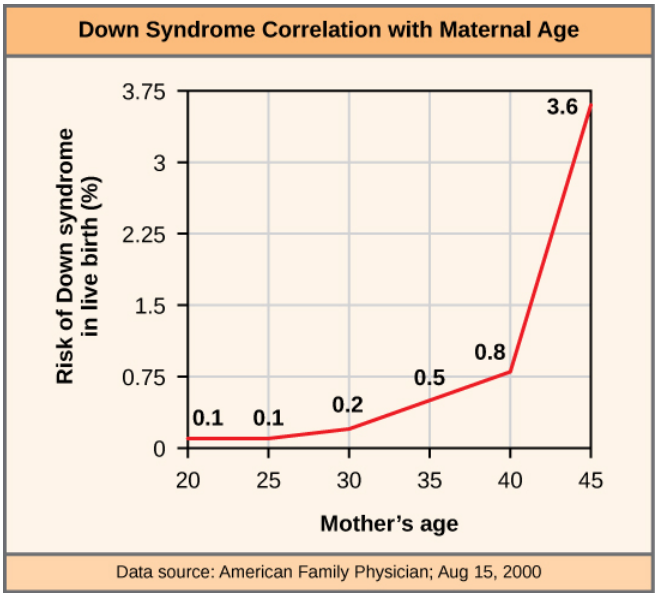


Figure 3.3.3.3: The incidence of having a fetus with trisomy 21 increases dramatically with maternal age.

Link to Learning



Visualize the addition of a chromosome that leads to Down syndrome in this video simulation.

Polyploidy

An individual with more than the correct number of chromosome sets (two for diploid species) is called polyploid. For instance, fertilization of an abnormal diploid egg with a normal haploid sperm would yield a triploid zygote. Polyploid animals are extremely rare, with only a few examples among the flatworms, crustaceans, amphibians, fish, and lizards. Polyploid animals are sterile because meiosis cannot proceed normally and instead produces mostly aneuploid daughter cells that cannot yield viable zygotes. Rarely, polyploid animals can reproduce asexually by haplodiploidy, in which an unfertilized egg divides mitotically to produce offspring. In contrast, polyploidy is very common in the plant kingdom, and polyploid plants tend to be larger and more robust than euploids of their species (Figure 3.3.3.4).



Figure 3.3.3.4: As with many polyploid plants, this triploid orange daylily (*Hemerocallis fulva*) is particularly large and robust, and grows flowers with triple the number of petals of its diploid counterparts. (credit: Steve Karg)

Sex Chromosome Nondisjunction in Humans

Humans display dramatic deleterious effects with autosomal trisomies and monosomies. Therefore, it may seem counterintuitive that human females and males can function normally, despite carrying different numbers of the X chromosome. Rather than a gain or loss of autosomes, variations in the number of sex chromosomes are associated with relatively mild effects. In part, this occurs because of a molecular process called X inactivation. Early in development, when female mammalian embryos consist of just a few thousand cells (relative to trillions in the newborn), one X chromosome in each cell inactivates by tightly condensing into a quiescent (dormant) structure called a Barr body. The chance that an X chromosome (maternally or paternally derived) is inactivated in each cell is random, but once the inactivation occurs, all cells derived from that one will have the same inactive X chromosome or Barr body. By this process, females compensate for their double genetic dose of X chromosome. In so-called "tortoiseshell" cats, embryonic X inactivation is observed as color variegation (Figure 3.3.3.5). Females that are heterozygous for an X-linked coat color gene will express one of two different coat colors over different regions of their body, corresponding to whichever X chromosome is inactivated in the embryonic cell progenitor of that region.



Figure 3.3.3.5: In cats, the gene for coat color is located on the X chromosome. In the embryonic development of female cats, one of the two X chromosomes is randomly inactivated in each cell, resulting in a tortoiseshell pattern if the cat has two different alleles for coat color. Male cats, having only one X chromosome, never exhibit a tortoiseshell coat color. (credit: Michael Bodega)

An individual carrying an abnormal number of X chromosomes will inactivate all but one X chromosome in each of her cells. However, even inactivated X chromosomes continue to express a few genes, and X chromosomes must reactivate for the proper maturation of female ovaries. As a result, X-chromosomal abnormalities are typically associated with mild mental and physical defects, as well as sterility. If the X chromosome is absent altogether, the individual will not develop in utero.

Several errors in sex chromosome number have been characterized. Individuals with three X chromosomes, called triplo-X, are phenotypically female but express developmental delays and reduced fertility. The XXY genotype, corresponding to one type of Klinefelter syndrome, corresponds to phenotypically male individuals with small testes, enlarged breasts, and reduced body hair. More complex types of Klinefelter syndrome exist in which the individual has as many as five X chromosomes. In all types, every X chromosome except one undergoes inactivation to compensate for the excess genetic dosage. This can be seen as several Barr bodies in each cell nucleus. Turner syndrome, characterized as an X0 genotype (i.e., only a single sex chromosome), corresponds to a phenotypically female individual with short stature, webbed skin in the neck region, hearing and cardiac impairments, and sterility.

Duplications and Deletions

In addition to the loss or gain of an entire chromosome, a chromosomal segment may be duplicated or lost. Duplications and deletions often produce offspring that survive but exhibit physical and mental abnormalities. Duplicated chromosomal segments may fuse to existing chromosomes or may be free in the nucleus. Cri-du-chat (from the French for “cry of the cat”) is a syndrome associated with nervous system abnormalities and identifiable physical features that result from a deletion of most of 5p (the small arm of chromosome 5) (Figure 3.3.3.6). Infants with this genotype emit a characteristic high-pitched cry on which the disorder’s name is based.

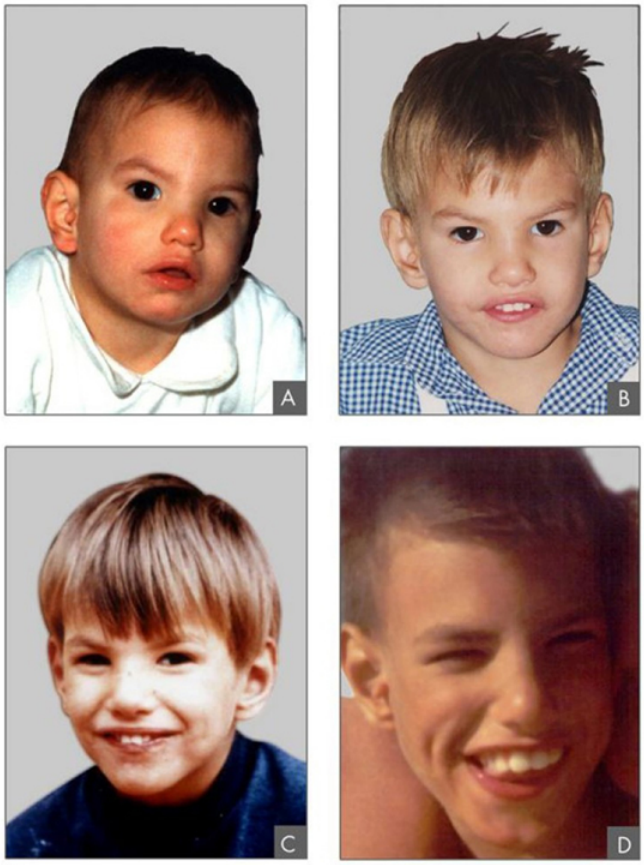


Figure 3.3.3.6: This individual with cri-du-chat syndrome is shown at two, four, nine, and 12 years of age. (credit: Paola Cerruti Mainardi)

Chromosomal Structural Rearrangements

Cytologists have characterized numerous structural rearrangements in chromosomes, but chromosome inversions and translocations are the most common. Both are identified during meiosis by the adaptive pairing of rearranged chromosomes with their former homologs to maintain appropriate gene alignment. If the genes carried on two homologs are not oriented correctly, a recombination event could result in the loss of genes from one chromosome and the gain of genes on the other. This would produce aneuploid gametes.

Chromosome Inversions

A chromosome inversion is the detachment, 180° rotation, and reinsertion of part of a chromosome. Inversions may occur in nature as a result of mechanical shear, or from the action of transposable elements (special DNA sequences capable of facilitating the rearrangement of chromosome segments with the help of enzymes that cut and paste DNA sequences). Unless they disrupt a gene sequence, inversions only change the orientation of genes and are likely to have more mild effects than aneuploid errors. However, altered gene orientation can result in functional changes because regulators of gene expression could be moved out of position with respect to their targets, causing aberrant levels of gene products.

An inversion can be pericentric and include the centromere, or paracentric and occur outside of the centromere (). A pericentric inversion that is asymmetric about the centromere can change the relative lengths of the chromosome arms, making these inversions easily identifiable.

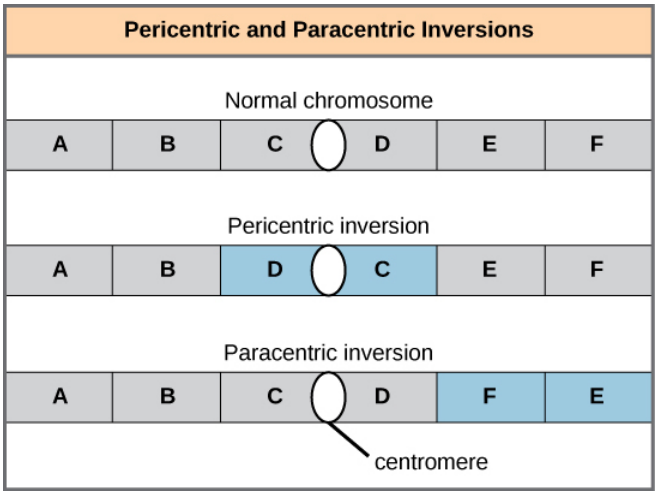


Figure 3.3.3.7: Pericentric inversions include the centromere, and paracentric inversions do not. A pericentric inversion can change the relative lengths of the chromosome arms; a paracentric inversion cannot.

When one homologous chromosome undergoes an inversion but the other does not, the individual is described as an inversion heterozygote. To maintain point-for-point synapsis during meiosis, one homolog must form a loop, and the other homolog must mold around it. Although this topology can ensure that the genes are correctly aligned, it also forces the homologs to stretch and can be associated with regions of imprecise synapsis (Figure 3.3.3.8).

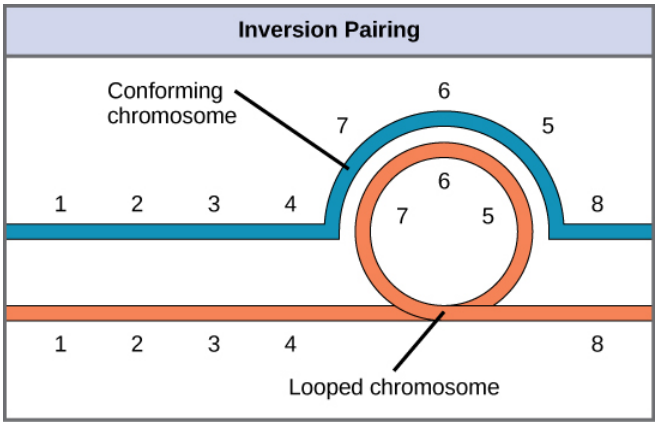


Figure 3.3.3.8: When one chromosome undergoes an inversion but the other does not, one chromosome must form an inverted loop to retain point-for-point interaction during synapsis. This inversion pairing is essential to maintaining gene alignment during meiosis and to allow for recombination.

Evolution Connection: The Chromosome 18 Inversion

Not all structural rearrangements of chromosomes produce nonviable, impaired, or infertile individuals. In rare instances, such a change can result in the evolution of a new species. In fact, a pericentric inversion in chromosome 18 appears to have contributed to the evolution of humans. This inversion is not present in our closest genetic relatives, the chimpanzees. Humans and chimpanzees differ cytogenetically by pericentric inversions on several chromosomes and by the fusion of two separate chromosomes in chimpanzees that correspond to chromosome two in humans.

The pericentric chromosome 18 inversion is believed to have occurred in early humans following their divergence from a common ancestor with chimpanzees approximately five million years ago. Researchers characterizing this inversion have suggested that approximately 19,000 nucleotide bases were duplicated on 18p, and the duplicated region inverted and reinserted on chromosome 18 of an ancestral human.

A comparison of human and chimpanzee genes in the region of this inversion indicates that two genes—*ROCK1* and *USP14*—that are adjacent on chimpanzee chromosome 17 (which corresponds to human chromosome 18) are more distantly positioned on human chromosome 18. This suggests that one of the inversion breakpoints occurred between these two genes. Interestingly, humans and chimpanzees express *USP14* at distinct levels in specific cell types, including cortical cells and

fibroblasts. Perhaps the chromosome 18 inversion in an ancestral human repositioned specific genes and reset their expression levels in a useful way. Because both *ROCK1* and *USP14* encode cellular enzymes, a change in their expression could alter cellular function. It is not known how this inversion contributed to hominid evolution, but it appears to be a significant factor in the divergence of humans from other primates.[1]

Translocations

A translocation occurs when a segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome. Translocations can be benign or have devastating effects depending on how the positions of genes are altered with respect to regulatory sequences. Notably, specific translocations have been associated with several cancers and with schizophrenia. Reciprocal translocations result from the exchange of chromosome segments between two nonhomologous chromosomes such that there is no gain or loss of genetic information (Figure 3.3.3.9).

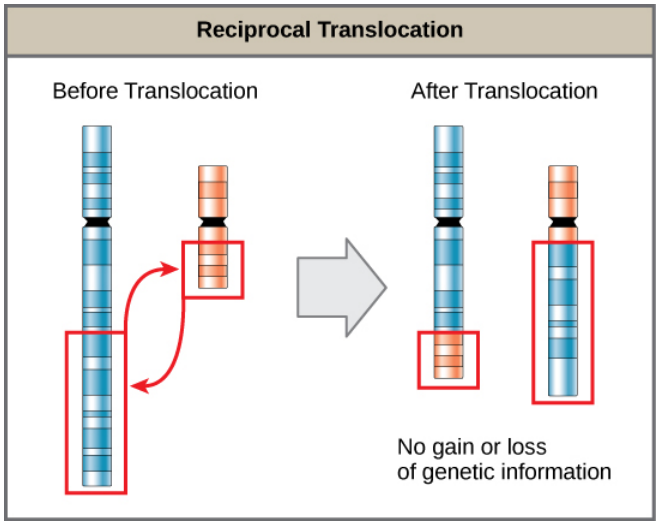


Figure 3.3.3.9: A reciprocal translocation occurs when a segment of DNA is transferred from one chromosome to another, nonhomologous chromosome. (credit: modification of work by National Human Genome Research/USA)

Summary

The number, size, shape, and banding pattern of chromosomes make them easily identifiable in a karyogram and allows for the assessment of many chromosomal abnormalities. Disorders in chromosome number, or aneuploidies, are typically lethal to the embryo, although a few trisomic genotypes are viable. Because of X inactivation, aberrations in sex chromosomes typically have milder phenotypic effects. Aneuploidies also include instances in which segments of a chromosome are duplicated or deleted. Chromosome structures may also be rearranged, for example by inversion or translocation. Both of these aberrations can result in problematic phenotypic effects. Because they force chromosomes to assume unnatural topologies during meiosis, inversions and translocations are often associated with reduced fertility because of the likelihood of nondisjunction.

Art Connections

Figure 3.3.3.2: Which of the following statements about nondisjunction is true?

A. Nondisjunction only results in gametes with n+1 or n–1 chromosomes.
B. Nondisjunction occurring during meiosis II results in 50 percent normal gametes.
C. Nondisjunction during meiosis I results in 50 percent normal gametes.
D. Nondisjunction always results in four different kinds of gametes.

Answer

B.

Footnotes

1. 1 Violaine Goidts et al., “Segmental duplication associated with the human-specific inversion of chromosome 18: a further example of the impact of segmental duplications on karyotype and genome evolution in primates,” *Human Genetics*. 115 (2004):116-122

Glossary

aneuploid
individual with an error in chromosome number; includes deletions and duplications of chromosome segments

autosome
any of the non-sex chromosomes

chromosome inversion
detachment, 180° rotation, and reinsertion of a chromosome arm

euploid
individual with the appropriate number of chromosomes for their species

karyogram
photographic image of a karyotype

karyotype
number and appearance of an individuals chromosomes; includes the size, banding patterns, and centromere position

monosomy
otherwise diploid genotype in which one chromosome is missing

nondisjunction
failure of synapsed homologs to completely separate and migrate to separate poles during the first cell division of meiosis

paracentric
inversion that occurs outside of the centromere

pericentric
inversion that involves the centromere

polyploid
individual with an incorrect number of chromosome sets

translocation
process by which one segment of a chromosome dissociates and reattaches to a different, nonhomologous chromosome

trisomy
otherwise diploid genotype in which one entire chromosome is duplicated

X inactivation
condensation of X chromosomes into Barr bodies during embryonic development in females to compensate for the double genetic dose

---

This page titled 3.3.3: Chromosomal Basis of Inherited Disorders is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **13.2: Chromosomal Basis of Inherited Disorders** by OpenStax is licensed CC BY 4.0.

3.3.E: Modern Understandings of Inheritance (Exercises)

13.1: Chromosomal Theory and Genetic Linkage

Review Questions

X-linked recessive traits in humans (or in *Drosophila*) are observed _____.

A. in more males than females
B. in more females than males
C. in males and females equally
D. in different distributions depending on the trait

Answer

A

The first suggestion that chromosomes may physically exchange segments came from the microscopic identification of _____.

A. synapsis
B. sister chromatids
C. chiasmata
D. alleles

Answer

C

Which recombination frequency corresponds to independent assortment and the absence of linkage?

A. 0
B. 0.25
C. 0.50
D. 0.75

Answer

C

Which recombination frequency corresponds to perfect linkage and violates the law of independent assortment?

A. 0
B. 0.25
C. 0.50
D. 0.75

Answer

A

Free Response

Explain how the Chromosomal Theory of Inheritance helped to advance our understanding of genetics.

Answer

The Chromosomal Theory of Inheritance proposed that genes reside on chromosomes. The understanding that chromosomes are linear arrays of genes explained linkage, and crossing over explained recombination.

13.2: Chromosomal Basis of Inherited Disorders

Review Questions

Which of the following codes describes position 12 on the long arm of chromosome 13?

A. 13p12
B. 13q12
C. 12p13
D. 12q13

Answer

B

In agriculture, polyploid crops (like coffee, strawberries, or bananas) tend to produce _____.

A. more uniformity
B. more variety
C. larger yields
D. smaller yields

Answer

C

Assume a pericentric inversion occurred in one of two homologs prior to meiosis. The other homolog remains normal. During meiosis, what structure—if any—would these homologs assume in order to pair accurately along their lengths?

A. V formation
B. cruciform
C. loop
D. pairing would not be possible

Answer

C

The genotype XXY corresponds to

A. Klinefelter syndrome
B. Turner syndrome
C. Triplo-X
D. Jacob syndrome

Answer

A

Abnormalities in the number of X chromosomes tends to have milder phenotypic effects than the same abnormalities in autosomes because of _____.

A. deletions
B. nonhomologous recombination

C. synapsis
D. X inactivation

Answer

D

By definition, a pericentric inversion includes the _____.

A. centromere
B. chiasma
C. telomere
D. synapse

Answer

A

Free Response

Using diagrams, illustrate how nondisjunction can result in an aneuploid zygote.

Answer

Exact diagram style will vary; diagram should look like Figure 13.2.2.

This page titled 3.3.E: Modern Understandings of Inheritance (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **13.E: Modern Understandings of Inheritance (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

3.4: DNA Structure and Function

Each human cell has 23 pairs of chromosomes: one set of chromosomes is inherited from the mother and the other set is inherited from the father. There is also a mitochondrial genome, inherited exclusively from the mother, which can be involved in inherited genetic disorders. On each chromosome, there are thousands of genes that are responsible for determining the genotype and phenotype of the individual. A gene is defined as a sequence of DNA that codes for a functional product. The human haploid genome contains 3 billion base pairs and has between 20,000 and 25,000 functional genes.

3.4.1: Prelude to DNA Structure and Function
3.4.2: Historical Basis of Modern Understanding
3.4.3: DNA Structure and Sequencing
3.4.4: Basics of DNA Replication
3.4.5: DNA Replication in Prokaryotes
3.4.6: DNA Replication in Eukaryotes
3.4.7: DNA Repair
3.4.E: DNA Structure and Function (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.4: DNA Structure and Function is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.4.1: Prelude to DNA Structure and Function



Figure 3.4.1.1: Dolly the sheep was the first large mammal to be cloned.

The three letters “DNA” have now become synonymous with crime solving, paternity testing, human identification, and genetic testing. DNA can be retrieved from hair, blood, or saliva. Each person’s DNA is unique, and it is possible to detect differences between individuals within a species on the basis of these unique features.

DNA analysis has many practical applications beyond forensics. In humans, DNA testing is applied to numerous uses: determining paternity, tracing genealogy, identifying pathogens, archeological research, tracing disease outbreaks, and studying human migration patterns. In the medical field, DNA is used in diagnostics, new vaccine development, and cancer therapy. It is now possible to determine predisposition to diseases by looking at genes.

Each human cell has 23 pairs of chromosomes: one set of chromosomes is inherited from the mother and the other set is inherited from the father. There is also a mitochondrial genome, inherited exclusively from the mother, which can be involved in inherited genetic disorders. On each chromosome, there are thousands of genes that are responsible for determining the genotype and phenotype of the individual. A gene is defined as a sequence of DNA that codes for a functional product. The human haploid genome contains 3 billion base pairs and has between 20,000 and 25,000 functional genes.

Video



This page titled 3.4.1: Prelude to DNA Structure and Function is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.0: Prelude to DNA Structure and Function** by OpenStax is licensed CC BY 4.0.

3.4.2: Historical Basis of Modern Understanding

Learning Objectives

- Explain transformation of DNA
- Describe the key experiments that helped identify that DNA is the genetic material
- State and explain Chargaff's rules

Modern understandings of DNA have evolved from the discovery of nucleic acid to the development of the double-helix model. In the 1860s, Friedrich Miescher (Figure 3.4.2.1), a physician by profession, was the first person to isolate phosphate-rich chemicals from white blood cells or leukocytes. He named these chemicals (which would eventually be known as RNA and DNA) nuclein because they were isolated from the nuclei of the cells.



Figure 3.4.2.1: Friedrich Miescher (1844–1895) discovered nucleic acids.

A half century later, British bacteriologist Frederick Griffith was perhaps the first person to show that hereditary information could be transferred from one cell to another "horizontally," rather than by descent. In 1928, he reported the first demonstration of bacterial transformation, a process in which external DNA is taken up by a cell, thereby changing morphology and physiology. He was working with *Streptococcus pneumoniae*, the bacterium that causes pneumonia. Griffith worked with two strains, rough (R) and smooth (S). The R strain is non-pathogenic (does not cause disease) and is called rough because its outer surface is a cell wall and lacks a capsule; as a result, the cell surface appears uneven under the microscope. The S strain is pathogenic (disease-causing) and has a capsule outside its cell wall. As a result, it has a smooth appearance under the microscope. Griffith injected the live R strain into mice and they survived. In another experiment, when he injected mice with the heat-killed S strain, they also survived. In a third set of experiments, a mixture of live R strain and heat-killed S strain were injected into mice, and—to his surprise—the mice died. Upon isolating the live bacteria from the dead mouse, only the S strain of bacteria was recovered. When this isolated S strain was injected into fresh mice, the mice died. Griffith concluded that something had passed from the heat-killed S strain into the live R strain and transformed it into the pathogenic S strain, and he called this the transforming principle (Figure 3.4.2.2). These experiments are now famously known as Griffith's transformation experiments.



Mouse injected with heat-killed virulant S strain lives.



Mouse injected with both heat-killed S strain and live non-virulant R strain dies.

Figure 3.4.2.2: Two strains of *S. pneumoniae* were used in Griffith's transformation experiments. The R strain is non-pathogenic. The S strain is pathogenic and causes death. When Griffith injected a mouse with the heat-killed S strain and a live R strain, the mouse died. The S strain was recovered from the dead mouse. Thus, Griffith concluded that something had passed from the heat-killed S strain to the R strain, transforming the R strain into S strain in the process. (credit "living mouse": modification of work by NIH; credit "dead mouse": modification of work by Sarah Marriage)

Scientists Oswald Avery, Colin MacLeod, and Maclyn McCarty (1944) were interested in exploring this transforming principle further. They isolated the S strain from the dead mice and isolated the proteins and nucleic acids, namely RNA and DNA, as these were possible candidates for the molecule of heredity. They conducted a systematic elimination study. They used enzymes that specifically degraded each component and then used each mixture separately to transform the R strain. They found that when DNA was degraded, the resulting mixture was no longer able to transform the bacteria, whereas all of the other combinations were able to transform the bacteria. This led them to conclude that DNA was the transforming principle.

Career Connection: Forensic Scientists and DNA Analysis

DNA evidence was used for the first time to solve an immigration case. The story started with a teenage boy returning to London from Ghana to be with his mother. Immigration authorities at the airport were suspicious of him, thinking that he was traveling on a forged passport. After much persuasion, he was allowed to go live with his mother, but the immigration authorities did not drop the case against him. All types of evidence, including photographs, were provided to the authorities, but deportation proceedings were started nevertheless. Around the same time, Dr. Alec Jeffreys of Leicester University in the United Kingdom had invented a technique known as DNA fingerprinting. The immigration authorities approached Dr. Jeffreys for help. He took DNA samples from the mother and three of her children, plus an unrelated mother, and compared the samples with the boy's DNA. Because the biological father was not in the picture, DNA from the three children was compared with the boy's DNA. He found a match in the boy's DNA for both the mother and his three siblings. He concluded that the boy was indeed the mother's son.

Forensic scientists analyze many items, including documents, handwriting, firearms, and biological samples. They analyze the DNA content of hair, semen, saliva, and blood, and compare it with a database of DNA profiles of known criminals. Analysis includes DNA isolation, sequencing, and sequence analysis; most forensic DNA analysis involves polymerase chain reaction (PCR) amplification of short tandem repeat (STR) loci and electrophoresis to determine the length of the PCR-amplified fragment. Only mitochondrial DNA is sequenced for forensics. Forensic scientists are expected to appear at court hearings to present their findings. They are usually employed in crime labs of city and state government agencies. Geneticists experimenting with DNA techniques also work for scientific and research organizations, pharmaceutical industries, and college and university labs. Students wishing to pursue a career as a forensic scientist should have at least a bachelor's degree in chemistry, biology, or physics, and preferably some experience working in a laboratory.

Experiments conducted by Martha Chase and Alfred Hershey in 1952 provided confirmatory evidence that DNA was the genetic material and not proteins. Chase and Hershey were studying a bacteriophage, which is a virus that infects bacteria. Viruses typically have a simple structure: a protein coat, called the capsid, and a nucleic acid core that contains the genetic material, either DNA or RNA. The bacteriophage infects the host bacterial cell by attaching to its surface, and then it injects its nucleic acids inside the cell. The phage DNA makes multiple copies of itself using the host machinery, and eventually the host cell bursts, releasing a large number of bacteriophages. Hershey and Chase labeled one batch of phage with radioactive sulfur, ^{35}S, to label the protein coat. Another batch of phage were labeled with radioactive phosphorus, ^{32}P. Because phosphorous is found in DNA, but not protein, the DNA and not the protein would be tagged with radioactive phosphorus.

Each batch of phage was allowed to infect the cells separately. After infection, the phage bacterial suspension was put in a blender, which caused the phage coat to be detached from the host cell. The phage and bacterial suspension was spun down in a centrifuge. The heavier bacterial cells settled down and formed a pellet, whereas the lighter phage particles stayed in the supernatant. In the tube that contained phage labeled with ^{35}S, the supernatant contained the radioactively labeled phage, whereas no radioactivity was detected in the pellet. In the tube that contained the phage labeled with ^{32}P, the radioactivity was detected in the pellet that contained the heavier bacterial cells, and no radioactivity was detected in the supernatant. Hershey and Chase concluded that it was the phage DNA that was injected into the cell and carried information to produce more phage particles, thus providing evidence that DNA was the genetic material and not proteins (Figure 3.4.2.3).

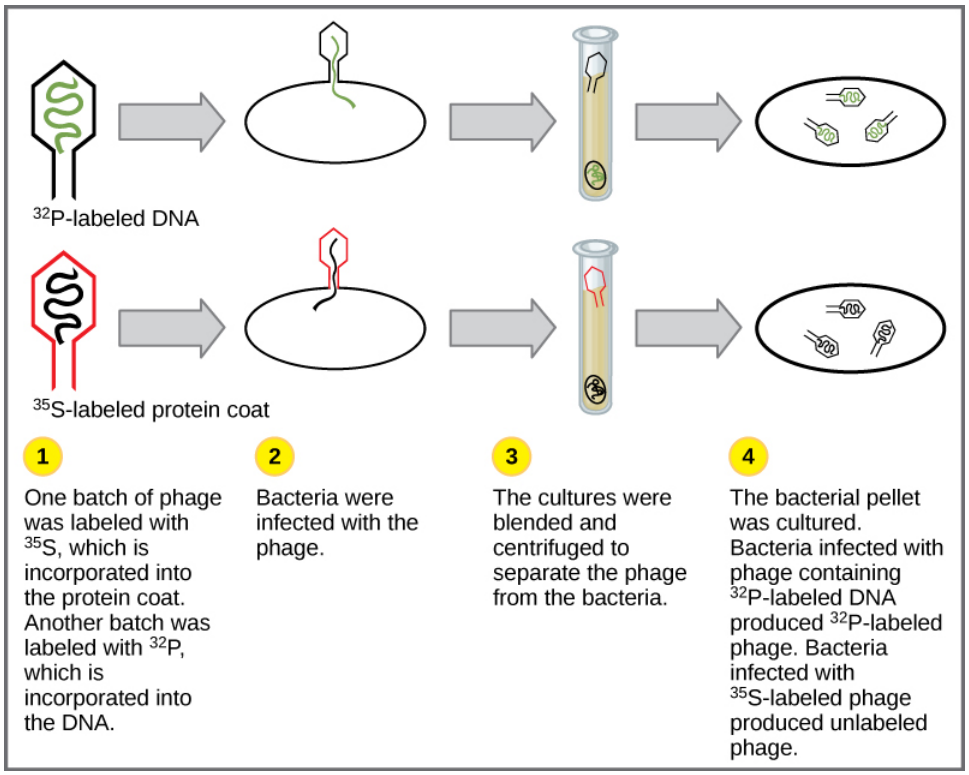


Figure 3.4.2.3: In Hershey and Chase's experiments, bacteria were infected with phage radiolabeled with either ^{35}S, which labels protein, or ^{32}P, which labels DNA. Only ^{32}P entered the bacterial cells, indicating that DNA is the genetic material.

Around this same time, Austrian biochemist Erwin Chargaff examined the content of DNA in different species and found that the amounts of adenine, thymine, guanine, and cytosine were not found in equal quantities, and that it varied from species to species, but not between individuals of the same species. He found that the amount of adenine equals the amount of thymine, and the amount of cytosine equals the amount of guanine, or A = T and G = C. This is also known as Chargaff's rules. This finding proved immensely useful when Watson and Crick were getting ready to propose their DNA double helix model.

Summary

DNA was first isolated from white blood cells by Friedrich Miescher, who called it nuclein because it was isolated from nuclei. Frederick Griffith's experiments with strains of *Streptococcus pneumoniae* provided the first hint that DNA may be the transforming principle. Avery, MacLeod, and McCarty proved that DNA is required for the transformation of bacteria. Later experiments by Hershey and Chase using bacteriophage T2 proved that DNA is the genetic material. Chargaff found that the ratio of A = T and C = G, and that the percentage content of A, T, G, and C is different for different species.

Glossary

transformation

process in which external DNA is taken up by a cell

This page titled 3.4.2: Historical Basis of Modern Understanding is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.1: Historical Basis of Modern Understanding** by OpenStax is licensed CC BY 4.0.

3.4.3: DNA Structure and Sequencing

Learning Objectives

- Describe the structure of DNA
- Explain the Sanger method of DNA sequencing
- Discuss the similarities and differences between eukaryotic and prokaryotic DNA

The building blocks of DNA are nucleotides. The important components of the nucleotide are a nitrogenous base, deoxyribose (5-carbon sugar), and a phosphate group (Figure 3.4.3.1). The nucleotide is named depending on the nitrogenous base. The nitrogenous base can be a purine such as adenine (A) and guanine (G), or a pyrimidine such as cytosine (C) and thymine (T).

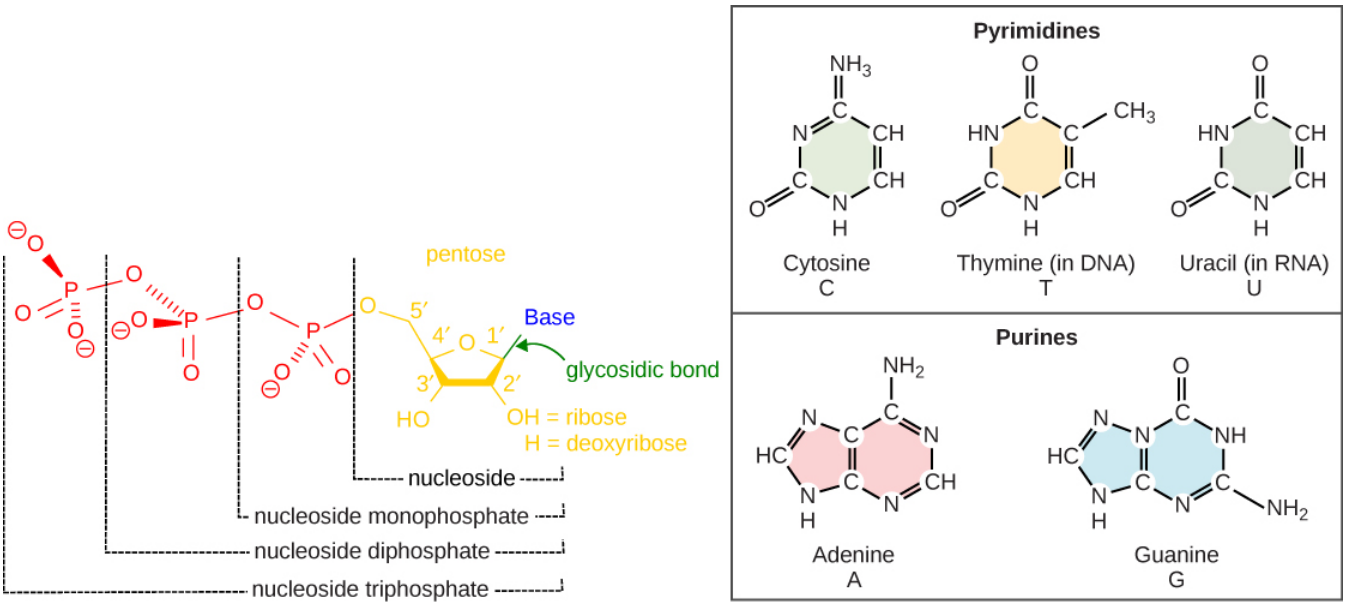


Figure 3.4.3.1: Each nucleotide is made up of a sugar, a phosphate group, and a nitrogenous base. The sugar is deoxyribose in DNA and ribose in RNA.

The nucleotides combine with each other by covalent bonds known as phosphodiester bonds or linkages. The purines have a double ring structure with a six-membered ring fused to a five-membered ring. Pyrimidines are smaller in size; they have a single six-membered ring structure. The carbon atoms of the five-carbon sugar are numbered 1', 2', 3', 4', and 5' (1' is read as “one prime”). The phosphate residue is attached to the hydroxyl group of the 5' carbon of one sugar of one nucleotide and the hydroxyl group of the 3' carbon of the sugar of the next nucleotide, thereby forming a 5'-3' phosphodiester bond.

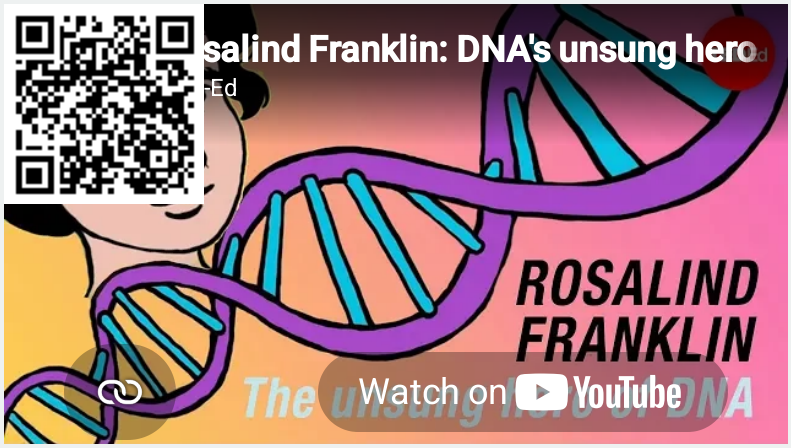
In the 1950s, Francis Crick and James Watson worked together to determine the structure of DNA at the University of Cambridge, England. Other scientists like Linus Pauling and Maurice Wilkins were also actively exploring this field. Pauling had discovered the secondary structure of proteins using X-ray crystallography. In Wilkins’ lab, researcher Rosalind Franklin was using X-ray diffraction methods to understand the structure of DNA. Watson and Crick were able to piece together the puzzle of the DNA molecule on the basis of Franklin's data because Crick had also studied X-ray diffraction (Figure 3.4.3.2). This is controversial because Franklin was not told that her work was being used by others and she was excluded from the discussions or findings. In 1962, James Watson, Francis Crick, and Maurice Wilkins were awarded the Nobel Prize in Medicine. Unfortunately, by then Franklin had died from cancer, likely due to her work with x-rays, and Nobel prizes are not awarded posthumously.



(a) (b)

Figure 3.4.3.2: The work of pioneering scientists (a) James Watson, Francis Crick, and Maclyn McCarty led to our present day understanding of DNA. Scientist Rosalind Franklin discovered (b) the X-ray diffraction pattern of DNA, which helped to elucidate its double helix structure. (credit a: modification of work by Marjorie McCarty, Public Library of Science)

Video



Watson and Crick proposed that DNA is made up of two strands that are twisted around each other to form a right-handed helix. Base pairing takes place between a purine and pyrimidine; namely, A pairs with T and G pairs with C. Adenine and thymine are complementary base pairs, and cytosine and guanine are also complementary base pairs. The base pairs are stabilized by hydrogen bonds; adenine and thymine form two hydrogen bonds and cytosine and guanine form three hydrogen bonds. The two strands are anti-parallel in nature; that is, the 3' end of one strand faces the 5' end of the other strand. The sugar and phosphate of the nucleotides form the backbone of the structure, whereas the nitrogenous bases are stacked inside. Each base pair is separated from the other base pair by a distance of 0.34 nm, and each turn of the helix measures 3.4 nm. Therefore, ten base pairs are present per turn of the helix. The diameter of the DNA double helix is 2 nm, and it is uniform throughout. Only the pairing between a purine and pyrimidine can explain the uniform diameter. The twisting of the two strands around each other results in the formation of uniformly spaced major and minor grooves (Figure 3.4.3.3).

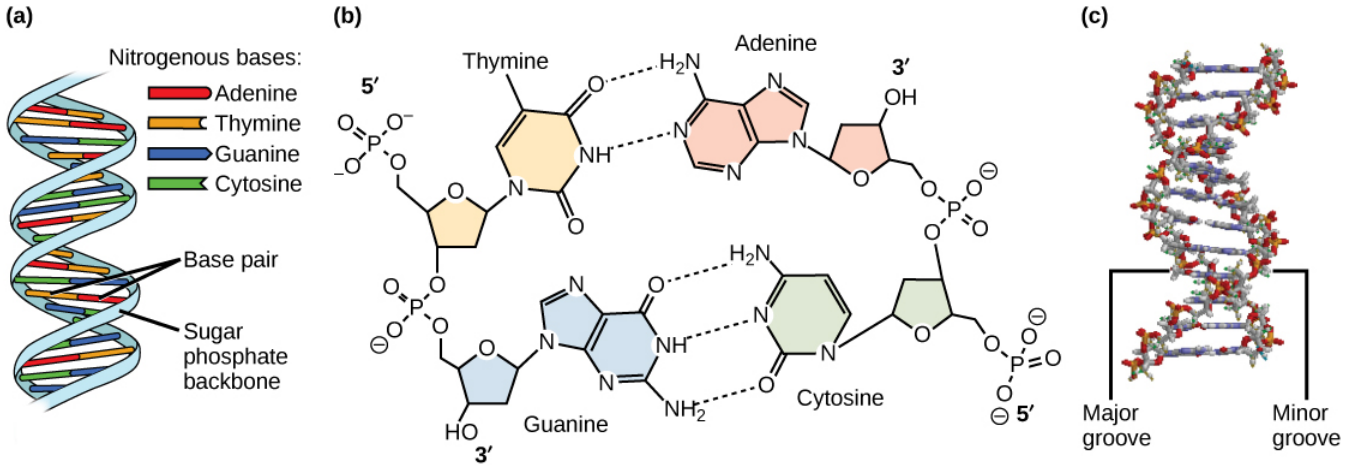


Figure 3.4.3.3: DNA has (a) a double helix structure and (b) phosphodiester bonds. The (c) major and minor grooves are binding sites for DNA binding proteins during processes such as transcription (the copying of RNA from DNA) and replication.

Video



DNA Sequencing Techniques

Until the 1990s, the sequencing of DNA (reading the sequence of DNA) was a relatively expensive and long process. Using radiolabeled nucleotides also compounded the problem through safety concerns. With currently available technology and automated machines, the process is cheap, safer, and can be completed in a matter of hours. Fred Sanger developed the sequencing method used for the human genome sequencing project, which is widely used today (Figure 3.4.3.4).

Video



The method is known as the dideoxy chain termination method. The sequencing method is based on the use of chain terminators, the dideoxynucleotides (ddNTPs). The dideoxynucleotides, or ddNTPSs, differ from the deoxynucleotides by the lack of a free 3' OH group on the five-carbon sugar. If a ddNTP is added to a growing a DNA strand, the chain is not extended any further because the free 3' OH group needed to add another nucleotide is not available. By using a predetermined ratio of deoxyribonucleotides to dideoxynucleotides, it is possible to generate DNA fragments of different sizes.

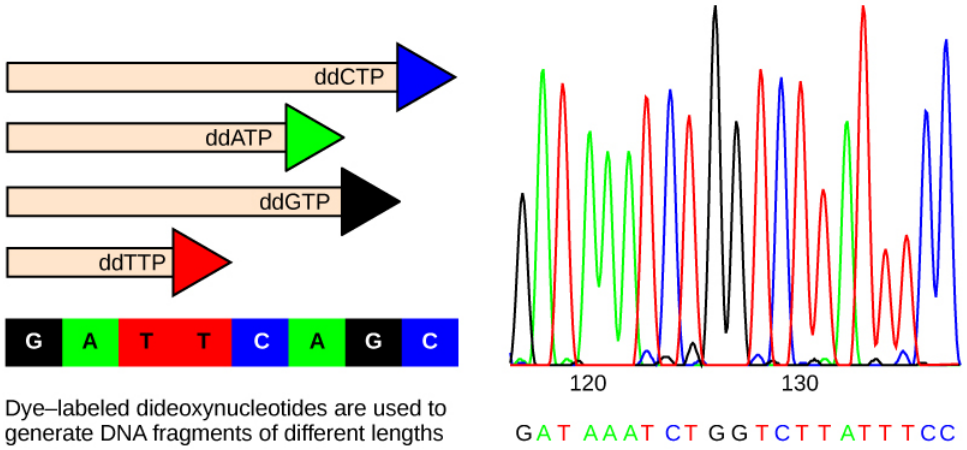


Figure 3.4.3.4: In Frederick Sanger's dideoxy chain termination method, dye-labeled dideoxynucleotides are used to generate DNA fragments that terminate at different points. The DNA is separated by capillary electrophoresis on the basis of size, and from the order of fragments formed, the DNA sequence can be read. The DNA sequence readout is shown on an electropherogram that is generated by a laser scanner.

The DNA sample to be sequenced is denatured or separated into two strands by heating it to high temperatures. The DNA is divided into four tubes in which a primer, DNA polymerase, and all four nucleotides (A, T, G, and C) are added. In addition to each of the four tubes, limited quantities of one of the four dideoxynucleotides are added to each tube respectively. The tubes are labeled as A, T, G, and C according to the ddNTP added. For detection purposes, each of the four dideoxynucleotides carries a different fluorescent label. Chain elongation continues until a fluorescent dideoxy nucleotide is incorporated, after which no further elongation takes place. After the reaction is over, electrophoresis is performed. Even a difference in length of a single base can be detected. The sequence is read from a laser scanner. For his work on DNA sequencing, Sanger received a Nobel Prize in chemistry in 1980.

Link to Learning



Sanger’s genome sequencing has led to a race to sequence human genomes at a rapid speed and low cost, often referred to as the $1000 in one day sequence. Learn more by selecting the Sequencing at Speed animation here.

Gel electrophoresis is a technique used to separate DNA fragments of different sizes. Usually the gel is made of a chemical called agarose. Agarose powder is added to a buffer and heated. After cooling, the gel solution is poured into a casting tray. Once the gel

has solidified, the DNA is loaded on the gel and electric current is applied. The DNA has a net negative charge and moves from the negative electrode toward the positive electrode. The electric current is applied for sufficient time to let the DNA separate according to size; the smallest fragments will be farthest from the well (where the DNA was loaded), and the heavier molecular weight fragments will be closest to the well. Once the DNA is separated, the gel is stained with a DNA-specific dye for viewing it (Figure 3.4.3.5).

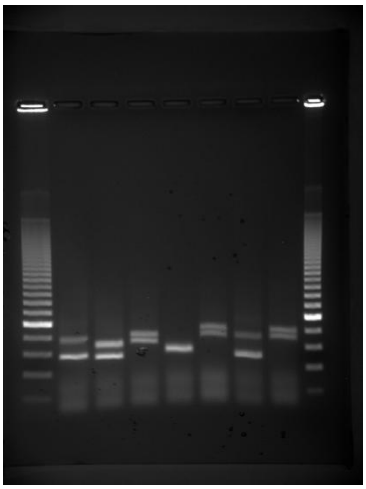


Figure 3.4.3.5: DNA can be separated on the basis of size using gel electrophoresis. (credit: James Jacob, Tompkins Cortland Community College)

Evolution Connection: Neanderthal Genome - How Are We Related?

The first draft sequence of the Neanderthal genome was recently published by Richard E. Green et al. in 2010.[1] Neanderthals are the closest ancestors of present-day humans. They were known to have lived in Europe and Western Asia before they disappeared from fossil records approximately 30,000 years ago. Green's team studied almost 40,000-year-old fossil remains that were selected from sites across the world. Extremely sophisticated means of sample preparation and DNA sequencing were employed because of the fragile nature of the bones and heavy microbial contamination. In their study, the scientists were able to sequence some four billion base pairs. The Neanderthal sequence was compared with that of present-day humans from across the world. After comparing the sequences, the researchers found that the Neanderthal genome had 2 to 3 percent greater similarity to people living outside Africa than to people in Africa. While current theories have suggested that all present-day humans can be traced to a small ancestral population in Africa, the data from the Neanderthal genome may contradict this view. Green and his colleagues also discovered DNA segments among people in Europe and Asia that are more similar to Neanderthal sequences than to other contemporary human sequences. Another interesting observation was that Neanderthals are as closely related to people from Papua New Guinea as to those from China or France. This is surprising because Neanderthal fossil remains have been located only in Europe and West Asia. Most likely, genetic exchange took place between Neanderthals and modern humans as modern humans emerged out of Africa, before the divergence of Europeans, East Asians, and Papua New Guineans.

Several genes seem to have undergone changes from Neanderthals during the evolution of present-day humans. These genes are involved in cranial structure, metabolism, skin morphology, and cognitive development. One of the genes that is of particular interest is *RUNX2*, which is different in modern day humans and Neanderthals. This gene is responsible for the prominent frontal bone, bell-shaped rib cage, and dental differences seen in Neanderthals. It is speculated that an evolutionary change in *RUNX2* was important in the origin of modern-day humans, and this affected the cranium and the upper body.

DNA Packaging in Cells

Video



When comparing prokaryotic cells to eukaryotic cells, prokaryotes are much simpler than eukaryotes in many of their features (Figure 3.4.3.6). Most prokaryotes contain a single, circular chromosome that is found in an area of the cytoplasm called the nucleoid.

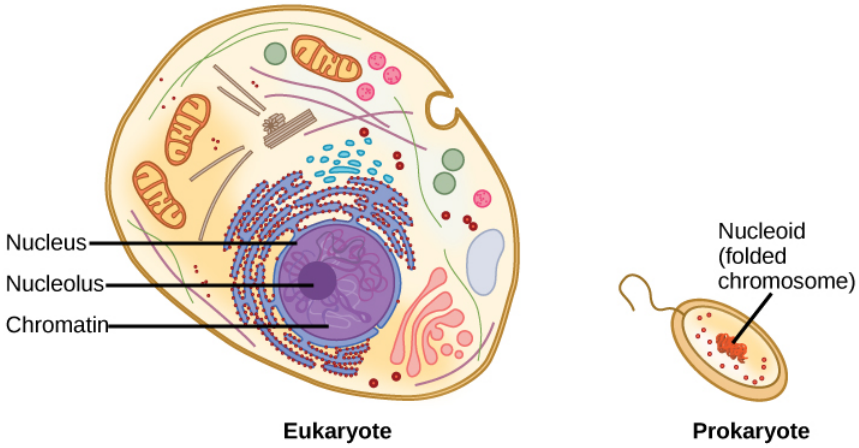


Figure 3.4.3.6: A eukaryote contains a well-defined nucleus, whereas in prokaryotes, the chromosome lies in the cytoplasm in an area called the nucleoid.

? Exercise 3.4.3.1

In eukaryotic cells, DNA and RNA synthesis occur in a separate compartment from protein synthesis. In prokaryotic cells, both processes occur together. What advantages might there be to separating the processes? What advantages might there be to having them occur together?

Answer

Compartmentalization enables a eukaryotic cell to divide processes into discrete steps so it can build more complex protein and RNA products. But there is an advantage to having a single compartment as well: RNA and protein synthesis occurs much more quickly in a prokaryotic cell.

The size of the genome in one of the most well-studied prokaryotes, *E.coli*, is 4.6 million base pairs (approximately 1.1 mm, if cut and stretched out). So how does this fit inside a small bacterial cell? The DNA is twisted by what is known as supercoiling. Supercoiling means that DNA is either under-wound (less than one turn of the helix per 10 base pairs) or over-wound (more than 1 turn per 10 base pairs) from its normal relaxed state. Some proteins are known to be involved in the supercoiling; other proteins and enzymes such as DNA gyrase help in maintaining the supercoiled structure.

Eukaryotes, whose chromosomes each consist of a linear DNA molecule, employ a different type of packing strategy to fit their DNA inside the nucleus (Figure 3.4.3.7). At the most basic level, DNA is wrapped around proteins known as histones to form structures called nucleosomes. The histones are evolutionarily conserved proteins that are rich in basic amino acids and form an octamer. The DNA (which is negatively charged because of the phosphate groups) is wrapped tightly around the histone core. This nucleosome is linked to the next one with the help of a linker DNA. This is also known as the “beads on a string” structure. This is further compacted into a 30 nm fiber, which is the diameter of the structure. At the metaphase stage, the chromosomes are at their most compact, are approximately 700 nm in width, and are found in association with scaffold proteins.

In interphase, eukaryotic chromosomes have two distinct regions that can be distinguished by staining. The tightly packaged region is known as heterochromatin, and the less dense region is known as euchromatin. Heterochromatin usually contains genes that are not expressed, and is found in the regions of the centromere and telomeres. The euchromatin usually contains genes that are transcribed, with DNA packaged around nucleosomes but not further compacted.

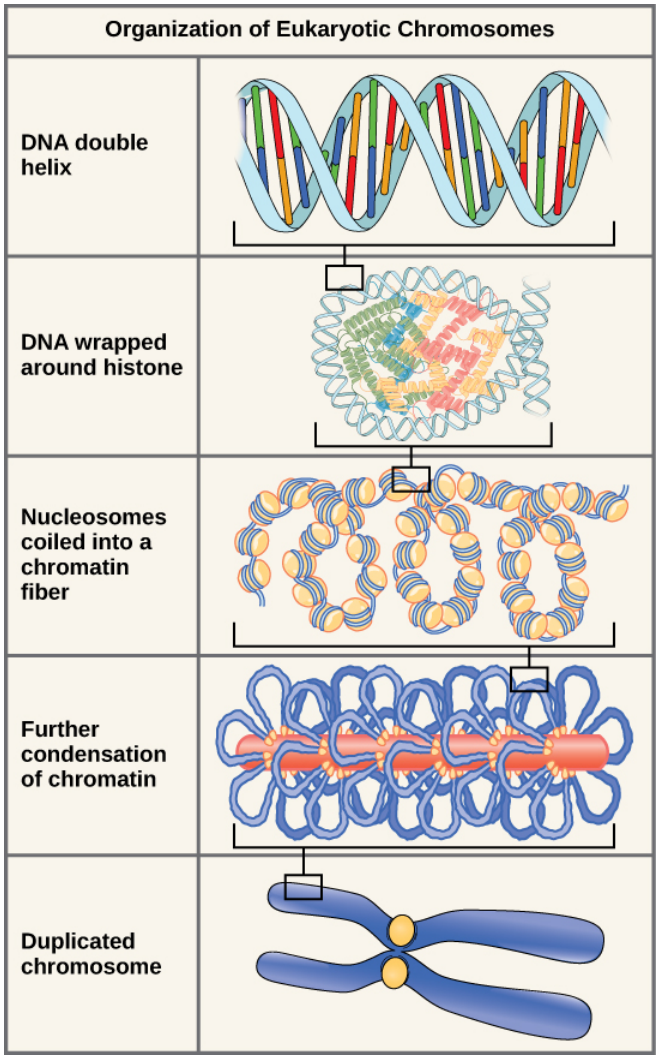


Figure 3.4.3.7: These figures illustrate the compaction of the eukaryotic chromosome.

Summary

The currently accepted model of the double-helix structure of DNA was proposed by Watson and Crick. Some of the salient features are that the two strands that make up the double helix are complementary and anti-parallel in nature. Deoxyribose sugars and phosphates form the backbone of the structure, and the nitrogenous bases are stacked inside. The diameter of the double helix, 2 nm, is uniform throughout. A purine always pairs with a pyrimidine; A pairs with T, and G pairs with C. One turn of the helix has ten base pairs. During cell division, each daughter cell receives a copy of the DNA by a process known as DNA replication. Prokaryotes are much simpler than eukaryotes in many of their features. Most prokaryotes contain a single, circular chromosome.

In general, eukaryotic chromosomes contain a linear DNA molecule packaged into nucleosomes, and have two distinct regions that can be distinguished by staining, reflecting different states of packaging and compaction.

Footnotes

1. 1 Richard E. Green et al., “A Draft Sequence of the Neandertal Genome,” *Science* 328 (2010): 710-22.

Glossary

electrophoresis

technique used to separate DNA fragments according to size

This page titled 3.4.3: DNA Structure and Sequencing is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.2: DNA Structure and Sequencing** by OpenStax is licensed CC BY 4.0.

3.4.4: Basics of DNA Replication

Learning Objects

- Explain how the structure of DNA reveals the replication process
- Describe the Meselson and Stahl experiments

The elucidation of the structure of the double helix provided a hint as to how DNA divides and makes copies of itself. This model suggests that the two strands of the double helix separate during replication, and each strand serves as a template from which the new complementary strand is copied. What was not clear was how the replication took place. There were three models suggested (Figure 3.4.4.1): *conservative, semi-conservative, and dispersive*.

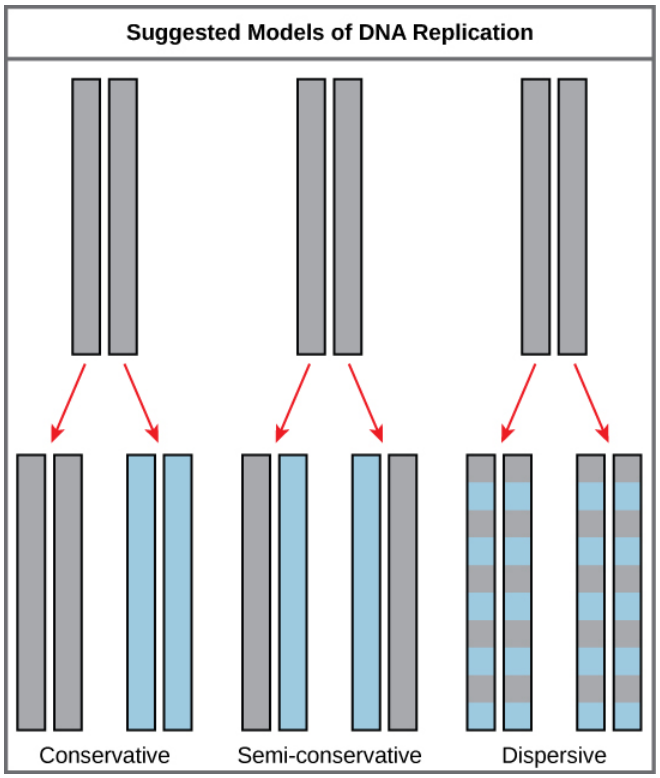


Figure 3.4.4.1: The three suggested models of DNA replication. Grey indicates the original DNA strands, and blue indicates newly synthesized DNA

In conservative replication, the parental DNA remains together, and the newly formed daughter strands are together. The semi-conservative method suggests that each of the two parental DNA strands act as a template for new DNA to be synthesized; after replication, each double-stranded DNA includes one parental or "old" strand and one "new" strand. In the dispersive model, both copies of DNA have double-stranded segments of parental DNA and newly synthesized DNA interspersed.

Meselson and Stahl were interested in understanding how DNA replicates. They grew *E. coli* for several generations in a medium containing a "heavy" isotope of nitrogen (^{15}N) that gets incorporated into nitrogenous bases, and eventually into the DNA (Figure 3.4.4.2).

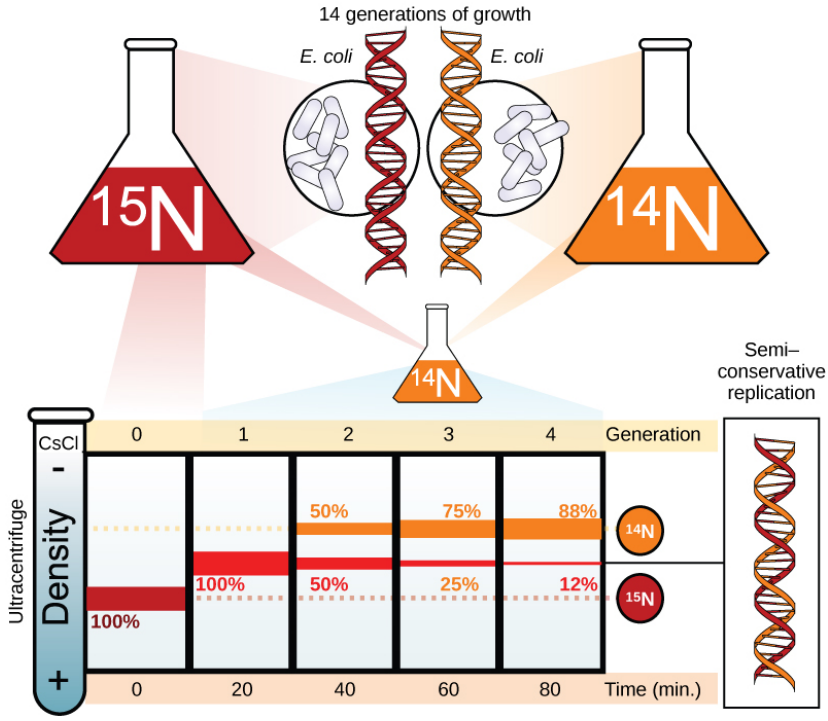


Figure 3.4.4.2: Meselson and Stahl experimented with E. coli grown first in heavy nitrogen (^{15}N) then in ^{14}N. DNA grown in ^{15}N (red band) is heavier than DNA grown in ^{14}N (orange band), and sediments to a lower level in cesium chloride solution in an ultracentrifuge. When DNA grown in ^{15}N is switched to media containing ^{14}N, after one round of cell division the DNA sediments halfway between the ^{15}N and ^{14}N levels, indicating that it now contains fifty percent ^{14}N. In subsequent cell divisions, an increasing amount of DNA contains ^{14}N only. This data supports the semi-conservative replication model. (credit: modification of work by Mariana Ruiz Villareal)

The *E. coli* culture was then shifted into medium containing ^{14}N and allowed to grow for one generation. The cells were harvested and the DNA was isolated. The DNA was centrifuged at high speeds in an ultracentrifuge. Some cells were allowed to grow for one more life cycle in ^{14}N and spun again. During the density gradient centrifugation, the DNA is loaded into a gradient (typically a salt such as cesium chloride or sucrose) and spun at high speeds of 50,000 to 60,000 rpm. Under these circumstances, the DNA will form a band according to its density in the gradient. DNA grown in ^{15}N will band at a higher density position than that grown in ^{14}N. Meselson and Stahl noted that after one generation of growth in ^{14}N after they had been shifted from ^{15}N, the single band observed was intermediate in position in between DNA of cells grown exclusively in ^{15}N and ^{14}N. This suggested either a semi-conservative or dispersive mode of replication. The DNA harvested from cells grown for two generations in ^{14}N formed two bands: one DNA band was at the intermediate position between ^{15}N and ^{14}N, and the other corresponded to the band of ^{14}N DNA. These results could only be explained if DNA replicates in a semi-conservative manner. Therefore, the other two modes were ruled out.

During DNA replication, each of the two strands that make up the double helix serves as a template from which new strands are copied. The new strand will be complementary to the parental or “old” strand. When two daughter DNA copies are formed, they have the same sequence and are divided equally into the two daughter cells.

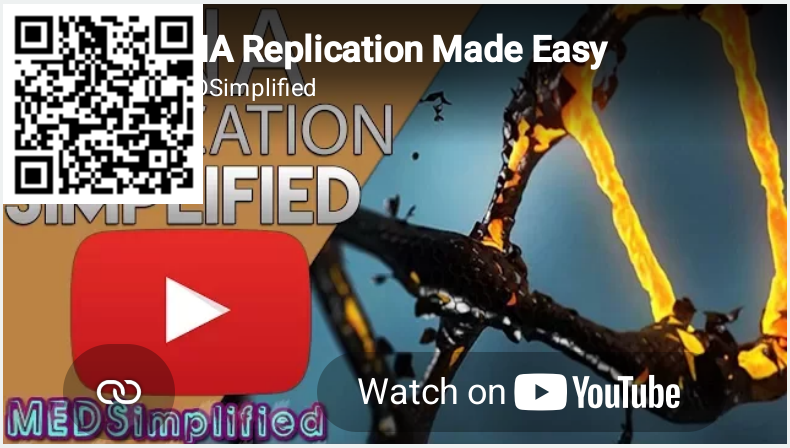
Video

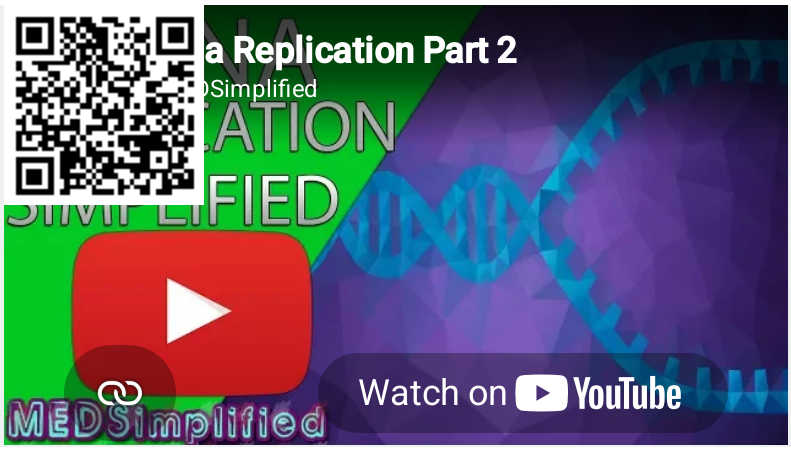

A Replication
REPLICATION
TEXAS EDUCATION AGENCY
Watch on YouTube

Video


A replication - 3D
genome
DNA polymerase
Watch on YouTube

Video


A Replication Made Easy
Simplified
MEDSimplified
Watch on YouTube



Summary

The model for DNA replication suggests that the two strands of the double helix separate during replication, and each strand serves as a template from which the new complementary strand is copied. In conservative replication, the parental DNA is conserved, and the daughter DNA is newly synthesized. The semi-conservative method suggests that each of the two parental DNA strands acts as template for new DNA to be synthesized; after replication, each double-stranded DNA includes one parental or “old” strand and one “new” strand. The dispersive mode suggested that the two copies of the DNA would have segments of parental DNA and newly synthesized DNA.

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.4.4: Basics of DNA Replication is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.3: Basics of DNA Replication** by OpenStax is licensed CC BY 4.0.

3.4.5: DNA Replication in Prokaryotes

Learning Objectives

- Explain the process of DNA replication in prokaryotes
- Discuss the role of different enzymes and proteins in supporting this process

DNA replication has been extremely well studied in prokaryotes primarily because of the small size of the genome and the mutants that are available. *E. coli* has 4.6 million base pairs in a single circular chromosome and all of it gets replicated in approximately 42 minutes, starting from a single origin of replication and proceeding around the circle in both directions. This means that approximately 1000 nucleotides are added per second. The process is quite rapid and occurs without many mistakes.

DNA replication employs a large number of proteins and enzymes, each of which plays a critical role during the process. One of the key players is the enzyme DNA polymerase, also known as DNA pol, which adds nucleotides one by one to the growing DNA chain that are complementary to the template strand. The addition of nucleotides requires energy; this energy is obtained from the nucleotides that have three phosphates attached to them, similar to ATP which has three phosphate groups attached. When the bond between the phosphates is broken, the energy released is used to form the phosphodiester bond between the incoming nucleotide and the growing chain. In prokaryotes, three main types of polymerases are known: DNA pol I, DNA pol II, and DNA pol III. It is now known that DNA pol III is the enzyme required for DNA synthesis; DNA pol I and DNA pol II are primarily required for repair.

How does the replication machinery know where to begin? It turns out that there are specific nucleotide sequences called origins of replication where replication begins. In *E. coli*, which has a single origin of replication on its one chromosome (as do most prokaryotes), it is approximately 245 base pairs long and is rich in AT sequences. The origin of replication is recognized by certain proteins that bind to this site. An enzyme called helicase unwinds the DNA by breaking the hydrogen bonds between the nitrogenous base pairs. ATP hydrolysis is required for this process. As the DNA opens up, Y-shaped structures called replication forks are formed. Two replication forks are formed at the origin of replication and these get extended bi- directionally as replication proceeds. Single-strand binding proteins coat the single strands of DNA near the replication fork to prevent the single-stranded DNA from winding back into a double helix. DNA polymerase is able to add nucleotides only in the 5' to 3' direction (a new DNA strand can be only extended in this direction). It also requires a free 3'-OH group to which it can add nucleotides by forming a phosphodiester bond between the 3'-OH end and the 5' phosphate of the next nucleotide. This essentially means that it cannot add nucleotides if a free 3'-OH group is not available. Then how does it add the first nucleotide? The problem is solved with the help of a primer that provides the free 3'-OH end. Another enzyme, RNA primase, synthesizes an RNA primer that is about five to ten nucleotides long and complementary to the DNA. Because this sequence primes the DNA synthesis, it is appropriately called the primer. DNA polymerase can now extend this RNA primer, adding nucleotides one by one that are complementary to the template strand (Figure 3.4.5.1).

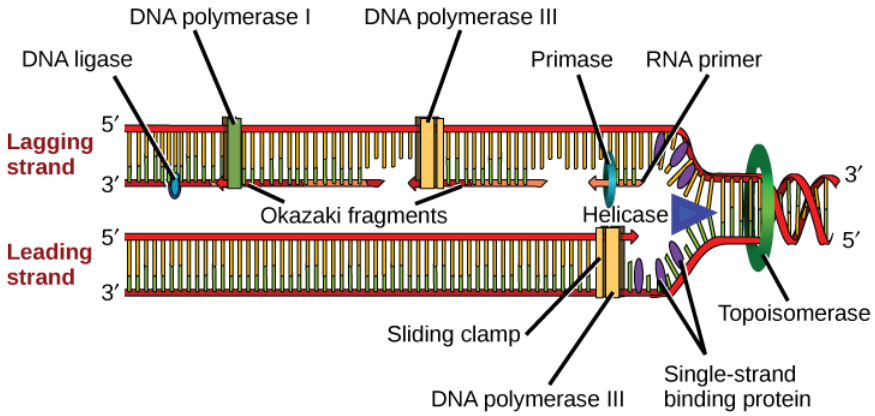


Figure 3.4.5.1: A replication fork is formed when helicase separates the DNA strands at the origin of replication. The DNA tends to become more highly coiled ahead of the replication fork. Topoisomerase breaks and reforms DNA's phosphate backbone ahead of the replication fork, thereby relieving the pressure that results from this supercoiling. Single-strand binding proteins bind to the single-stranded DNA to prevent the helix from re-forming. Primase synthesizes an RNA primer. DNA polymerase III uses this primer to synthesize the daughter DNA strand. On the leading strand, DNA is synthesized continuously, whereas on the lagging strand, DNA is synthesized in short stretches called Okazaki fragments. DNA polymerase I replaces the RNA primer with DNA. DNA ligase seals the gaps between the Okazaki fragments, joining the fragments into a single DNA molecule. (credit: modification of work by Mariana Ruiz Villareal)

? Exercise 3.4.5.1

You isolate a cell strain in which the joining together of Okazaki fragments is impaired and suspect that a mutation has occurred in an enzyme found at the replication fork. Which enzyme is most likely to be mutated?

Answer

DNA ligase, as this enzyme joins together Okazaki fragments.

The replication fork moves at the rate of 1000 nucleotides per second. DNA polymerase can only extend in the 5' to 3' direction, which poses a slight problem at the replication fork. As we know, the DNA double helix is anti-parallel; that is, one strand is in the 5' to 3' direction and the other is oriented in the 3' to 5' direction. One strand, which is complementary to the 3' to 5' parental DNA strand, is synthesized continuously towards the replication fork because the polymerase can add nucleotides in this direction. This continuously synthesized strand is known as the leading strand. The other strand, complementary to the 5' to 3' parental DNA, is extended away from the replication fork, in small fragments known as Okazaki fragments, each requiring a primer to start the synthesis. Okazaki fragments are named after the Japanese scientist who first discovered them. The strand with the Okazaki fragments is known as the lagging strand.

The leading strand can be extended by one primer alone, whereas the lagging strand needs a new primer for each of the short Okazaki fragments. The overall direction of the lagging strand will be 3' to 5', and that of the leading strand 5' to 3'. A protein called the sliding clamp holds the DNA polymerase in place as it continues to add nucleotides. The sliding clamp is a ring-shaped protein that binds to the DNA and holds the polymerase in place. Topoisomerase prevents the over-winding of the DNA double helix ahead of the replication fork as the DNA is opening up; it does so by causing temporary nicks in the DNA helix and then resealing it. As synthesis proceeds, the RNA primers are replaced by DNA. The primers are removed by the exonuclease activity of DNA pol I, and the gaps are filled in by deoxyribonucleotides. The nicks that remain between the newly synthesized DNA (that replaced the RNA primer) and the previously synthesized DNA are sealed by the enzyme DNA ligase that catalyzes the formation of phosphodiester linkage between the 3'-OH end of one nucleotide and the 5' phosphate end of the other fragment.

Once the chromosome has been completely replicated, the two DNA copies move into two different cells during cell division. The process of DNA replication can be summarized as follows.

DNA replication steps

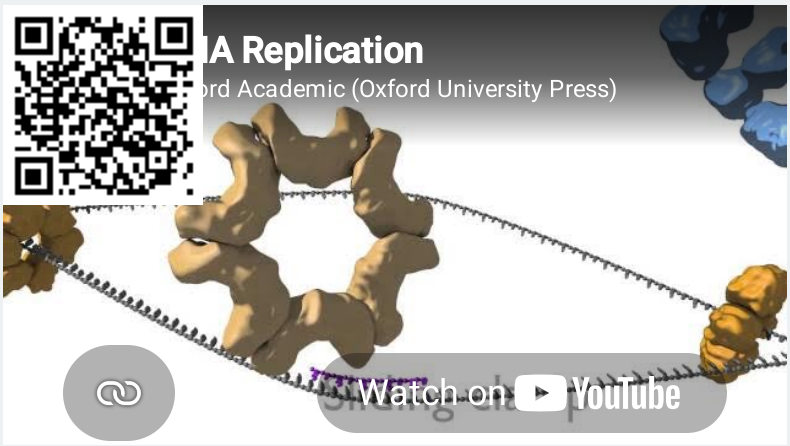
1. DNA unwinds at the origin of replication.
2. Helicase opens up the DNA-forming replication forks; these are extended bidirectionally.
3. Single-strand binding proteins coat the DNA around the replication fork to prevent rewinding of the DNA.
4. Topoisomerase binds at the region ahead of the replication fork to prevent supercoiling.
5. Primase synthesizes RNA primers complementary to the DNA strand.
6. DNA polymerase starts adding nucleotides to the 3'-OH end of the primer.
7. Elongation of both the lagging and the leading strand continues.
8. RNA primers are removed by exonuclease activity.
9. Gaps are filled by DNA pol by adding dNTPs.
10. The gap between the two DNA fragments is sealed by DNA ligase, which helps in the formation of phosphodiester bonds.

Table 3.4.5.1 summarizes the enzymes involved in prokaryotic DNA replication and the functions of each.

Table 3.4.5.1: Prokaryotic DNA Replication: Enzymes and Their Function

Enzyme/protein	Specific Function
DNA pol I	Exonuclease activity removes RNA primer and replaces with newly synthesized DNA
DNA pol II	Repair function
DNA pol III	Main enzyme that adds nucleotides in the 5'-3' direction
Helicase	Opens the DNA helix by breaking hydrogen bonds between the nitrogenous bases
Ligase	Seals the gaps between the Okazaki fragments to create one continuous DNA strand
Primase	Synthesizes RNA primers needed to start replication
Sliding Clamp	Helps to hold the DNA polymerase in place when nucleotides are being added
Topoisomerase	Helps relieve the stress on DNA when unwinding by causing breaks and then resealing the DNA
Single-strand binding proteins (SSB)	Binds to single-stranded DNA to avoid DNA rewinding back.

Link to Learning



Review the full process of DNA replication here.

Summary

Replication in prokaryotes starts from a sequence found on the chromosome called the origin of replication—the point at which the DNA opens up. Helicase opens up the DNA double helix, resulting in the formation of the replication fork. Single-strand binding proteins bind to the single-stranded DNA near the replication fork to keep the fork open. Primase synthesizes an RNA primer to initiate synthesis by DNA polymerase, which can add nucleotides only in the 5' to 3' direction. One strand is synthesized continuously in the direction of the replication fork; this is called the leading strand. The other strand is synthesized in a direction away from the replication fork, in short stretches of DNA known as Okazaki fragments. This strand is known as the lagging strand. Once replication is completed, the RNA primers are replaced by DNA nucleotides and the DNA is sealed with DNA ligase, which creates phosphodiester bonds between the 3'-OH of one end and the 5' phosphate of the other strand.

Glossary

helicase
: during replication, this enzyme helps to open up the DNA helix by breaking the hydrogen bonds

lagging strand
: during replication, the strand that is replicated in short fragments and away from the replication fork

leading strand
: strand that is synthesized continuously in the 5'-3' direction which is synthesized in the direction of the replication fork

ligase
: enzyme that catalyzes the formation of a phosphodiester linkage between the 3' OH and 5' phosphate ends of the DNA

Okazaki fragment
: DNA fragment that is synthesized in short stretches on the lagging strand

primase
: enzyme that synthesizes the RNA primer; the primer is needed for DNA pol to start synthesis of a new DNA strand

primer
: short stretch of nucleotides that is required to initiate replication; in the case of replication, the primer has RNA nucleotides

replication fork
: Y-shaped structure formed during initiation of replication

single-strand binding protein
: during replication, protein that binds to the single-stranded DNA; this helps in keeping the two strands of DNA apart so that they may serve as templates

sliding clamp
: ring-shaped protein that holds the DNA pol on the DNA strand

topoisomerase
: enzyme that causes underwinding or overwinding of DNA when DNA replication is taking place

---

This page titled 3.4.5: DNA Replication in Prokaryotes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.4: DNA Replication in Prokaryotes** by OpenStax is licensed CC BY 4.0.

3.4.6: DNA Replication in Eukaryotes

Learning Objectives

- Discuss the similarities and differences between DNA replication in eukaryotes and prokaryotes
- State the role of telomerase in DNA replication

Eukaryotic genomes are much more complex and larger in size than prokaryotic genomes. The human genome has three billion base pairs per haploid set of chromosomes, and 6 billion base pairs are replicated during the S phase of the cell cycle. There are multiple origins of replication on the eukaryotic chromosome; humans can have up to 100,000 origins of replication. The rate of replication is approximately 100 nucleotides per second, much slower than prokaryotic replication. In yeast, which is a eukaryote, special sequences known as Autonomously Replicating Sequences (ARS) are found on the chromosomes. These are equivalent to the origin of replication in *E. coli*.

The number of DNA polymerases in eukaryotes is much more than prokaryotes: 14 are known, of which five are known to have major roles during replication and have been well studied. They are known as pol α, pol β, pol γ, pol δ, and pol ε.

The essential steps of replication are the same as in prokaryotes. Before replication can start, the DNA has to be made available as template. Eukaryotic DNA is bound to basic proteins known as histones to form structures called nucleosomes. The chromatin (the complex between DNA and proteins) may undergo some chemical modifications, so that the DNA may be able to slide off the proteins or be accessible to the enzymes of the DNA replication machinery. At the origin of replication, a pre-replication complex is made with other initiator proteins. Other proteins are then recruited to start the replication process (Table 3.4.6.1).

A helicase using the energy from ATP hydrolysis opens up the DNA helix. Replication forks are formed at each replication origin as the DNA unwinds. The opening of the double helix causes over-winding, or supercoiling, in the DNA ahead of the replication fork. These are resolved with the action of topoisomerases. Primers are formed by the enzyme primase, and using the primer, DNA pol can start synthesis. While the leading strand is continuously synthesized by the enzyme pol δ, the lagging strand is synthesized by pol ε. A sliding clamp protein known as PCNA (Proliferating Cell Nuclear Antigen) holds the DNA pol in place so that it does not slide off the DNA. RNase H removes the RNA primer, which is then replaced with DNA nucleotides. The Okazaki fragments in the lagging strand are joined together after the replacement of the RNA primers with DNA. The gaps that remain are sealed by DNA ligase, which forms the phosphodiester bond.

Telomere replication

Unlike prokaryotic chromosomes, eukaryotic chromosomes are linear. As you've learned, the enzyme DNA pol can add nucleotides only in the 5' to 3' direction. In the leading strand, synthesis continues until the end of the chromosome is reached. On the lagging strand, DNA is synthesized in short stretches, each of which is initiated by a separate primer. When the replication fork reaches the end of the linear chromosome, there is no place for a primer to be made for the DNA fragment to be copied at the end of the chromosome. These ends thus remain unpaired, and over time these ends may get progressively shorter as cells continue to divide.

The ends of the linear chromosomes are known as telomeres, which have repetitive sequences that code for no particular gene. In a way, these telomeres protect the genes from getting deleted as cells continue to divide. In humans, a six base pair sequence, TTAGGG, is repeated 100 to 1000 times. The discovery of the enzyme telomerase (Figure 3.4.6.1) helped in the understanding of how chromosome ends are maintained. The telomerase enzyme contains a catalytic part and a built-in RNA template. It attaches to the end of the chromosome, and complementary bases to the RNA template are added on the 3' end of the DNA strand. Once the 3' end of the lagging strand template is sufficiently elongated, DNA polymerase can add the nucleotides complementary to the ends of the chromosomes. Thus, the ends of the chromosomes are replicated.

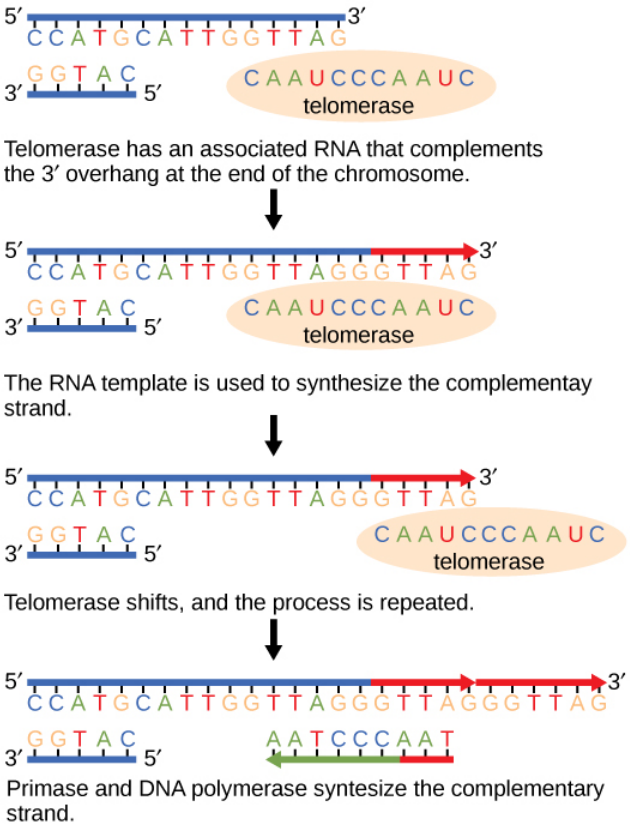


Figure 3.4.6.1: The ends of linear chromosomes are maintained by the action of the telomerase enzyme.

Telomerase is typically active in germ cells and adult stem cells. It is not active in adult somatic cells. For her discovery of telomerase and its action, Elizabeth Blackburn (Figure 3.4.6.2) received the Nobel Prize for Medicine and Physiology in 2009.



Figure 3.4.6.2: Elizabeth Blackburn, 2009 Nobel Laureate, is the scientist who discovered how telomerase works. (credit: US Embassy Sweden)

Telomerase and Aging

Cells that undergo cell division continue to have their telomeres shortened because most somatic cells do not make telomerase. This essentially means that telomere shortening is associated with aging. With the advent of modern medicine, preventative health care, and healthier lifestyles, the human life span has increased, and there is an increasing demand for people to look younger and have a better quality of life as they grow older.

In 2010, scientists found that telomerase can reverse some age-related conditions in mice. This may have potential in regenerative medicine.[1] Telomerase-deficient mice were used in these studies; these mice have tissue atrophy, stem cell depletion, organ system failure, and impaired tissue injury responses. Telomerase reactivation in these mice caused extension of telomeres, reduced DNA damage, reversed neurodegeneration, and improved the function of the testes, spleen, and intestines. Thus, telomere reactivation may have potential for treating age-related diseases in humans.

Cancer is characterized by uncontrolled cell division of abnormal cells. The cells accumulate mutations, proliferate uncontrollably, and can migrate to different parts of the body through a process called metastasis. Scientists have observed that cancerous cells have considerably shortened telomeres and that telomerase is active in these cells. Interestingly, only after the telomeres were

shortened in the cancer cells did the telomerase become active. If the action of telomerase in these cells can be inhibited by drugs during cancer therapy, then the cancerous cells could potentially be stopped from further division.

Table 3.4.6.1: Difference between Prokaryotic and Eukaryotic Replication

Property	Prokaryotes	Eukaryotes
Origin of replication	Single	Multiple
Rate of replication	1000 nucleotides/s	50 to 100 nucleotides/s
DNA polymerase types	5	14
Telomerase	Not present	Present
RNA primer removal	DNA pol I	RNase H
Strand elongation	DNA pol III	Pol δ, pol ε
Sliding clamp	Sliding clamp	PCNA

Summary

Replication in eukaryotes starts at multiple origins of replication. The mechanism is quite similar to prokaryotes. A primer is required to initiate synthesis, which is then extended by DNA polymerase as it adds nucleotides one by one to the growing chain. The leading strand is synthesized continuously, whereas the lagging strand is synthesized in short stretches called Okazaki fragments. The RNA primers are replaced with DNA nucleotides; the DNA remains one continuous strand by linking the DNA fragments with DNA ligase. The ends of the chromosomes pose a problem as polymerase is unable to extend them without a primer. Telomerase, an enzyme with an inbuilt RNA template, extends the ends by copying the RNA template and extending one end of the chromosome. DNA polymerase can then extend the DNA using the primer. In this way, the ends of the chromosomes are protected.

Footnotes

1. 1 Jaskelioff et al., “Telomerase reactivation reverses tissue degeneration in aged telomerase-deficient mice,” *Nature* 469 (2011): 102-7.

Glossary

telomerase

enzyme that contains a catalytic part and an inbuilt RNA template; it functions to maintain telomeres at chromosome ends

telomere

DNA at the end of linear chromosomes

This page titled 3.4.6: DNA Replication in Eukaryotes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

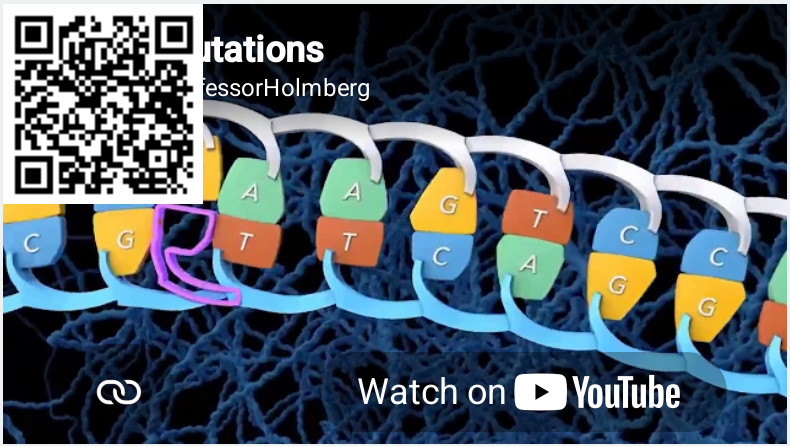
- **14.5: DNA Replication in Eukaryotes** by OpenStax is licensed CC BY 4.0.

3.4.7: DNA Repair

Learning Objectives

- Discuss the different types of mutations in DNA
- Explain DNA repair mechanisms

Video



DNA replication is a highly accurate process, but mistakes can occasionally occur, such as a DNA polymerase inserting a wrong base. Uncorrected mistakes may sometimes lead to serious consequences, such as cancer. Repair mechanisms correct the mistakes. In rare cases, mistakes are not corrected, leading to mutations; in other cases, repair enzymes are themselves mutated or defective.

Most of the mistakes during DNA replication are promptly corrected by DNA polymerase by proofreading the base that has been just added (Figure 3.4.7.1). In proofreading, the DNA pol reads the newly added base before adding the next one, so a correction can be made. The polymerase checks whether the newly added base has paired correctly with the base in the template strand. If it is the right base, the next nucleotide is added. If an incorrect base has been added, the enzyme makes a cut at the phosphodiester bond and releases the wrong nucleotide. This is performed by the exonuclease action of DNA pol III. Once the incorrect nucleotide has been removed, a new one will be added again.

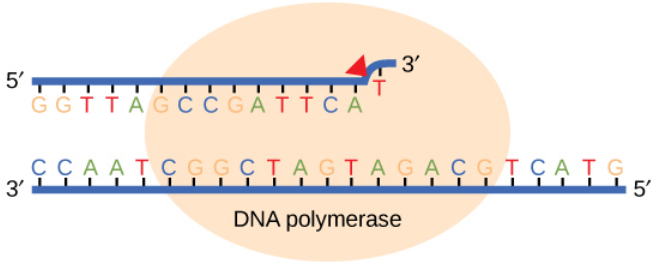


Figure 3.4.7.1: Proofreading by DNA polymerase corrects errors during replication.

Some errors are not corrected during replication, but are instead corrected after replication is completed; this type of repair is known as mismatch repair (Figure 3.4.7.2). The enzymes recognize the incorrectly added nucleotide and excise it; this is then replaced by the correct base. If this remains uncorrected, it may lead to more permanent damage. How do mismatch repair enzymes recognize which of the two bases is the incorrect one? In *E. coli*, after replication, the nitrogenous base adenine acquires a methyl group; the parental DNA strand will have methyl groups, whereas the newly synthesized strand lacks them. Thus, DNA polymerase is able to remove the wrongly incorporated bases from the newly synthesized, non-methylated strand. In eukaryotes, the mechanism is not very well understood, but it is believed to involve recognition of unsealed nicks in the new strand, as well as a short-term continuing association of some of the replication proteins with the new daughter strand after replication has completed.

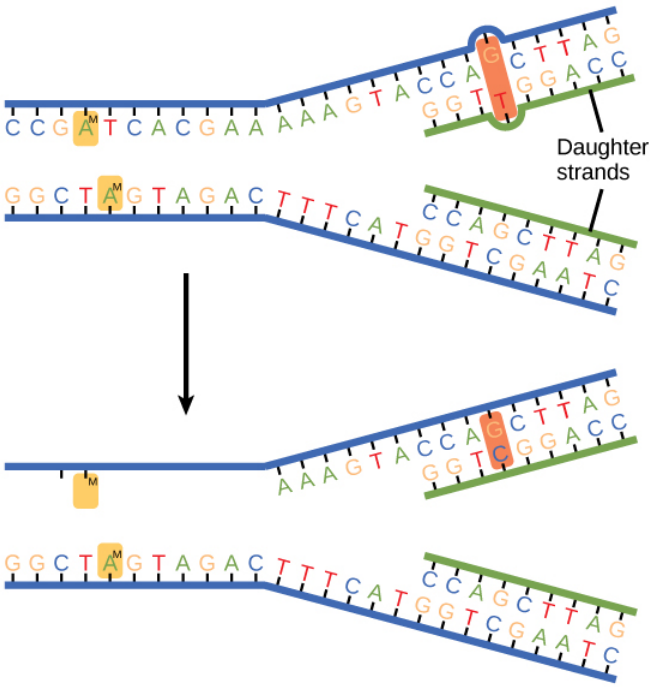


Figure 3.4.7.2: In mismatch repair, the incorrectly added base is detected after replication. The mismatch repair proteins detect this base and remove it from the newly synthesized strand by nuclease action. The gap is now filled with the correctly paired base.

In another type of repair mechanism, nucleotide excision repair, enzymes replace incorrect bases by making a cut on both the 3' and 5' ends of the incorrect base (Figure 3.4.7.3). The segment of DNA is removed and replaced with the correctly paired nucleotides by the action of DNA pol. Once the bases are filled in, the remaining gap is sealed with a phosphodiester linkage catalyzed by DNA ligase. This repair mechanism is often employed when UV exposure causes the formation of pyrimidine dimers.

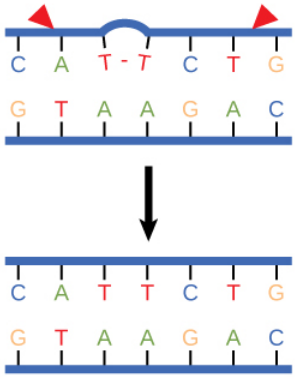


Figure 3.4.7.3: Nucleotide excision repairs thymine dimers. When exposed to UV, thymines lying adjacent to each other can form thymine dimers. In normal cells, they are excised and replaced.

A well-studied example of mistakes not being corrected is seen in people suffering from xeroderma pigmentosa (Figure 3.4.7.4). Affected individuals have skin that is highly sensitive to UV rays from the sun. When individuals are exposed to UV, pyrimidine dimers, especially those of thymine, are formed; people with xeroderma pigmentosa are not able to repair the damage. These are not repaired because of a defect in the nucleotide excision repair enzymes, whereas in normal individuals, the thymine dimers are excised and the defect is corrected. The thymine dimers distort the structure of the DNA double helix, and this may cause problems during DNA replication. People with xeroderma pigmentosa may have a higher risk of contracting skin cancer than those who dont have the condition.



Figure 3.4.7.4: Xeroderma pigmentosa is a condition in which thymine dimerization from exposure to UV is not repaired. Exposure to sunlight results in skin lesions. (credit: James Halpern et al.)

Errors during DNA replication are not the only reason why mutations arise in DNA. Mutations, variations in the nucleotide sequence of a genome, can also occur because of damage to DNA. Such mutations may be of two types: induced or spontaneous. Induced mutations are those that result from an exposure to chemicals, UV rays, x-rays, or some other environmental agent. Spontaneous mutations occur without any exposure to any environmental agent; they are a result of natural reactions taking place within the body.

Mutations may have a wide range of effects. Some mutations are not expressed; these are known as silent mutations. Point mutations are those mutations that affect a single base pair. The most common nucleotide mutations are substitutions, in which one base is replaced by another. These can be of two types, either transitions or transversions. Transition substitution refers to a purine or pyrimidine being replaced by a base of the same kind; for example, a purine such as adenine may be replaced by the purine guanine. Transversion substitution refers to a purine being replaced by a pyrimidine, or vice versa; for example, cytosine, a pyrimidine, is replaced by adenine, a purine. Mutations can also be the result of the addition of a base, known as an insertion, or the removal of a base, also known as deletion. Sometimes a piece of DNA from one chromosome may get translocated to another chromosome or to another region of the same chromosome; this is also known as translocation. These mutation types are shown in Figure 3.4.7.5.

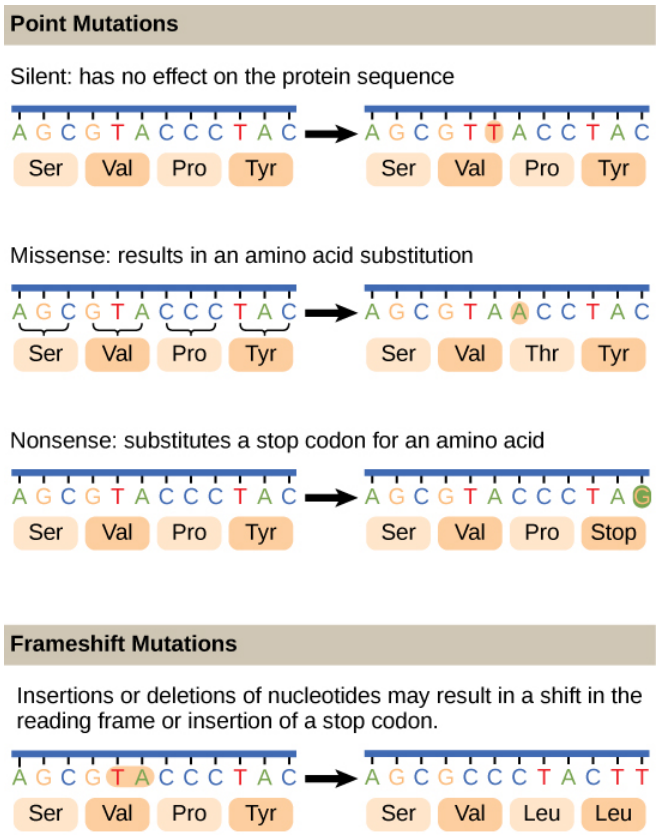


Figure 3.4.7.5: Mutations can lead to changes in the protein sequence encoded by the DNA.

? Exercise 3.4.7.1

A frameshift mutation that results in the insertion of three nucleotides is often less deleterious than a mutation that results in the insertion of one nucleotide. Why?

Answer

If three nucleotides are added, one additional amino acid will be incorporated into the protein chain, but the reading frame won't shift.

Mutations in repair genes have been known to cause cancer. Many mutated repair genes have been implicated in certain forms of pancreatic cancer, colon cancer, and colorectal cancer. Mutations can affect either somatic cells or germ cells. If many mutations accumulate in a somatic cell, they may lead to problems such as the uncontrolled cell division observed in cancer. If a mutation takes place in germ cells, the mutation will be passed on to the next generation, as in the case of hemophilia and xeroderma pigmentosa.

Summary

DNA polymerase can make mistakes while adding nucleotides. It edits the DNA by proofreading every newly added base. Incorrect bases are removed and replaced by the correct base, and then a new base is added. Most mistakes are corrected during replication, although when this does not happen, the mismatch repair mechanism is employed. Mismatch repair enzymes recognize the wrongly incorporated base and excise it from the DNA, replacing it with the correct base. In yet another type of repair, nucleotide excision repair, the incorrect base is removed along with a few bases on the 5' and 3' end, and these are replaced by copying the template with the help of DNA polymerase. The ends of the newly synthesized fragment are attached to the rest of the DNA using DNA ligase, which creates a phosphodiester bond.

Most mistakes are corrected, and if they are not, they may result in a mutation defined as a permanent change in the DNA sequence. Mutations can be of many types, such as substitution, deletion, insertion, and translocation. Mutations in repair genes may lead to serious consequences such as cancer. Mutations can be induced or may occur spontaneously.

Glossary

induced mutation
: mutation that results from exposure to chemicals or environmental agents

mutation
: variation in the nucleotide sequence of a genome

mismatch repair
: type of repair mechanism in which mismatched bases are removed after replication

nucleotide excision repair
: type of DNA repair mechanism in which the wrong base, along with a few nucleotides upstream or downstream, are removed

proofreading
: function of DNA pol in which it reads the newly added base before adding the next one

point mutation
: mutation that affects a single base

silent mutation
: mutation that is not expressed

spontaneous mutation
: mutation that takes place in the cells as a result of chemical reactions taking place naturally without exposure to any external agent

transition substitution
: when a purine is replaced with a purine or a pyrimidine is replaced with another pyrimidine

transversion substitution
: when a purine is replaced by a pyrimidine or a pyrimidine is replaced by a purine

---

This page titled 3.4.7: DNA Repair is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.6: DNA Repair** by OpenStax is licensed CC BY 4.0.

3.4.E: DNA Structure and Function (Exercises)

14.1: Historical Basis of Modern Understanding

Modern understandings of DNA have evolved from the discovery of nucleic acid to the development of the double-helix model. In the 1860s, Friedrich Miescher, a physician by profession, was the first person to isolate phosphate-rich chemicals from white blood cells or leukocytes. He named these chemicals (which would eventually be known as RNA and DNA) nuclein because they were isolated from the nuclei of the cells.

Review Questions

If DNA of a particular species was analyzed and it was found that it contains 27 percent A, what would be the percentage of C?

A. 27 percent
B. 30 percent
C. 23 percent
D. 54 percent

Answer

C

The experiments by Hershey and Chase helped confirm that DNA was the hereditary material on the basis of the finding that:

A. radioactive phage were found in the pellet
B. radioactive cells were found in the supernatant
C. radioactive sulfur was found inside the cell
D. radioactive phosphorus was found in the cell

Answer

D

Free Response

Explain Griffith's transformation experiments. What did he conclude from them?

Answer

Live R cells acquired genetic information from the heat-killed S cells that “transformed” the R cells into S cells.

Why were radioactive sulfur and phosphorous used to label bacteriophage in Hershey and Chase's experiments?

Answer

Sulfur is an element found in proteins and phosphorus is a component of nucleic acids.

14.2: DNA Structure and Sequencing

The building blocks of DNA are nucleotides. The important components of the nucleotide are a nitrogenous base, deoxyribose (5-carbon sugar), and a phosphate group. The nucleotide is named depending on the nitrogenous base. The nitrogenous base can be a purine such as adenine (A) and guanine (G), or a pyrimidine such as cytosine (C) and thymine (T).

Review Questions

DNA double helix does not have which of the following?

A. antiparallel configuration

B. complementary base pairing
C. major and minor grooves
D. uracil

Answer

D

In eukaryotes, what is the DNA wrapped around?

A. single-stranded binding proteins
B. sliding clamp
C. polymerase
D. histones

Answer

D

Free Response

Provide a brief summary of the Sanger sequencing method.

Answer

The template DNA strand is mixed with a DNA polymerase, a primer, the 4 deoxynucleotides, and a limiting concentration of 4 dideoxynucleotides. DNA polymerase synthesizes a strand complementary to the template. Incorporation of ddNTPs at different locations results in DNA fragments that have terminated at every possible base in the template. These fragments are separated by gel electrophoresis and visualized by a laser detector to determine the sequence of bases.

Describe the structure and complementary base pairing of DNA.

Answer

DNA has two strands in anti-parallel orientation. The sugar-phosphate linkages form a backbone on the outside, and the bases are paired on the inside: A with T, and G with C, like rungs on a spiral ladder.

14.3: Basics of DNA Replication

The elucidation of the structure of the double helix provided a hint as to how DNA divides and makes copies of itself. This model suggests that the two strands of the double helix separate during replication, and each strand serves as a template from which the new complementary strand is copied. What was not clear was how the replication took place. There were three models suggested: conservative, semi-conservative, and dispersive.

Review Questions

Meselson and Stahl's experiments proved that DNA replicates by which mode?

a. conservative
b. semi-conservative
c. dispersive
d. none of the above

Answer

B

If the sequence of the 5'-3' strand is AATGCTAC, then the complementary sequence has the following sequence:

a. 3'-AATGCTAC-5'
b. 3'-CATCGTAA-5'
c. 3'-TTACGATG-5'
d. 3'-GTAGCATT-5'

Answer

C

Free Response

How did the scientific community learn that DNA replication takes place in a semi-conservative fashion?

Answer

Meselson's experiments with *E. coli* grown in ^{15}N deduced this finding.

14.4: DNA Replication in Prokaryotes

DNA replication has been extremely well studied in prokaryotes primarily because of the small size of the genome and the mutants that are available. E. coli has 4.6 million base pairs in a single circular chromosome and all of it gets replicated in approximately 42 minutes, starting from a single origin of replication and proceeding around the circle in both directions. This means that approximately 1000 nucleotides are added per second. The process is quite rapid and occurs without many mistake

Review Questions

Which of the following components is not involved during the formation of the replication fork?

A. single-strand binding proteins
B. helicase
C. origin of replication
D. ligase

Answer

D

Which of the following does the enzyme primase synthesize?

A. DNA primer
B. RNA primer
C. Okazaki fragments
D. phosphodiester linkage

Answer

B

In which direction does DNA replication take place?

A. 5'-3'
B. 3'-5'
C. 5'
D. 3'

Answer

A

Free Response

DNA replication is bidirectional and discontinuous; explain your understanding of those concepts.

Answer

At an origin of replication, two replication forks are formed that are extended in two directions. On the lagging strand, Okazaki fragments are formed in a discontinuous manner.

What are Okazaki fragments and how they are formed?

Answer

Short DNA fragments are formed on the lagging strand synthesized in a direction away from the replication fork. These are synthesized by DNA pol.

If the rate of replication in a particular prokaryote is 900 nucleotides per second, how long would it take 1.2 million base pair genomes to make two copies?

Answer

1333 seconds or 22.2 minutes.

Explain the events taking place at the replication fork. If the gene for helicase is mutated, what part of replication will be affected?

Answer

At the replication fork, the events taking place are helicase action, binding of single-strand binding proteins, primer synthesis, and synthesis of new strands. If there is a mutated helicase gene, the replication fork will not be extended.

What is the role of a primer in DNA replication? What would happen if you forgot to add a primer in a tube containing the reaction mix for a DNA sequencing reaction?

Answer

Primer provides a 3'-OH group for DNA pol to start adding nucleotides. There would be no reaction in the tube without a primer, and no bands would be visible on the electrophoresis.

14.5: DNA Replication in Eukaryotes

Eukaryotic genomes are much more complex and larger in size than prokaryotic genomes. The human genome has three billion base pairs per haploid set of chromosomes, and 6 billion base pairs are replicated during the S phase of the cell cycle. There are multiple origins of replication on the eukaryotic chromosome; humans can have up to 100,000 origins of replication

Review Questions

The ends of the linear chromosomes are maintained by

A. helicase
B. primase
C. DNA pol
D. telomerase

Answer

D

Free Response

How do the linear chromosomes in eukaryotes ensure that its ends are replicated completely?

Answer

Telomerase has an inbuilt RNA template that extends the 3' end, so primer is synthesized and extended. Thus, the ends are protected.

14.6: DNA Repair

DNA replication is a highly accurate process, but mistakes can occasionally occur, such as a DNA polymerase inserting a wrong base. Uncorrected mistakes may sometimes lead to serious consequences, such as cancer. Repair mechanisms correct the mistakes. In rare cases, mistakes are not corrected, leading to mutations; in other cases, repair enzymes are themselves mutated or defective.

Review Questions

During proofreading, which of the following enzymes reads the DNA?

A. primase
B. topoisomerase
C. DNA pol
D. helicase

Answer

C

The initial mechanism for repairing nucleotide errors in DNA is _____.

A. mismatch repair
B. DNA polymerase proofreading
C. nucleotide excision repair
D. thymine dimers

Answer

B

Free Response

What is the consequence of mutation of a mismatch repair enzyme? How will this affect the function of a gene?

Answer

Mutations are not repaired, as in the case of xeroderma pigmentosa. Gene function may be affected or it may not be expressed.

This page titled 3.4.E: DNA Structure and Function (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **14.E: DNA Structure and Function (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

3.5: Genes Expression

Since the rediscovery of Mendel's work in 1900, the definition of the gene has progressed from an abstract unit of heredity to a tangible molecular entity capable of replication, expression, and mutation. Genes are composed of DNA and are linearly arranged on chromosomes. Genes specify the sequences of amino acids, which are the building blocks of proteins. In turn, proteins are responsible for orchestrating nearly every function of the cell. Both genes and the proteins they encode are absolutely essential to life as we know it.

3.5.1: Prelude to Genes and Proteins
3.5.2: The Genetic Code
3.5.3: Prokaryotic Transcription
3.5.4: Eukaryotic Transcription
3.5.5: RNA Processing in Eukaryotes
3.5.6: Ribosomes and Protein Synthesis
3.5.E: Genes and Proteins (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.5: Genes Expression is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.5.1: Prelude to Genes and Proteins

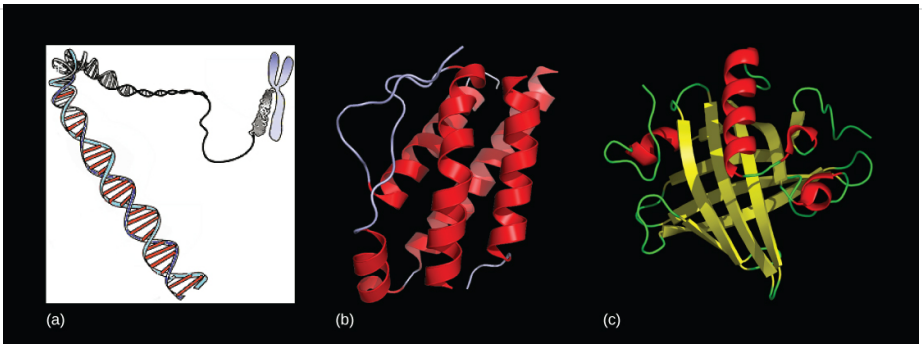


Figure 3.5.1.1: Genes, which are carried on (a) chromosomes, are linearly organized instructions for making the RNA and protein molecules that are necessary for all of the processes of life. The (b) interleukin-2 protein and (c) alpha-2u-globulin protein are just two examples of the array of different molecular structures that are encoded by genes. (credit “chromosome: National Human Genome Research Institute; credit “interleukin-2”: Ramin Herati/Created from PDB 1M47 and rendered with Pymol; credit “alpha-2u-globulin”: Darren Logan/rendered with AISMIG)

Since the rediscovery of Mendel’s work in 1900, the definition of the gene has progressed from an abstract unit of heredity to a tangible molecular entity capable of replication, expression, and mutation (Figure 3.5.1.1). Genes are composed of DNA and are linearly arranged on chromosomes. Genes specify the sequences of amino acids, which are the building blocks of proteins. In turn, proteins are responsible for orchestrating nearly every function of the cell. Both genes and the proteins they encode are absolutely essential to life as we know it.

Video



This page titled 3.5.1: Prelude to Genes and Proteins is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.0: Prelude to Genes and Proteins** by OpenStax is licensed CC BY 4.0.

3.5.2: The Genetic Code

Learning Objecttives

- Explain the “central dogma” of protein synthesis
- Describe the genetic code and how the nucleotide sequence prescribes the amino acid and the protein sequence

The cellular process of transcription generates messenger RNA (mRNA), a mobile molecular copy of one or more genes with an alphabet of A, C, G, and uracil (U). Translation of the mRNA template converts nucleotide-based genetic information into a protein product. Protein sequences consist of 20 commonly occurring amino acids; therefore, it can be said that the protein alphabet consists of 20 letters (Figure 3.5.2.1). Each amino acid is defined by a three-nucleotide sequence called the triplet codon. Different amino acids have different chemistries (such as acidic versus basic, or polar and nonpolar) and different structural constraints. Variation in amino acid sequence gives rise to enormous variation in protein structure and function.

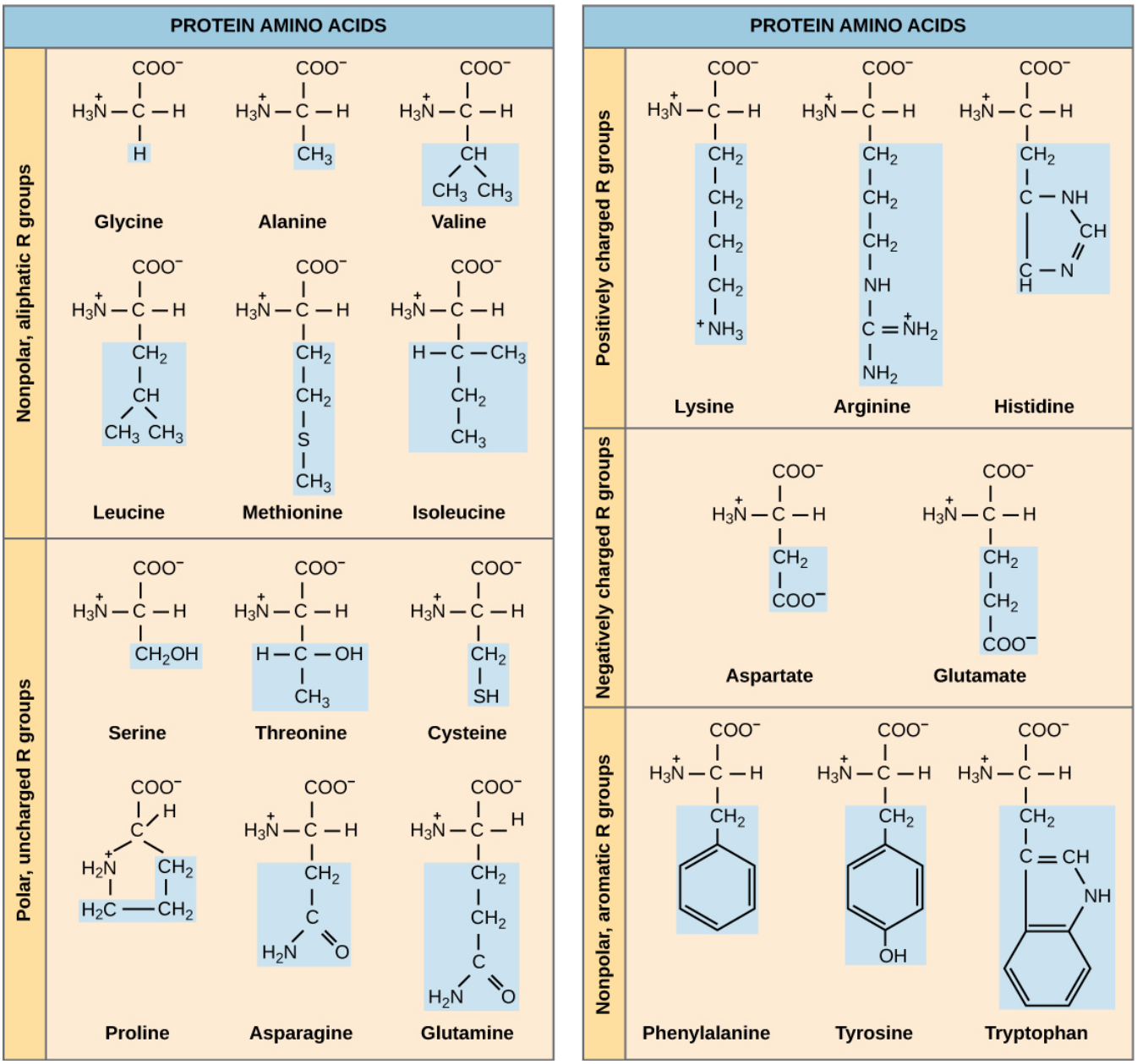


Figure 3.5.2.1: Structures of the 20 amino acids found in proteins are shown. Each amino acid is composed of an amino group (NH_3^+), a carboxyl group (COO^-), and a side chain (blue). The side chain may be nonpolar, polar, or charged, as well as large or small. It is the variety of amino acid side chains that gives rise to the incredible variation of protein structure and function.

https://bio.libretexts.org/@go/page/82937

Video



The Central Dogma: DNA Encodes RNA; RNA Encodes Protein

The flow of genetic information in cells from DNA to mRNA to protein is described by the Central Dogma (Figure 3.5.2.2), which states that genes specify the sequence of mRNAs, which in turn specify the sequence of proteins. The decoding of one molecule to another is performed by specific proteins and RNAs. Because the information stored in DNA is so central to cellular function, it makes intuitive sense that the cell would make mRNA copies of this information for protein synthesis, while keeping the DNA itself intact and protected. The copying of DNA to RNA is relatively straightforward, with one nucleotide being added to the mRNA strand for every nucleotide read in the DNA strand. The translation to protein is a bit more complex because three mRNA nucleotides correspond to one amino acid in the polypeptide sequence. However, the translation to protein is still systematic and colinear, such that nucleotides 1 to 3 correspond to amino acid 1, nucleotides 4 to 6 correspond to amino acid 2, and so on.

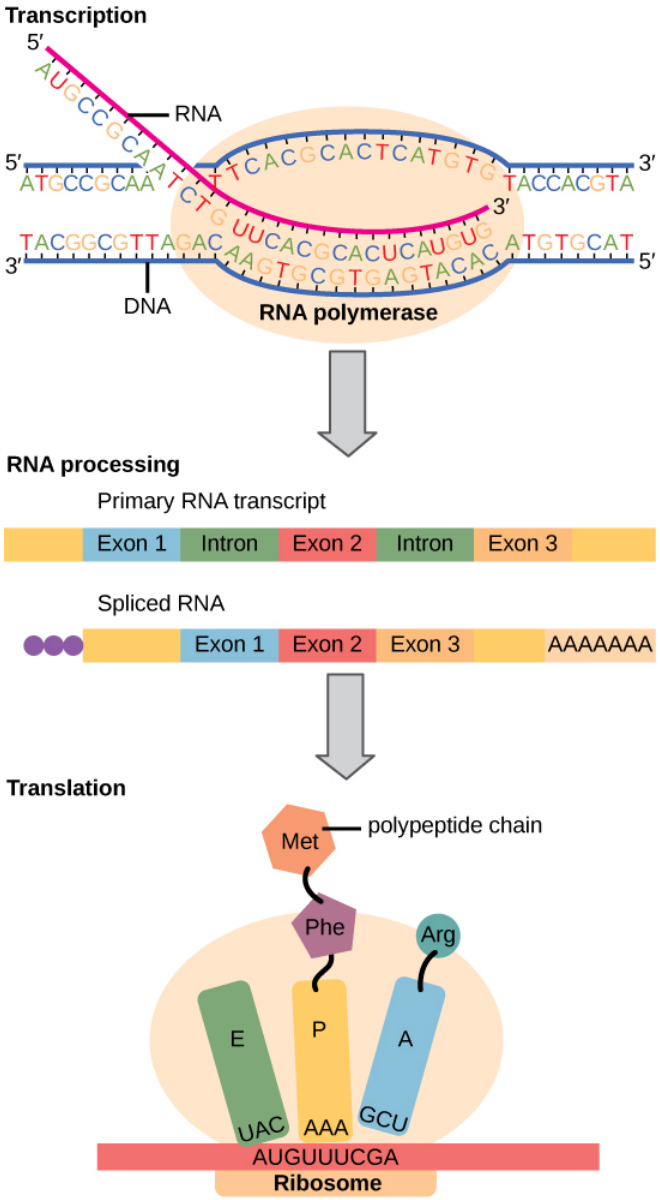
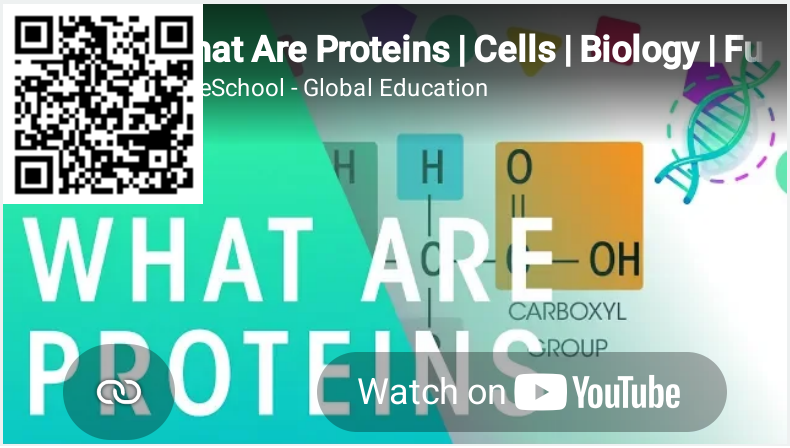


Figure 3.5.2.2: Instructions on DNA are transcribed onto messenger RNA. Ribosomes are able to read the genetic information inscribed on a strand of messenger RNA and use this information to string amino acids together into a protein.

Video



Video



The Genetic Code Is Degenerate and Universal

Given the different numbers of "letters" in the mRNA and protein "alphabets," scientists theorized that combinations of nucleotides corresponded to single amino acids. Nucleotide doublets would not be sufficient to specify every amino acid because there are only 16 possible two-nucleotide combinations (4^2). In contrast, there are 64 possible nucleotide triplets (4^3), which is far more than the number of amino acids. Scientists theorized that amino acids were encoded by nucleotide triplets and that the genetic code was degenerate. In other words, a given amino acid could be encoded by more than one nucleotide triplet. This was later confirmed experimentally; Francis Crick and Sydney Brenner used the chemical mutagen proflavin to insert one, two, or three nucleotides into the gene of a virus. When one or two nucleotides were inserted, protein synthesis was completely abolished. When three nucleotides were inserted, the protein was synthesized and functional. This demonstrated that three nucleotides specify each amino acid. These nucleotide triplets are called codons. The insertion of one or two nucleotides completely changed the triplet reading frame, thereby altering the message for every subsequent amino acid (Figure 3.5.2.4). Though insertion of three nucleotides caused an extra amino acid to be inserted during translation, the integrity of the rest of the protein was maintained.

Scientists painstakingly solved the genetic code by translating synthetic mRNAs in vitro and sequencing the proteins they specified (Figure 3.5.2.3).

Second letter

First letter	U	C	A	G	Third letter
U	UUU Phe UUC Phe UUA Leu UUG Leu	UCU Ser UCC Ser UCA Ser UCG Ser	UAU Tyr UAC Tyr **UAA Stop** **UAG Stop**	UGU Cys UGC Cys **UGA Stop** UGG Trp	U C A G
C	CUU Leu CUC Leu CUA Leu CUG Leu	CCU Pro CCC Pro CCA Pro CCG Pro	CAU His CAC His CAA Gln CAG Gln	CGU Arg CGC Arg CGA Arg CGG Arg	U C A G
A	AUU Ile AUC Ile AUA Ile **AUG Met**	ACU Thr ACC Thr ACA Thr ACG Thr	AAU Asn AAC Asn AAA Lys AAG Lys	AGU Ser AGC Ser AGA Arg AGG Arg	U C A G
G	GUU Val GUC Val GUA Val GUG Val	GCU Ala GCC Ala GCA Ala GCG Ala	GAU Asp GAC Asp GAA Glu GAG Glu	GGU Gly GGC Gly GGA Gly GGG Gly	U C A G

Figure 3.5.2.3: This figure shows the genetic code for translating each nucleotide triplet in mRNA into an amino acid or a termination signal in a nascent protein. (credit: modification of work by NIH)

In addition to instructing the addition of a specific amino acid to a polypeptide chain, three of the 64 codons terminate protein synthesis and release the polypeptide from the translation machinery. These triplets are called nonsense codons, or stop codons.

Another codon, AUG, also has a special function. In addition to specifying the amino acid methionine, it also serves as the start codon to initiate translation. The reading frame for translation is set by the AUG start codon near the 5' end of the mRNA.

The genetic code is universal. With a few exceptions, virtually all species use the same genetic code for protein synthesis. Conservation of codons means that a purified mRNA encoding the globin protein in horses could be transferred to a tulip cell, and the tulip would synthesize horse globin. That there is only one genetic code is powerful evidence that all of life on Earth shares a common origin, especially considering that there are about 10^{84} possible combinations of 20 amino acids and 64 triplet codons.

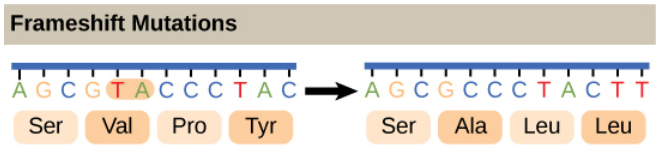


Figure 3.5.2.4: The deletion of two nucleotides shifts the reading frame of an mRNA and changes the entire protein message, creating a nonfunctional protein or terminating protein synthesis altogether.

Degeneracy is believed to be a cellular mechanism to reduce the negative impact of random mutations. Codons that specify the same amino acid typically only differ by one nucleotide. In addition, amino acids with chemically similar side chains are encoded by similar codons. This nuance of the genetic code ensures that a single-nucleotide substitution mutation might either specify the same amino acid but have no effect or specify a similar amino acid, preventing the protein from being rendered completely nonfunctional.

Scientific Method Connection: Which Has More DNA: A Kiwi or a Strawberry?

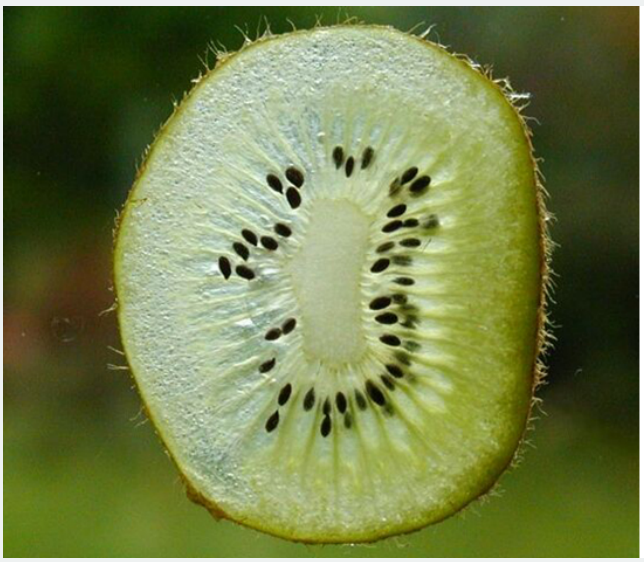




Figure 3.5.2.5: Do you think that a kiwi or a strawberry has more DNA per fruit? (credit “kiwi”: "Kelbv"/Flickr; credit: “strawberry”: Alisdair McDiarmid)

Question: Would a kiwifruit and strawberry that are approximately the same size (Figure 3.5.2.5) also have approximately the same amount of DNA?

Background: Genes are carried on chromosomes and are made of DNA. All mammals are diploid, meaning they have two copies of each chromosome. However, not all plants are diploid. The common strawberry is octoploid (8*n*) and the cultivated kiwi is hexaploid (6*n*). Research the total number of chromosomes in the cells of each of these fruits and think about how this might correspond to the amount of DNA in these fruits’ cell nuclei. Read about the technique of DNA isolation to understand how each step in the isolation protocol helps liberate and precipitate DNA.

Hypothesis: Hypothesize whether you would be able to detect a difference in DNA quantity from similarly sized strawberries and kiwis. Which fruit do you think would yield more DNA?

Test your hypothesis: Isolate the DNA from a strawberry and a kiwi that are similarly sized. Perform the experiment in at least triplicate for each fruit.

1. Prepare a bottle of DNA extraction buffer from 900 mL water, 50 mL dish detergent, and two teaspoons of table salt. Mix by inversion (cap it and turn it upside down a few times).
2. Grind a strawberry and a kiwifruit by hand in a plastic bag, or using a mortar and pestle, or with a metal bowl and the end of a blunt instrument. Grind for at least two minutes per fruit.
3. Add 10 mL of the DNA extraction buffer to each fruit, and mix well for at least one minute.
4. Remove cellular debris by filtering each fruit mixture through cheesecloth or porous cloth and into a funnel placed in a test tube or an appropriate container.
5. Pour ice-cold ethanol or isopropanol (rubbing alcohol) into the test tube. You should observe white, precipitated DNA.
6. Gather the DNA from each fruit by winding it around separate glass rods.

Record your observations: Because you are not quantitatively measuring DNA volume, you can record for each trial whether the two fruits produced the same or different amounts of DNA as observed by eye. If one or the other fruit produced noticeably more DNA, record this as well. Determine whether your observations are consistent with several pieces of each fruit.

Analyze your data: Did you notice an obvious difference in the amount of DNA produced by each fruit? Were your results reproducible?

Draw a conclusion: Given what you know about the number of chromosomes in each fruit, can you conclude that chromosome number necessarily correlates to DNA amount? Can you identify any drawbacks to this procedure? If you had access to a laboratory, how could you standardize your comparison and make it more quantitative?

Summary

The genetic code refers to the DNA alphabet (A, T, C, G), the RNA alphabet (A, U, C, G), and the polypeptide alphabet (20 amino acids). The Central Dogma describes the flow of genetic information in the cell from genes to mRNA to proteins. Genes are used to make mRNA by the process of transcription; mRNA is used to synthesize proteins by the process of translation. The genetic code is degenerate because 64 triplet codons in mRNA specify only 20 amino acids and three nonsense codons. Almost every species on the planet uses the same genetic code.

Glossary

Central Dogma
states that genes specify the sequence of mRNAs, which in turn specify the sequence of proteins

codon
three consecutive nucleotides in mRNA that specify the insertion of an amino acid or the release of a polypeptide chain during translation

colinear
in terms of RNA and protein, three “units” of RNA (nucleotides) specify one “unit” of protein (amino acid) in a consecutive fashion

degeneracy
(of the genetic code) describes that a given amino acid can be encoded by more than one nucleotide triplet; the code is degenerate, but not ambiguous

nonsense codon
one of the three mRNA codons that specifies termination of translation

reading frame
sequence of triplet codons in mRNA that specify a particular protein; a ribosome shift of one or two nucleotides in either direction completely abolishes synthesis of that protein

This page titled 3.5.2: The Genetic Code is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.1: The Genetic Code** by OpenStax is licensed CC BY 4.0.

3.5.3: Prokaryotic Transcription

Learning Objectives

- List the different steps in prokaryotic transcription
- Discuss the role of promoters in prokaryotic transcription
- Describe how and when transcription is terminated

The prokaryotes, which include bacteria and archaea, are mostly single-celled organisms that, by definition, lack membrane-bound nuclei and other organelles. A bacterial chromosome is a covalently closed circle that, unlike eukaryotic chromosomes, is not organized around histone proteins. The central region of the cell in which prokaryotic DNA resides is called the nucleoid. In addition, prokaryotes often have abundant plasmids, which are shorter circular DNA molecules that may only contain one or a few genes. Plasmids can be transferred independently of the bacterial chromosome during cell division and often carry traits such as antibiotic resistance.

Transcription in prokaryotes (and in eukaryotes) requires the DNA double helix to partially unwind in the region of mRNA synthesis. The region of unwinding is called a transcription bubble. Transcription always proceeds from the same DNA strand for each gene, which is called the template strand. The mRNA product is complementary to the template strand and is almost identical to the other DNA strand, called the nontemplate strand. The only difference is that in mRNA, all of the T nucleotides are replaced with U nucleotides. In an RNA double helix, A can bind U via two hydrogen bonds, just as in A–T pairing in a DNA double helix.

The nucleotide pair in the DNA double helix that corresponds to the site from which the first 5' mRNA nucleotide is transcribed is called the +1 site, or the initiation site. Nucleotides preceding the initiation site are given negative numbers and are designated upstream. Conversely, nucleotides following the initiation site are denoted with "+" numbering and are called downstream nucleotides.

Initiation of Transcription in Prokaryotes

Prokaryotes do not have membrane-enclosed nuclei. Therefore, the processes of transcription, translation, and mRNA degradation can all occur simultaneously. The intracellular level of a bacterial protein can quickly be amplified by multiple transcription and translation events occurring concurrently on the same DNA template. Prokaryotic transcription often covers more than one gene and produces polycistronic mRNAs that specify more than one protein.

Our discussion here will exemplify transcription by describing this process in *Escherichia coli*, a well-studied bacterial species. Although some differences exist between transcription in *E. coli* and transcription in archaea, an understanding of *E. coli* transcription can be applied to virtually all bacterial species.

Prokaryotic RNA Polymerase

Prokaryotes use the same RNA polymerase to transcribe all of their genes. In *E. coli*, the polymerase is composed of five polypeptide subunits, two of which are identical. Four of these subunits, denoted α, α, β, and β' comprise the polymerase core enzyme. These subunits assemble every time a gene is transcribed, and they disassemble once transcription is complete. Each subunit has a unique role; the two α-subunits are necessary to assemble the polymerase on the DNA; the β-subunit binds to the ribonucleoside triphosphate that will become part of the nascent "recently born" mRNA molecule; and the β' binds the DNA template strand. The fifth subunit, σ, is involved only in transcription initiation. It confers transcriptional specificity such that the polymerase begins to synthesize mRNA from an appropriate initiation site. Without σ, the core enzyme would transcribe from random sites and would produce mRNA molecules that specified protein gibberish. The polymerase comprised of all five subunits is called the holoenzyme.

Prokaryotic Promoters

A promoter is a DNA sequence onto which the transcription machinery binds and initiates transcription. In most cases, promoters exist upstream of the genes they regulate. The specific sequence of a promoter is very important because it determines whether the corresponding gene is transcribed all the time, some of the time, or infrequently. Although promoters vary among prokaryotic genomes, a few elements are conserved. At the -10 and -35 regions upstream of the initiation site, there are two promoter consensus

sequences, or regions that are similar across all promoters and across various bacterial species (Figure 3.5.3.1). The -10 consensus sequence, called the -10 region, is TATAAT. The -35 sequence, TTGACA, is recognized and bound by σ. Once this interaction is made, the subunits of the core enzyme bind to the site. The A–T-rich -10 region facilitates unwinding of the DNA template, and several phosphodiester bonds are made. The transcription initiation phase ends with the production of abortive transcripts, which are polymers of approximately 10 nucleotides that are made and released.

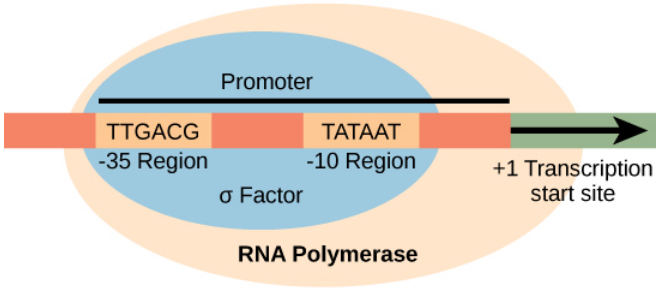
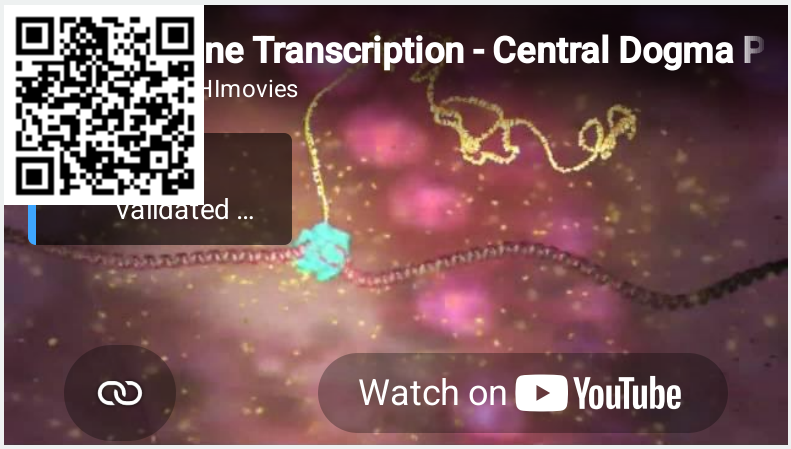


Figure 3.5.3.1: The σ subunit of prokaryotic RNA polymerase recognizes consensus sequences found in the promoter region upstream of the transcription start sight. The σ subunit dissociates from the polymerase after transcription has been initiated.

Link to Learning



View this MolecularMovies animation to see the first part of transcription and the base sequence repetition of the TATA box.

Elongation and Termination in Prokaryotes

The transcription elongation phase begins with the release of the σ subunit from the polymerase. The dissociation of σ allows the core enzyme to proceed along the DNA template, synthesizing mRNA in the 5' to 3' direction at a rate of approximately 40 nucleotides per second. As elongation proceeds, the DNA is continuously unwound ahead of the core enzyme and rewound behind it (Figure 3.5.3.2). The base pairing between DNA and RNA is not stable enough to maintain the stability of the mRNA synthesis components. Instead, the RNA polymerase acts as a stable linker between the DNA template and the nascent RNA strands to ensure that elongation is not interrupted prematurely.

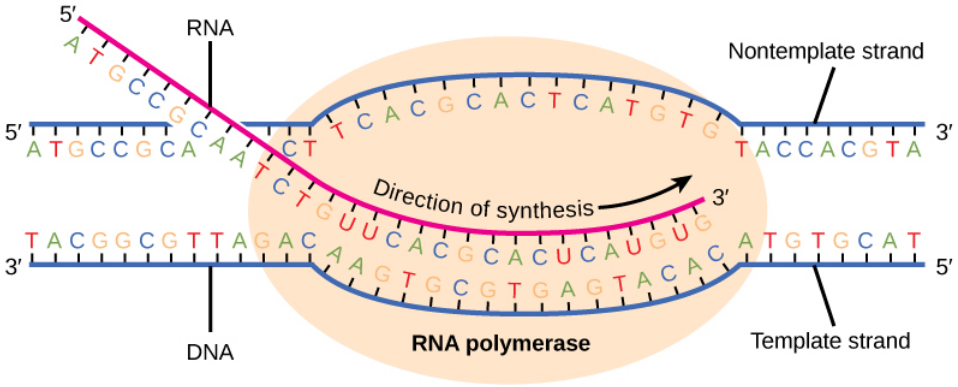


Figure 3.5.3.2: During elongation, the prokaryotic RNA polymerase tracks along the DNA template, synthesizes mRNA in the 5' to 3' direction, and unwinds and rewinds the DNA as it is read.

Prokaryotic Termination Signals

Once a gene is transcribed, the prokaryotic polymerase needs to be instructed to dissociate from the DNA template and liberate the newly made mRNA. Depending on the gene being transcribed, there are two kinds of termination signals. One is protein-based and the other is RNA-based. Rho-dependent termination is controlled by the rho protein, which tracks along behind the polymerase on the growing mRNA chain. Near the end of the gene, the polymerase encounters a run of G nucleotides on the DNA template and it stalls. As a result, the rho protein collides with the polymerase. The interaction with rho releases the mRNA from the transcription bubble.

Rho-independent termination is controlled by specific sequences in the DNA template strand. As the polymerase nears the end of the gene being transcribed, it encounters a region rich in C–G nucleotides. The mRNA folds back on itself, and the complementary C–G nucleotides bind together. The result is a stable hairpin that causes the polymerase to stall as soon as it begins to transcribe a region rich in A–T nucleotides. The complementary U–A region of the mRNA transcript forms only a weak interaction with the template DNA. This, coupled with the stalled polymerase, induces enough instability for the core enzyme to break away and liberate the new mRNA transcript.

Upon termination, the process of transcription is complete. By the time termination occurs, the prokaryotic transcript would already have been used to begin synthesis of numerous copies of the encoded protein because these processes can occur concurrently. The unification of transcription, translation, and even mRNA degradation is possible because all of these processes occur in the same 5' to 3' direction, and because there is no membranous compartmentalization in the prokaryotic cell (Figure 3.5.3.3). In contrast, the presence of a nucleus in eukaryotic cells precludes simultaneous transcription and translation.

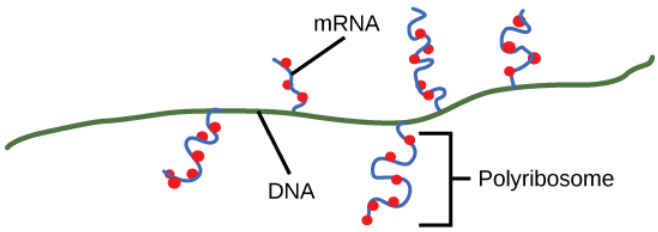
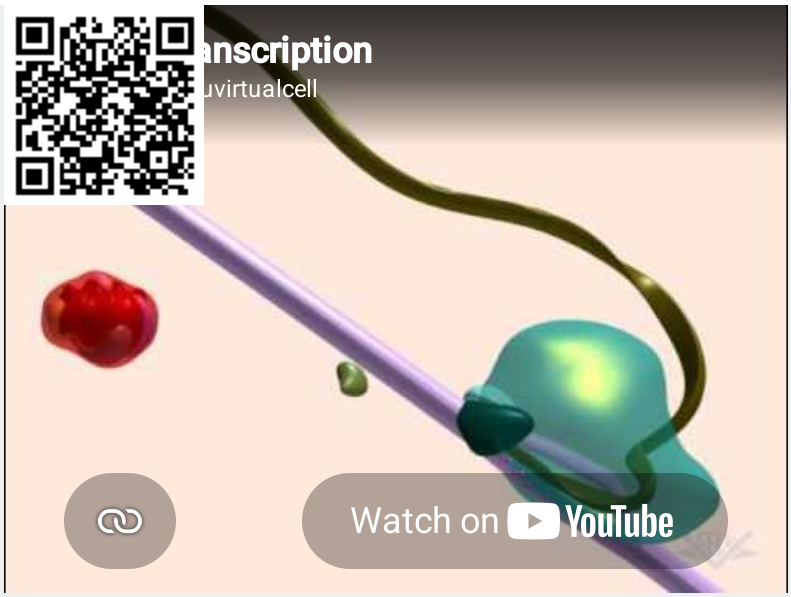


Figure 3.5.3.3: Multiple polymerases can transcribe a single bacterial gene while numerous ribosomes concurrently translate the mRNA transcripts into polypeptides. In this way, a specific protein can rapidly reach a high concentration in the bacterial cell.

Link to Learning



Visit this BioStudio animation to see the process of prokaryotic transcription.

Summary

In prokaryotes, mRNA synthesis is initiated at a promoter sequence on the DNA template comprising two consensus sequences that recruit RNA polymerase. The prokaryotic polymerase consists of a core enzyme of four protein subunits and a σ protein that assists only with initiation. Elongation synthesizes mRNA in the 5' to 3' direction at a rate of 40 nucleotides per second. Termination liberates the mRNA and occurs either by rho protein interaction or by the formation of an mRNA hairpin.

Glossary

consensus
DNA sequence that is used by many species to perform the same or similar functions

core enzyme
prokaryotic RNA polymerase consisting of α, α, β, and β' but missing σ; this complex performs elongation

downstream
nucleotides following the initiation site in the direction of mRNA transcription; in general, sequences that are toward the 3' end relative to a site on the mRNA

hairpin
structure of RNA when it folds back on itself and forms intramolecular hydrogen bonds between complementary nucleotides

holoenzyme
prokaryotic RNA polymerase consisting of α, α, β, β', and σ; this complex is responsible for transcription initiation

initiation site
nucleotide from which mRNA synthesis proceeds in the 5' to 3' direction; denoted with a “+1”

nontemplate strand
strand of DNA that is not used to transcribe mRNA; this strand is identical to the mRNA except that T nucleotides in the DNA are replaced by U nucleotides in the mRNA

plasmid

extrachromosomal, covalently closed, circular DNA molecule that may only contain one or a few genes; common in prokaryotes

promoter

DNA sequence to which RNA polymerase and associated factors bind and initiate transcription

Rho-dependent termination

in prokaryotes, termination of transcription by an interaction between RNA polymerase and the rho protein at a run of G nucleotides on the DNA template

Rho-independent

termination sequence-dependent termination of prokaryotic mRNA synthesis; caused by hairpin formation in the mRNA that stalls the polymerase

TATA box

conserved promoter sequence in eukaryotes and prokaryotes that helps to establish the initiation site for transcription

template strand

strand of DNA that specifies the complementary mRNA molecule

transcription bubble

region of locally unwound DNA that allows for transcription of mRNA

upstream

nucleotides preceding the initiation site; in general, sequences toward the 5' end relative to a site on the mRNA

This page titled 3.5.3: Prokaryotic Transcription is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.2: Prokaryotic Transcription** by OpenStax is licensed CC BY 4.0.

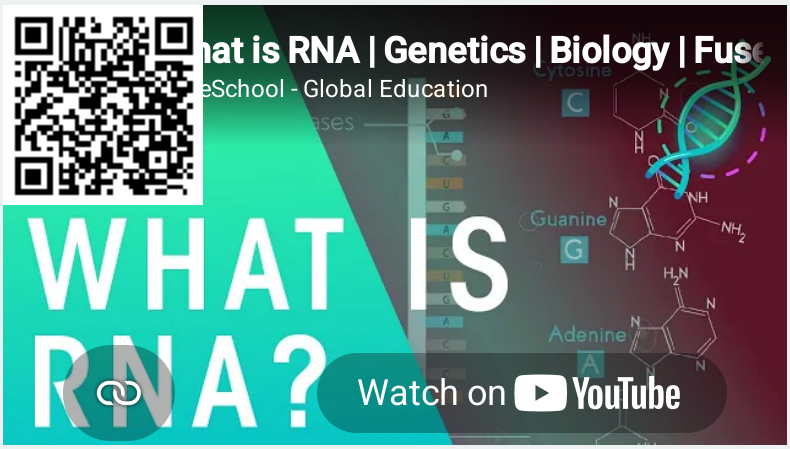
3.5.4: Eukaryotic Transcription

Learning Objectives

- List the steps in eukaryotic transcription
- Discuss the role of RNA polymerases in transcription
- Compare and contrast the three RNA polymerases
- Explain the significance of transcription factors

Prokaryotes and eukaryotes perform fundamentally the same process of transcription, with a few key differences. The most important difference between prokaryotes and eukaryotes is the latter's membrane-bound nucleus and organelles. With the genes bound in a nucleus, the eukaryotic cell must be able to transport its mRNA to the cytoplasm and must protect its mRNA from degrading before it is translated. Eukaryotes also employ three different polymerases that each transcribe a different subset of genes. Eukaryotic mRNAs are usually monogenic, meaning that they specify a single protein.

Video



Initiation of Transcription in Eukaryotes

Unlike the prokaryotic polymerase that can bind to a DNA template on its own, eukaryotes require several other proteins, called transcription factors, to first bind to the promoter region and then help recruit the appropriate polymerase.

Video



The Three Eukaryotic RNA Polymerases

The features of eukaryotic mRNA synthesis are markedly more complex those of prokaryotes. Instead of a single polymerase comprising five subunits, the eukaryotes have three polymerases that are each made up of 10 subunits or more. Each eukaryotic polymerase also requires a distinct set of transcription factors to bring it to the DNA template.

RNA polymerase I is located in the nucleolus, a specialized nuclear substructure in which ribosomal RNA (rRNA) is transcribed, processed, and assembled into ribosomes (Table 3.5.4.1). The rRNA molecules are considered structural RNAs because they have a cellular role but are not translated into protein. The rRNAs are components of the ribosome and are essential to the process of translation. RNA polymerase I synthesizes all of the rRNAs except for the 5S rRNA molecule. The “S” designation applies to “Svedberg” units, a nonadditive value that characterizes the speed at which a particle sediments during centrifugation.

Table 3.5.4.1: Locations, Products, and Sensitivities of the Three Eukaryotic RNA Polymerases

RNA Polymerase	Cellular Compartment	Product of Transcription	α-Amanitin Sensitivity
I	Nucleolus	All rRNAs except 5S rRNA	Insensitive
II	Nucleus	All protein-coding nuclear pre-mRNAs	Extremely sensitive
III	Nucleus	5S rRNA, tRNAs, and small nuclear RNAs	Moderately sensitive

RNA polymerase II is located in the nucleus and synthesizes all protein-coding nuclear pre-mRNAs. Eukaryotic pre-mRNAs undergo extensive processing after transcription but before translation. For clarity, this module’s discussion of transcription and translation in eukaryotes will use the term “mRNAs” to describe only the mature, processed molecules that are ready to be translated. RNA polymerase II is responsible for transcribing the overwhelming majority of eukaryotic genes.

RNA polymerase III is also located in the nucleus. This polymerase transcribes a variety of structural RNAs that includes the 5S pre-rRNA, transfer pre-RNAs (pre-tRNAs), and small nuclear pre-RNAs. The tRNAs have a critical role in translation; they serve as the adaptor molecules between the mRNA template and the growing polypeptide chain. Small nuclear RNAs have a variety of functions, including “splicing” pre-mRNAs and regulating transcription factors.

A scientist characterizing a new gene can determine which polymerase transcribes it by testing whether the gene is expressed in the presence of a particular mushroom poison, α-amanitin (table above). Interestingly, α-amanitin produced by *Amanita phalloides*, the Death Cap mushroom, affects the three polymerases very differently. RNA polymerase I is completely insensitive to α-amanitin, meaning that the polymerase can transcribe DNA in vitro in the presence of this poison. In contrast, RNA polymerase II is extremely sensitive to α-amanitin, and RNA polymerase III is moderately sensitive. Knowing the transcribing polymerase can clue a researcher into the general function of the gene being studied. Because RNA polymerase II transcribes the vast majority of genes, we will focus on this polymerase in our subsequent discussions about eukaryotic transcription factors and promoters.

Structure of an RNA Polymerase II Promoter

Eukaryotic promoters are much larger and more complex than prokaryotic promoters, but both have a TATA box. For example, in the mouse thymidine kinase gene, the TATA box is located at approximately -30 relative to the initiation (+1) site (Figure 3.5.4.1). For this gene, the exact TATA box sequence is TATAAAA, as read in the 5' to 3' direction on the nontemplate strand. This sequence is not identical to the *E. coli* TATA box, but it conserves the A–T rich element. The thermostability of A–T bonds is low and this helps the DNA template to locally unwind in preparation for transcription.

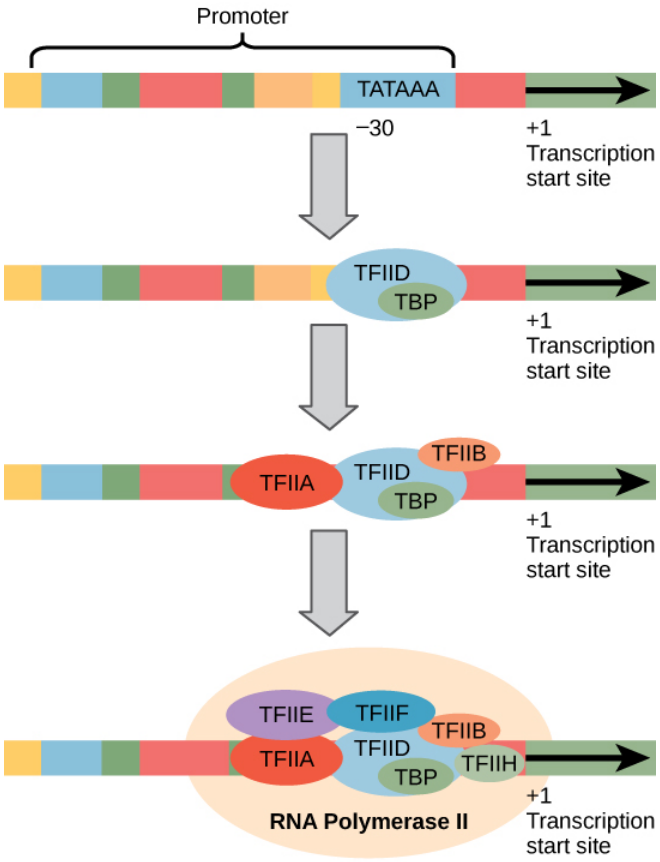


Figure 3.5.4.1: A generalized promoter of a gene transcribed by RNA polymerase II is shown. Transcription factors recognize the promoter. RNA polymerase II then binds and forms the transcription initiation complex.

Art Connection

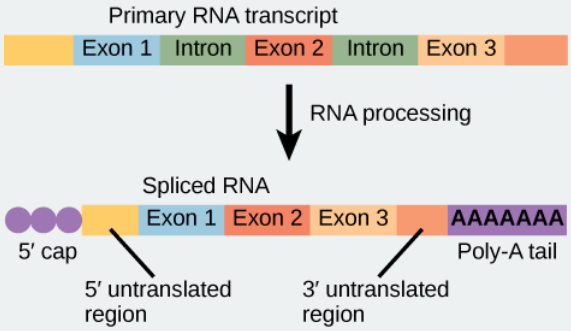


Figure 3.5.4.2: Eukaryotic mRNA contains introns that must be spliced out. A 5′ cap and 3′ poly-A tail are also added.

A scientist splices a eukaryotic promoter in front of a bacterial gene and inserts the gene in a bacterial chromosome. Would you expect the bacteria to transcribe the gene?

The mouse genome includes one gene and two pseudogenes for cytoplasmic thymidine kinase. Pseudogenes are genes that have lost their protein-coding ability or are no longer expressed by the cell. These pseudogenes are copied from mRNA and incorporated into the chromosome. For example, the mouse thymidine kinase promoter also has a conserved CAAT box (GGCCAATCT) at approximately -80. This sequence is essential and is involved in binding transcription factors. Further upstream of the TATA box, eukaryotic promoters may also contain one or more GC-rich boxes (GGCG) or octamer boxes (ATTTGCAT). These elements bind cellular factors that increase the efficiency of transcription initiation and are often identified in more “active” genes that are constantly being expressed by the cell.

Transcription Factors for RNA Polymerase II

The complexity of eukaryotic transcription does not end with the polymerases and promoters. An army of basal transcription factors, enhancers, and silencers also help to regulate the frequency with which pre-mRNA is synthesized from a gene. Enhancers and silencers affect the efficiency of transcription but are not necessary for transcription to proceed. Basal transcription factors are crucial in the formation of a preinitiation complex on the DNA template that subsequently recruits RNA polymerase II for transcription initiation.

The names of the basal transcription factors begin with "TFII" (this is the transcription factor for RNA polymerase II) and are specified with the letters A–J. The transcription factors systematically fall into place on the DNA template, with each one further stabilizing the preinitiation complex and contributing to the recruitment of RNA polymerase II.

The processes of bringing RNA polymerases I and III to the DNA template involve slightly less complex collections of transcription factors, but the general theme is the same. Eukaryotic transcription is a tightly regulated process that requires a variety of proteins to interact with each other and with the DNA strand. Although the process of transcription in eukaryotes involves a greater metabolic investment than in prokaryotes, it ensures that the cell transcribes precisely the pre-mRNAs that it needs for protein synthesis.

Evolution Connection: The Evolution of Promoters

The evolution of genes may be a familiar concept. Mutations can occur in genes during DNA replication, and the result may or may not be beneficial to the cell. By altering an enzyme, structural protein, or some other factor, the process of mutation can transform functions or physical features. However, eukaryotic promoters and other gene regulatory sequences may evolve as well. For instance, consider a gene that, over many generations, becomes more valuable to the cell. Maybe the gene encodes a structural protein that the cell needs to synthesize in abundance for a certain function. If this is the case, it would be beneficial to the cell for that gene's promoter to recruit transcription factors more efficiently and increase gene expression.

Scientists examining the evolution of promoter sequences have reported varying results. In part, this is because it is difficult to infer exactly where a eukaryotic promoter begins and ends. Some promoters occur within genes; others are located very far upstream, or even downstream, of the genes they are regulating. However, when researchers limited their examination to human core promoter sequences that were defined experimentally as sequences that bind the preinitiation complex, they found that promoters evolve even faster than protein-coding genes.

It is still unclear how promoter evolution might correspond to the evolution of humans or other higher organisms. However, the evolution of a promoter to effectively make more or less of a given gene product is an intriguing alternative to the evolution of the genes themselves.[1]

Promoter Structures for RNA Polymerases I and III

In eukaryotes, the conserved promoter elements differ for genes transcribed by RNA polymerases I, II, and III. RNA polymerase I transcribes genes that have two GC-rich promoter sequences in the -45 to +20 region. These sequences alone are sufficient for transcription initiation to occur, but promoters with additional sequences in the region from -180 to -105 upstream of the initiation site will further enhance initiation. Genes that are transcribed by RNA polymerase III have upstream promoters or promoters that occur within the genes themselves.

Eukaryotic Elongation and Termination

Following the formation of the preinitiation complex, the polymerase is released from the other transcription factors, and elongation is allowed to proceed as it does in prokaryotes with the polymerase synthesizing pre-mRNA in the 5' to 3' direction. As discussed previously, RNA polymerase II transcribes the major share of eukaryotic genes, so this section will focus on how this polymerase accomplishes elongation and termination.

Although the enzymatic process of elongation is essentially the same in eukaryotes and prokaryotes, the DNA template is more complex. When eukaryotic cells are not dividing, their genes exist as a diffuse mass of DNA and proteins called chromatin. The DNA is tightly packaged around charged histone proteins at repeated intervals. These DNA–histone complexes, collectively called nucleosomes, are regularly spaced and include 146 nucleotides of DNA wound around eight histones like thread around a spool.

For polynucleotide synthesis to occur, the transcription machinery needs to move histones out of the way every time it encounters a nucleosome. This is accomplished by a special protein complex called FACT, which stands for “facilitates chromatin transcription.” This complex pulls histones away from the DNA template as the polymerase moves along it. Once the pre-mRNA is synthesized, the FACT complex replaces the histones to recreate the nucleosomes.

The termination of transcription is different for the different polymerases. Unlike in prokaryotes, elongation by RNA polymerase II in eukaryotes takes place 1,000–2,000 nucleotides beyond the end of the gene being transcribed. This pre-mRNA tail is subsequently removed by cleavage during mRNA processing. On the other hand, RNA polymerases I and III require termination signals. Genes transcribed by RNA polymerase I contain a specific 18-nucleotide sequence that is recognized by a termination protein. The process of termination in RNA polymerase III involves an mRNA hairpin similar to rho-independent termination of transcription in prokaryotes.

Summary

Transcription in eukaryotes involves one of three types of polymerases, depending on the gene being transcribed. RNA polymerase II transcribes all of the protein-coding genes, whereas RNA polymerase I transcribes rRNA genes, and RNA polymerase III transcribes rRNA, tRNA, and small nuclear RNA genes. The initiation of transcription in eukaryotes involves the binding of several transcription factors to complex promoter sequences that are usually located upstream of the gene being copied. The mRNA is synthesized in the 5' to 3' direction, and the FACT complex moves and reassembles nucleosomes as the polymerase passes by. Whereas RNA polymerases I and III terminate transcription by protein- or RNA hairpin-dependent methods, RNA polymerase II transcribes for 1,000 or more nucleotides beyond the gene template and cleaves the excess during pre-mRNA processing.

Art Connections

Figure 3.5.4.2: A scientist splices a eukaryotic promoter in front of a bacterial gene and inserts the gene in a bacterial chromosome. Would you expect the bacteria to transcribe the gene?

Answer

No. Prokaryotes use different promoters than eukaryotes.

Footnotes

1. 1 H Liang et al., “Fast evolution of core promoters in primate genomes,” *Molecular Biology and Evolution* 25 (2008): 1239–44.

Glossary

CAAT box
(GGCCAATCT) essential eukaryotic promoter sequence involved in binding transcription factors

FACT
complex that “facilitates chromatin transcription” by disassembling nucleosomes ahead of a transcribing RNA polymerase II and reassembling them after the polymerase passes by

GC-rich box
(GGCG) nonessential eukaryotic promoter sequence that binds cellular factors to increase the efficiency of transcription; may be present several times in a promoter

Octamer box
(ATTTGCAT) nonessential eukaryotic promoter sequence that binds cellular factors to increase the efficiency of transcription; may be present several times in a promoter

preinitiation complex
cluster of transcription factors and other proteins that recruit RNA polymerase II for transcription of a DNA template

small nuclear RNA

molecules synthesized by RNA polymerase III that have a variety of functions, including splicing pre-mRNAs and regulating transcription factors

---

This page titled 3.5.4: Eukaryotic Transcription is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.3: Eukaryotic Transcription** by OpenStax is licensed CC BY 4.0.

3.5.5: RNA Processing in Eukaryotes

Learning Objectives

- Describe the different steps in RNA processing
- Understand the significance of exons, introns, and splicing
- Explain how tRNAs and rRNAs are processed

After transcription, eukaryotic pre-mRNAs must undergo several processing steps before they can be translated. Eukaryotic (and prokaryotic) tRNAs and rRNAs also undergo processing before they can function as components in the protein synthesis machinery.

mRNA Processing

The eukaryotic pre-mRNA undergoes extensive processing before it is ready to be translated. The additional steps involved in eukaryotic mRNA maturation create a molecule with a much longer half-life than a prokaryotic mRNA. Eukaryotic mRNAs last for several hours, whereas the typical *E. coli* mRNA lasts no more than five seconds.

Pre-mRNAs are first coated in RNA-stabilizing proteins; these protect the pre-mRNA from degradation while it is processed and exported out of the nucleus. The three most important steps of pre-mRNA processing are the addition of stabilizing and signaling factors at the 5' and 3' ends of the molecule, and the removal of intervening sequences that do not specify the appropriate amino acids. In rare cases, the mRNA transcript can be “edited” after it is transcribed.

Video



5' Capping

While the pre-mRNA is still being synthesized, a 7-methylguanosine cap is added to the 5' end of the growing transcript by a phosphate linkage. This moiety (functional group) protects the nascent mRNA from degradation. In addition, factors involved in protein synthesis recognize the cap to help initiate translation by ribosomes.

3' Poly-A Tail

Once elongation is complete, the pre-mRNA is cleaved by an endonuclease between an AAUAAA consensus sequence and a GU-rich sequence, leaving the AAUAAA sequence on the pre-mRNA. An enzyme called poly-A polymerase then adds a string of approximately 200 A residues, called the poly-A tail. This modification further protects the pre-mRNA from degradation and signals the export of the cellular factors that the transcript needs to the cytoplasm.

Pre-mRNA Splicing

Eukaryotic genes are composed of exons, which correspond to protein-coding sequences (*ex*-on signifies that they are *ex*pressed), and *int*ervening sequences called introns (*int*-ron denotes their *int*ervening role), which may be involved in gene regulation but are

removed from the pre-mRNA during processing. Intron sequences in mRNA do not encode functional proteins.

The discovery of introns came as a surprise to researchers in the 1970s who expected that pre-mRNAs would specify protein sequences without further processing, as they had observed in prokaryotes. The genes of higher eukaryotes very often contain one or more introns. These regions may correspond to regulatory sequences; however, the biological significance of having many introns or having very long introns in a gene is unclear. It is possible that introns slow down gene expression because it takes longer to transcribe pre-mRNAs with lots of introns. Alternatively, introns may be nonfunctional sequence remnants left over from the fusion of ancient genes throughout evolution. This is supported by the fact that separate exons often encode separate protein subunits or domains. For the most part, the sequences of introns can be mutated without ultimately affecting the protein product.

All of a pre-mRNA's introns must be completely and precisely removed before protein synthesis. If the process errs by even a single nucleotide, the reading frame of the rejoined exons would shift, and the resulting protein would be dysfunctional. The process of removing introns and reconnecting exons is called splicing (Figure 3.5.5.2). Introns are removed and degraded while the pre-mRNA is still in the nucleus. Splicing occurs by a sequence-specific mechanism that ensures introns will be removed and exons rejoined with the accuracy and precision of a single nucleotide. The splicing of pre-mRNAs is conducted by complexes of proteins and RNA molecules called spliceosomes.

Art Connection

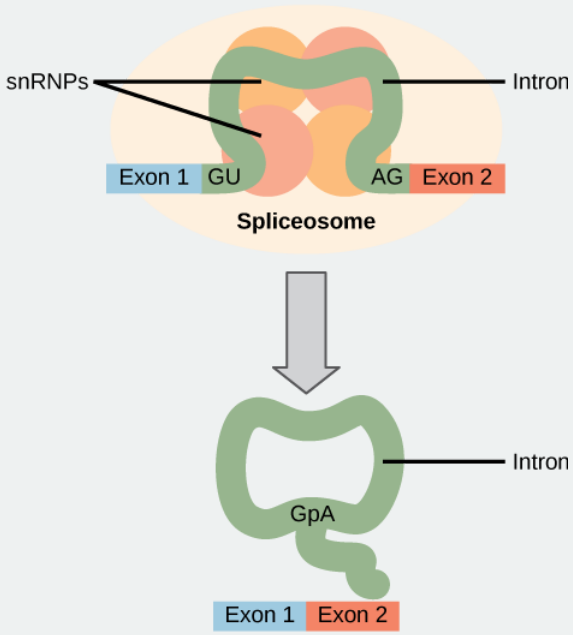
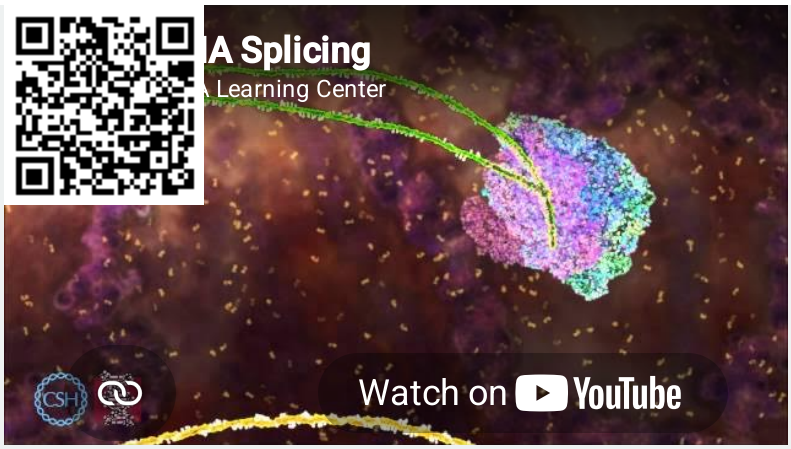


Figure 3.5.5.2: Pre-mRNA splicing involves the precise removal of introns from the primary RNA transcript. The splicing process is catalyzed by protein complexes called spliceosomes that are composed of proteins and RNA molecules called snRNAs. Spliceosomes recognize sequences at the 5' and 3' end of the intron.

Errors in splicing are implicated in cancers and other human diseases. What kinds of mutations might lead to splicing errors? Think of different possible outcomes if splicing errors occur.

Note that more than 70 individual introns can be present, and each has to undergo the process of splicing—in addition to 5' capping and the addition of a poly-A tail—just to generate a single, translatable mRNA molecule.

Link to Learning



See how introns are removed during RNA splicing at this website.

Processing of tRNAs and rRNAs

The tRNAs and rRNAs are structural molecules that have roles in protein synthesis; however, these RNAs are not themselves translated. Pre-rRNAs are transcribed, processed, and assembled into ribosomes in the nucleolus. Pre-tRNAs are transcribed and processed in the nucleus and then released into the cytoplasm where they are linked to free amino acids for protein synthesis.

Most of the tRNAs and rRNAs in eukaryotes and prokaryotes are first transcribed as a long precursor molecule that spans multiple rRNAs or tRNAs. Enzymes then cleave the precursors into subunits corresponding to each structural RNA. Some of the bases of pre-rRNAs are methylated; that is, a $–CH_3$ moiety (methyl functional group) is added for stability. Pre-tRNA molecules also undergo methylation. As with pre-mRNAs, subunit excision occurs in eukaryotic pre-RNAs destined to become tRNAs or rRNAs.

Mature rRNAs make up approximately 50 percent of each ribosome. Some of a ribosome's RNA molecules are purely structural, whereas others have catalytic or binding activities. Mature tRNAs take on a three-dimensional structure through intramolecular hydrogen bonding to position the amino acid binding site at one end and the anticodon at the other end (Figure 3.5.5.3). The anticodon is a three-nucleotide sequence in a tRNA that interacts with an mRNA codon through complementary base pairing.

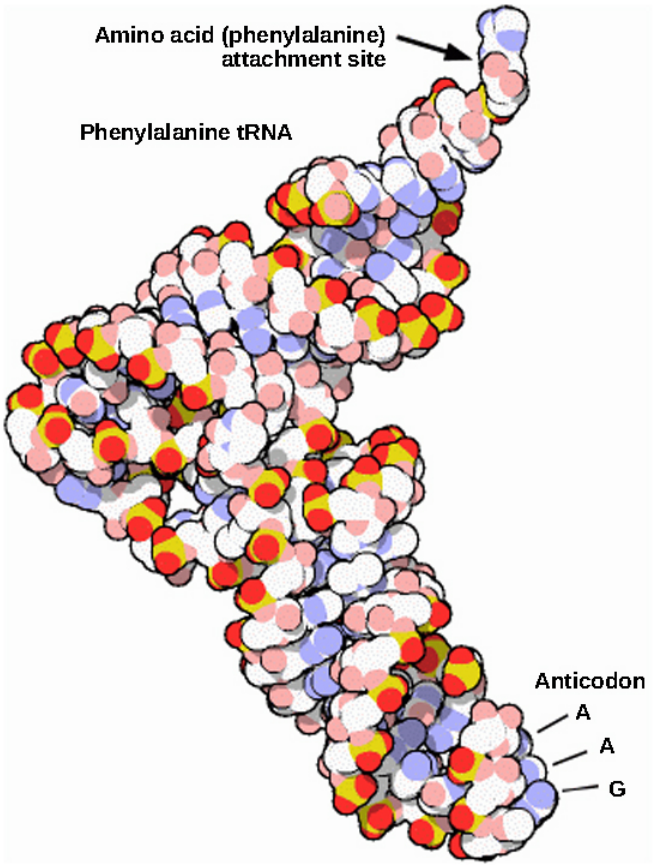


Figure 3.5.5.3: This is a space-filling model of a tRNA molecule that adds the amino acid phenylalanine to a growing polypeptide chain. The anticodon AAG binds the Codon UUC on the mRNA. The amino acid phenylalanine is attached to the other end of the tRNA.

Summary

Eukaryotic pre-mRNAs are modified with a 5' methylguanosine cap and a poly-A tail. These structures protect the mature mRNA from degradation and help export it from the nucleus. Pre-mRNAs also undergo splicing, in which introns are removed and exons are reconnected with single-nucleotide accuracy. Only finished mRNAs that have undergone 5' capping, 3' polyadenylation, and intron splicing are exported from the nucleus to the cytoplasm. Pre-rRNAs and pre-tRNAs may be processed by intramolecular cleavage, splicing, methylation, and chemical conversion of nucleotides. Rarely, RNA editing is also performed to insert missing bases after an mRNA has been synthesized.

Art Connections

Figure 3.5.5.2: Errors in splicing are implicated in cancers and other human diseases. What kinds of mutations might lead to splicing errors? Think of different possible outcomes if splicing errors occur.

Answer

Mutations in the spliceosome recognition sequence at each end of the intron, or in the proteins and RNAs that make up the spliceosome, may impair splicing. Mutations may also add new spliceosome recognition sites. Splicing errors could lead to introns being retained in spliced RNA, exons being excised, or changes in the location of the splice site.

Glossary

7-methylguanosine cap

modification added to the 5' end of pre-mRNAs to protect mRNA from degradation and assist translation

anticodon

three-nucleotide sequence in a tRNA molecule that corresponds to an mRNA codon

exon

sequence present in protein-coding mRNA after completion of pre-mRNA splicing

intron

non–protein-coding intervening sequences that are spliced from mRNA during processing

poly-A tail

modification added to the 3' end of pre-mRNAs to protect mRNA from degradation and assist mRNA export from the nucleus

RNA editing

direct alteration of one or more nucleotides in an mRNA that has already been synthesized

splicing

process of removing introns and reconnecting exons in a pre-mRNA

This page titled 3.5.5: RNA Processing in Eukaryotes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.4: RNA Processing in Eukaryotes** by OpenStax is licensed CC BY 4.0.

3.5.6: Ribosomes and Protein Synthesis

Learning Objectives

- Describe the different steps in protein synthesis
- Discuss the role of ribosomes in protein synthesis

The synthesis of proteins consumes more of a cell's energy than any other metabolic process. In turn, proteins account for more mass than any other component of living organisms (with the exception of water), and proteins perform virtually every function of a cell. The process of translation, or protein synthesis, involves the decoding of an mRNA message into a polypeptide product. Amino acids are covalently strung together by interlinking peptide bonds in lengths ranging from approximately 50 amino acid residues to more than 1,000. Each individual amino acid has an amino group (NH_2) and a carboxyl (COOH) group. Polypeptides are formed when the amino group of one amino acid forms an amide (i.e., peptide) bond with the carboxyl group of another amino acid (Figure 3.5.6.1). This reaction is catalyzed by ribosomes and generates one water molecule.

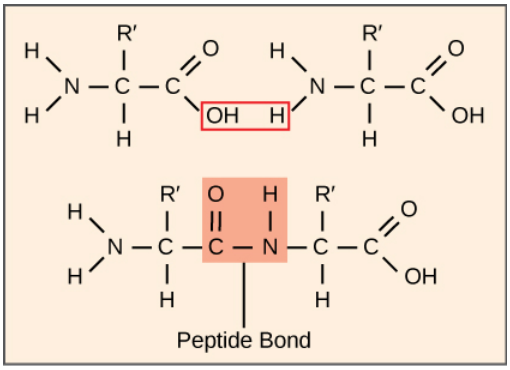


Figure 3.5.6.1: A peptide bond links the carboxyl end of one amino acid with the amino end of another, expelling one water molecule. For simplicity in this image, only the functional groups involved in the peptide bond are shown. The R and R' designations refer to the rest of each amino acid structure.

The Protein Synthesis Machinery

In addition to the mRNA template, many molecules and macromolecules contribute to the process of translation. The composition of each component may vary across species; for instance, ribosomes may consist of different numbers of rRNAs and polypeptides depending on the organism. However, the general structures and functions of the protein synthesis machinery are comparable from bacteria to human cells. Translation requires the input of an mRNA template, ribosomes, tRNAs, and various enzymatic factors.

Ribosomes

Even before an mRNA is translated, a cell must invest energy to build each of its ribosomes. In *E. coli*, there are between 10,000 and 70,000 ribosomes present in each cell at any given time. A ribosome is a complex macromolecule composed of structural and catalytic rRNAs, and many distinct polypeptides. In eukaryotes, the nucleolus is completely specialized for the synthesis and assembly of rRNAs.

Ribosomes exist in the cytoplasm in prokaryotes and in the cytoplasm and rough endoplasmic reticulum in eukaryotes. Mitochondria and chloroplasts also have their own ribosomes in the matrix and stroma, which look more similar to prokaryotic ribosomes (and have similar drug sensitivities) than the ribosomes just outside their outer membranes in the cytoplasm. Ribosomes dissociate into large and small subunits when they are not synthesizing proteins and reassociate during the initiation of translation. In *E. coli*, the small subunit is described as 30S, and the large subunit is 50S, for a total of 70S (recall that Svedberg units are not additive). Mammalian ribosomes have a small 40S subunit and a large 60S subunit, for a total of 80S. The small subunit is responsible for binding the mRNA template, whereas the large subunit sequentially binds tRNAs. Each mRNA molecule is simultaneously translated by many ribosomes, all synthesizing protein in the same direction: reading the mRNA from 5' to 3' and synthesizing the polypeptide from the N terminus to the C terminus. The complete mRNA/poly-ribosome structure is called a polysome.

Video



tRNAs

The tRNAs are structural RNA molecules that were transcribed from genes by RNA polymerase III. Depending on the species, 40 to 60 types of tRNAs exist in the cytoplasm. Serving as adaptors, specific tRNAs bind to sequences on the mRNA template and add the corresponding amino acid to the polypeptide chain. Therefore, tRNAs are the molecules that actually “translate” the language of RNA into the language of proteins.

Of the 64 possible mRNA codons—or triplet combinations of A, U, G, and C—three specify the termination of protein synthesis and 61 specify the addition of amino acids to the polypeptide chain. Of these 61, one codon (AUG) also encodes the initiation of translation. Each tRNA anticodon can base pair with one of the mRNA codons and add an amino acid or terminate translation, according to the genetic code. For instance, if the sequence CUA occurred on an mRNA template in the proper reading frame, it would bind a tRNA expressing the complementary sequence, GAU, which would be linked to the amino acid leucine.

As the adaptor molecules of translation, it is surprising that tRNAs can fit so much specificity into such a small package. Consider that tRNAs need to interact with three factors: 1) they must be recognized by the correct aminoacyl synthetase (see below); 2) they must be recognized by ribosomes; and 3) they must bind to the correct sequence in mRNA.

Aminoacyl tRNA Synthetases

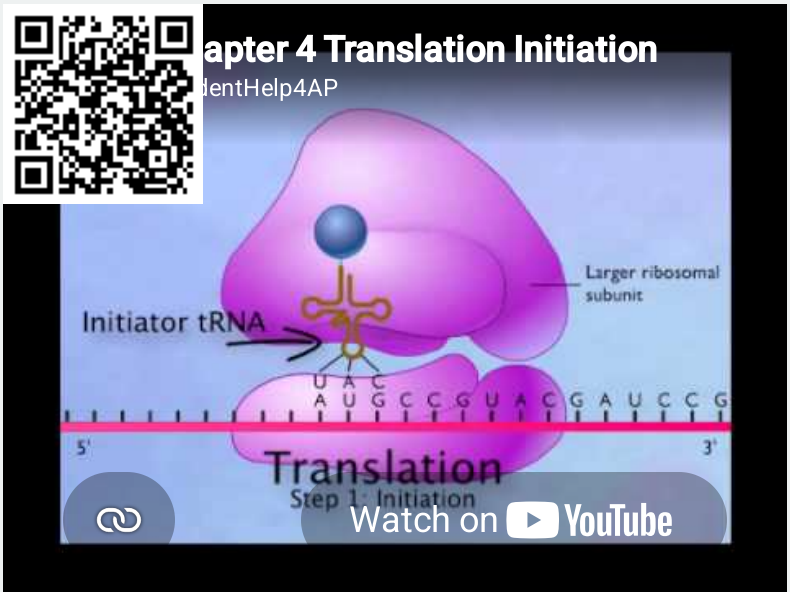
The process of pre-tRNA synthesis by RNA polymerase III only creates the RNA portion of the adaptor molecule. The corresponding amino acid must be added later, once the tRNA is processed and exported to the cytoplasm. Through the process of tRNA “charging,” each tRNA molecule is linked to its correct amino acid by a group of enzymes called aminoacyl tRNA synthetases. At least one type of aminoacyl tRNA synthetase exists for each of the 20 amino acids; the exact number of aminoacyl tRNA synthetases varies by species. These enzymes first bind and hydrolyze ATP to catalyze a high-energy bond between an amino acid and adenosine monophosphate (AMP); a pyrophosphate molecule is expelled in this reaction. The activated amino acid is then transferred to the tRNA, and AMP is released.

The Mechanism of Protein Synthesis

As with mRNA synthesis, protein synthesis can be divided into three phases: initiation, elongation, and termination. The process of translation is similar in prokaryotes and eukaryotes. Here we’ll explore how translation occurs in *E. coli*, a representative prokaryote, and specify any differences between prokaryotic and eukaryotic translation.

Initiation of Translation

Video



Protein synthesis begins with the formation of an initiation complex. In *E. coli*, this complex involves the small 30S ribosome, the mRNA template, three initiation factors (IFs; IF-1, IF-2, and IF-3), and a special initiator tRNA, called $\mathrm{tRNA_f^{Met}}$. The initiator tRNA interacts with the start codon AUG (or rarely, GUG), links to a formylated methionine called fMet, and can also bind IF-2. Formylated methionine is inserted by $\mathrm{fMet-tRNA_f^{Met}}$ at the beginning of every polypeptide chain synthesized by *E. coli*, but it is usually clipped off after translation is complete. When an in-frame AUG is encountered during translation elongation, a non-formylated methionine is inserted by a regular Met-$\mathrm{tRNA^{Met}}$.

In *E. coli* mRNA, a sequence upstream of the first AUG codon, called the Shine-Dalgarno sequence (AGGAGG), interacts with the rRNA molecules that compose the ribosome. This interaction anchors the 30S ribosomal subunit at the correct location on the mRNA template. Guanosine triphosphate (GTP), which is a purine nucleotide triphosphate, acts as an energy source during translation—both at the start of elongation and during the ribosome's translocation.

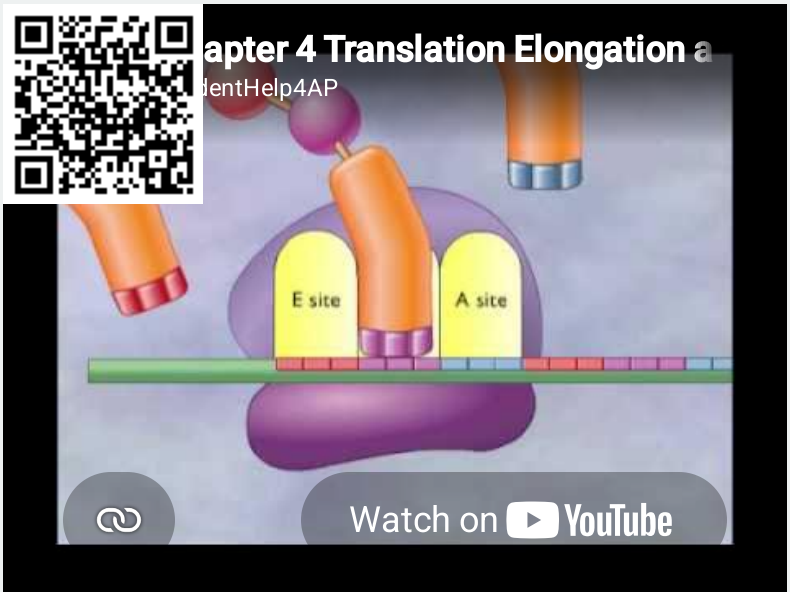
In eukaryotes, a similar initiation complex forms, comprising mRNA, the 40S small ribosomal subunit, IFs, and nucleoside triphosphates (GTP and ATP). The charged initiator tRNA, called Met-$\mathrm{tRNA_i}$, does not bind fMet in eukaryotes, but is distinct from other Met-tRNAs in that it can bind IFs.

Instead of depositing at the Shine-Dalgarno sequence, the eukaryotic initiation complex recognizes the 7-methylguanosine cap at the 5' end of the mRNA. A cap-binding protein (CBP) and several other IFs assist the movement of the ribosome to the 5' cap. Once at the cap, the initiation complex tracks along the mRNA in the 5' to 3' direction, searching for the AUG start codon. Many eukaryotic mRNAs are translated from the first AUG, but this is not always the case. According to Kozak's rules, the nucleotides around the AUG indicate whether it is the correct start codon. Kozak's rules state that the following consensus sequence must appear around the AUG of vertebrate genes: 5'-gccRccAUGG-3'. The R (for purine) indicates a site that can be either A or G, but cannot be C or U. Essentially, the closer the sequence is to this consensus, the higher the efficiency of translation.

Once the appropriate AUG is identified, the other proteins and CBP dissociate, and the 60S subunit binds to the complex of Met-$\mathrm{tRNA_i}$, mRNA, and the 40S subunit. This step completes the initiation of translation in eukaryotes.

Translation, Elongation, and Termination

Video



In prokaryotes and eukaryotes, the basics of elongation are the same, so we will review elongation from the perspective of *E. coli*. The 50S ribosomal subunit of *E. coli* consists of three compartments: the A (aminoacyl) site binds incoming charged aminoacyl tRNAs. The P (peptidyl) site binds charged tRNAs carrying amino acids that have formed peptide bonds with the growing polypeptide chain but have not yet dissociated from their corresponding tRNA. The E (exit) site releases dissociated tRNAs so that they can be recharged with free amino acids. There is one exception to this assembly line of tRNAs: in *E. coli*, $\mathrm{fMet-tRNA_f^{Met}}$ is capable of entering the P site directly without first entering the A site. Similarly, the eukaryotic Met-$\mathrm{tRNA_i}$, with help from other proteins of the initiation complex, binds directly to the P site. In both cases, this creates an initiation complex with a free A site ready to accept the tRNA corresponding to the first codon after the AUG.

During translation elongation, the mRNA template provides specificity. As the ribosome moves along the mRNA, each mRNA codon comes into register, and specific binding with the corresponding charged tRNA anticodon is ensured. If mRNA were not present in the elongation complex, the ribosome would bind tRNAs nonspecifically.

Elongation proceeds with charged tRNAs entering the A site and then shifting to the P site followed by the E site with each single-codon “step” of the ribosome. Ribosomal steps are induced by conformational changes that advance the ribosome by three bases in the 3' direction. The energy for each step of the ribosome is donated by an elongation factor that hydrolyzes GTP. Peptide bonds form between the amino group of the amino acid attached to the A-site tRNA and the carboxyl group of the amino acid attached to the P-site tRNA. The formation of each peptide bond is catalyzed by peptidyl transferase, an RNA-based enzyme that is integrated into the 50S ribosomal subunit. The energy for each peptide bond formation is derived from GTP hydrolysis, which is catalyzed by a separate elongation factor. The amino acid bound to the P-site tRNA is also linked to the growing polypeptide chain. As the ribosome steps across the mRNA, the former P-site tRNA enters the E site, detaches from the amino acid, and is expelled (Figure 3.5.6.2). Amazingly, the *E. coli* translation apparatus takes only 0.05 seconds to add each amino acid, meaning that a 200-amino acid protein can be translated in just 10 seconds.

Art Connection

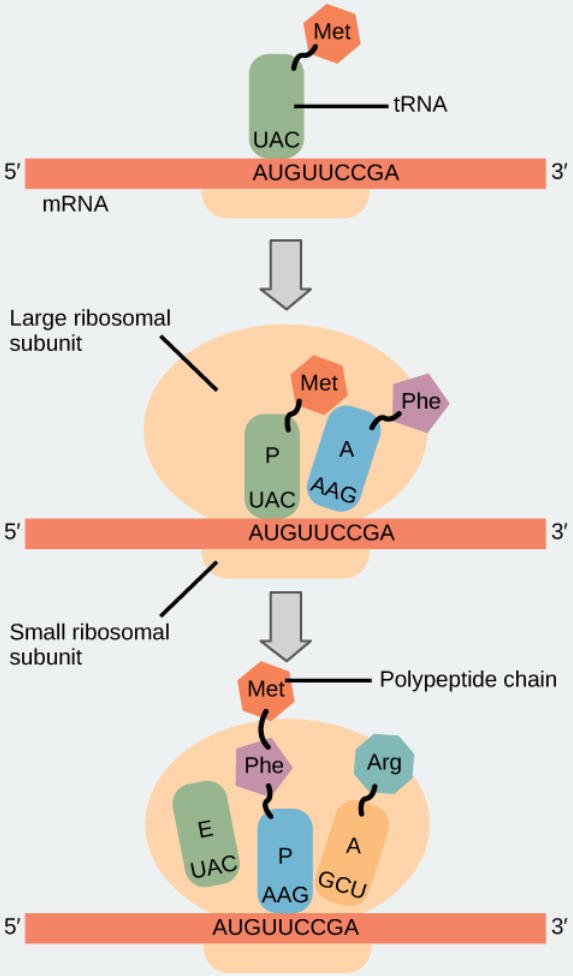


Figure 3.5.6.2: Translation begins when an initiator tRNA anticodon recognizes a codon on mRNA. The large ribosomal subunit joins the small subunit, and a second tRNA is recruited. As the mRNA moves relative to the ribosome, the polypeptide chain is formed. Entry of a release factor into the A site terminates translation and the components dissociate.

Many antibiotics inhibit bacterial protein synthesis. For example, tetracycline blocks the A site on the bacterial ribosome, and chloramphenicol blocks peptidyl transfer. What specific effect would you expect each of these antibiotics to have on protein synthesis?

Tetracycline would directly affect:

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Chloramphenicol would directly affect

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Termination of translation occurs when a nonsense codon (UAA, UAG, or UGA) is encountered. Upon aligning with the A site, these nonsense codons are recognized by release factors in prokaryotes and eukaryotes that instruct peptidyl transferase to add a water molecule to the carboxyl end of the P-site amino acid. This reaction forces the P-site amino acid to detach from its tRNA, and the newly made protein is released. The small and large ribosomal subunits dissociate from the mRNA and from each other;

they are recruited almost immediately into another translation initiation complex. After many ribosomes have completed translation, the mRNA is degraded so the nucleotides can be reused in another transcription reaction.

Protein Folding, Modification, and Targeting

During and after translation, individual amino acids may be chemically modified, signal sequences may be appended, and the new protein “folds” into a distinct three-dimensional structure as a result of intramolecular interactions. A signal sequence is a short tail of amino acids that directs a protein to a specific cellular compartment. These sequences at the amino end or the carboxyl end of the protein can be thought of as the protein’s “train ticket” to its ultimate destination. Other cellular factors recognize each signal sequence and help transport the protein from the cytoplasm to its correct compartment. For instance, a specific sequence at the amino terminus will direct a protein to the mitochondria or chloroplasts (in plants). Once the protein reaches its cellular destination, the signal sequence is usually clipped off.

Many proteins fold spontaneously, but some proteins require helper molecules, called chaperones, to prevent them from aggregating during the complicated process of folding. Even if a protein is properly specified by its corresponding mRNA, it could take on a completely dysfunctional shape if abnormal temperature or pH conditions prevent it from folding correctly.

Summary

The players in translation include the mRNA template, ribosomes, tRNAs, and various enzymatic factors. The small ribosomal subunit forms on the mRNA template either at the Shine-Dalgarno sequence (prokaryotes) or the 5' cap (eukaryotes). Translation begins at the initiating AUG on the mRNA, specifying methionine. The formation of peptide bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. Charged tRNAs enter the ribosomal A site, and their amino acid bonds with the amino acid at the P site. The entire mRNA is translated in three-nucleotide “steps” of the ribosome. When a nonsense codon is encountered, a release factor binds and dissociates the components and frees the new protein. Folding of the protein occurs during and after translation.

Art Connections

Figure 3.5.6.2: Many antibiotics inhibit bacterial protein synthesis. For example, tetracycline blocks the A site on the bacterial ribosome, and chloramphenicol blocks peptidyl transfer. What specific effect would you expect each of these antibiotics to have on protein synthesis?

Tetracycline would directly affect:

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Chloramphenicol would directly affect

a. tRNA binding to the ribosome
b. ribosome assembly
c. growth of the protein chain

Answer

Tetracycline: a; Chloramphenicol: c.

Glossary

aminoacyl tRNA synthetase

enzyme that “charges” tRNA molecules by catalyzing a bond between the tRNA and a corresponding amino acid

initiator tRNA

in prokaryotes, called $\mathrm{tRNA_f^{Met}}$; in eukaryotes, called $\mathrm{tRNA_i}$; a tRNA that interacts with a start codon, binds directly to the ribosome P site, and links to a special methionine to begin a polypeptide chain

Kozak's rules

determines the correct initiation AUG in a eukaryotic mRNA; the following consensus sequence must appear around the AUG: 5'-GCC(**purine**)CCAUG**G**-3'; the bolded bases are most important

peptidyl transferase

RNA-based enzyme that is integrated into the 50S ribosomal subunit and catalyzes the formation of peptide bonds

polysome

mRNA molecule simultaneously being translated by many ribosomes all going in the same direction

Shine-Dalgarno sequence

(AGGAGG); initiates prokaryotic translation by interacting with rRNA molecules comprising the 30S ribosome

signal sequence

short tail of amino acids that directs a protein to a specific cellular compartment

start codon

AUG (or rarely, GUG) on an mRNA from which translation begins; always specifies methionine

---

This page titled 3.5.6: Ribosomes and Protein Synthesis is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.5: Ribosomes and Protein Synthesis** by OpenStax is licensed CC BY 4.0.

3.5.E: Genes and Proteins (Exercises)

15.1: The Genetic Code

Review Questions

The AUC and AUA codons in mRNA both specify isoleucine. What feature of the genetic code explains this?

A. complementarity
B. nonsense codons
C. universality
D. degeneracy

Answer

D

How many nucleotides are in 12 mRNA codons?

A. 12
B. 24
C. 36
D. 48

Answer

C

Free Response

Imagine if there were 200 commonly occurring amino acids instead of 20. Given what you know about the genetic code, what would be the shortest possible codon length? Explain.

Answer

For 200 commonly occurring amino acids, codons consisting of four types of nucleotides would have to be at least four nucleotides long, because $4^4 = 256$. There would be much less degeneracy in this case.

Discuss how degeneracy of the genetic code makes cells more robust to mutations.

Answer

Codons that specify the same amino acid typically only differ by one nucleotide. In addition, amino acids with chemically similar side chains are encoded by similar codons. This nuance of the genetic code ensures that a single-nucleotide substitution mutation might either specify the same amino acid and have no effect, or may specify a similar amino acid, preventing the protein from being rendered completely nonfunctional.

15.2: Prokaryotic Transcription

Review Questions

Which subunit of the *E. coli* polymerase confers specificity to transcription?

A. α
B. β
C. β'

D. σ

Answer

D

The -10 and -35 regions of prokaryotic promoters are called consensus sequences because _____.

A. they are identical in all bacterial species
B. they are similar in all bacterial species
C. they exist in all organisms
D. they have the same function in all organisms

Answer

B

Free Response

If mRNA is complementary to the DNA template strand and the DNA template strand is complementary to the DNA nontemplate strand, then why are base sequences of mRNA and the DNA nontemplate strand not identical? Could they ever be?

Answer

DNA is different from RNA in that T nucleotides in DNA are replaced with U nucleotides in RNA. Therefore, they could never be identical in base sequence.

In your own words, describe the difference between rho-dependent and rho-independent termination of transcription in prokaryotes.

Answer

Rho-dependent termination is controlled by the rho protein, which tracks along behind the polymerase on the growing mRNA chain. Near the end of the gene, the polymerase stalls at a run of G nucleotides on the DNA template. The rho protein collides with the polymerase and releases mRNA from the transcription bubble. Rho-independent termination is controlled by specific sequences in the DNA template strand. As the polymerase nears the end of the gene being transcribed, it encounters a region rich in C–G nucleotides. This creates an mRNA hairpin that causes the polymerase to stall right as it begins to transcribe a region rich in A–T nucleotides. Because A–U bonds are less thermostable, the core enzyme falls away.

15.3: Eukaryotic Transcription

Review Questions

Which feature of promoters can be found in both prokaryotes and eukaryotes?

A. GC box
B. TATA box
C. octamer box
D. -10 and -35 sequences

Answer

B

https://bio.libretexts.org/@go/page/82942

What transcripts will be most affected by low levels of α-amanitin?

A. 18S and 28S rRNAs
B. pre-mRNAs
C. 5S rRNAs and tRNAs
D. other small nuclear RNAs

Answer

B

15.4: RNA Processing in Eukaryotes

Review Questions

Which pre-mRNA processing step is important for initiating translation?

A. poly-A tail
B. RNA editing
C. splicing
D. 7-methylguanosine cap

Answer

D

What processing step enhances the stability of pre-tRNAs and pre-rRNAs?

A. methylation
B. nucleotide modification
C. cleavage
D. splicing

Answer

A

15.5: Ribosomes and Protein Synthesis

Review Questions

The RNA components of ribosomes are synthesized in the _____.

A. cytoplasm
B. nucleus
C. nucleolus
D. endoplasmic reticulum

Answer

C

In any given species, there are at least how many types of aminoacyl tRNA synthetases?

A. 20
B. 40
C. 100
D. 200

Answer

A

Free Response

Transcribe and translate the following DNA sequence (nontemplate strand): 5'-ATGGCCGGTTATTAAGCA-3'

Answer

The mRNA would be: 5'-AUGGCCGGUUAUUAAGCA-3'. The protein would be: MAGY. Even though there are six codons, the fifth codon corresponds to a stop, so the sixth codon would not be translated.

Explain how single nucleotide changes can have vastly different effects on protein function.

Answer

Nucleotide changes in the third position of codons may not change the amino acid and would have no effect on the protein. Other nucleotide changes that change important amino acids or create or delete start or stop codons would have severe effects on the amino acid sequence of the protein.

This page titled 3.5.E: Genes and Proteins (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **15.E: Genes and Proteins (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

3.6: Gene Regulation

Whereas each cell shares the same genome and DNA sequence, each cell does not turn on, or express, the same set of genes. Each cell type needs a different set of proteins to perform its function. Therefore, only a small subset of proteins is expressed in a cell. For the proteins to be expressed, the DNA must be transcribed into RNA and the RNA must be translated into protein. In a given cell type, not all genes encoded in the DNA are transcribed into RNA or translated into protein because specific cells in our body have specific functions. Specialized proteins that make up the eye (iris, lens, and cornea) are only expressed in the eye, whereas the specialized proteins in the heart (pacemaker cells, heart muscle, and valves) are only expressed in the heart. At any given time, only a subset of all of the genes encoded by our DNA are expressed and translated into proteins. The expression of specific genes is a highly regulated process with many levels and stages of control. This complexity ensures the proper expression in the proper cell at the proper time.

3.6.1: Prelude to Gene Expression
3.6.2: Regulation of Gene Expression
3.6.3: Prokaryotic Gene Regulation
3.6.4: Eukaryotic Epigenetic Gene Regulation
3.6.5: Eukaryotic Transcription Gene Regulation
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
3.6.8: Cancer and Gene Regulation
3.6.E: Gene Expression (Exercises)

This page titled 3.6: Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.6.1: Prelude to Gene Expression

Each somatic cell in the body generally contains the same DNA. A few exceptions include red blood cells, which contain no DNA in their mature state, and some immune system cells that rearrange their DNA while producing antibodies. In general, however, the genes that determine whether you have green eyes, brown hair, and how fast you metabolize food are the same in the cells in your eyes and your liver, even though these organs function quite differently. If each cell has the same DNA, how is it that cells or organs are different? Why do cells in the eye differ so dramatically from cells in the liver?

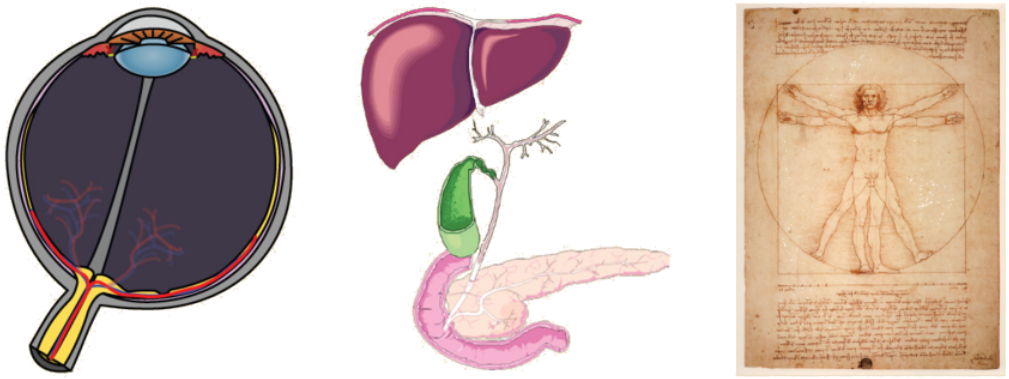


Figure 3.6.1.1: The genetic content of each somatic cell in an organism is the same, but not all genes are expressed in every cell. The control of which genes are expressed dictates whether a cell is (a) an eye cell or (b) a liver cell. It is the differential gene expression patterns that arise in different cells that give rise to (c) a complete organism.

Whereas each cell shares the same genome and DNA sequence, each cell does not turn on, or express, the same set of genes. Each cell type needs a different set of proteins to perform its function. Therefore, only a small subset of proteins is expressed in a cell. For the proteins to be expressed, the DNA must be transcribed into RNA and the RNA must be translated into protein. In a given cell type, not all genes encoded in the DNA are transcribed into RNA or translated into protein because specific cells in our body have specific functions. Specialized proteins that make up the eye (iris, lens, and cornea) are only expressed in the eye, whereas the specialized proteins in the heart (pacemaker cells, heart muscle, and valves) are only expressed in the heart. At any given time, only a subset of all of the genes encoded by our DNA are expressed and translated into proteins. The expression of specific genes is a highly regulated process with many levels and stages of control. This complexity ensures the proper expression in the proper cell at the proper time.

This page titled 3.6.1: Prelude to Gene Expression is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.0: Prelude to Gene Expression** by OpenStax is licensed CC BY 4.0.

3.6.2: Regulation of Gene Expression

Skills to Develop

- Discuss why every cell does not express all of its genes
- Describe how prokaryotic gene regulation occurs at the transcriptional level
- Discuss how eukaryotic gene regulation occurs at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels

For a cell to function properly, necessary proteins must be synthesized at the proper time. All cells control or regulate the synthesis of proteins from information encoded in their DNA. The process of turning on a gene to produce RNA and protein is called gene expression. Whether in a simple unicellular organism or a complex multi-cellular organism, each cell controls when and how its genes are expressed. For this to occur, there must be a mechanism to control when a gene is expressed to make RNA and protein, how much of the protein is made, and when it is time to stop making that protein because it is no longer needed.

The regulation of gene expression conserves energy and space. It would require a significant amount of energy for an organism to express every gene at all times, so it is more energy efficient to turn on the genes only when they are required. In addition, only expressing a subset of genes in each cell saves space because DNA must be unwound from its tightly coiled structure to transcribe and translate the DNA. Cells would have to be enormous if every protein were expressed in every cell all the time.

The control of gene expression is extremely complex. Malfunctions in this process are detrimental to the cell and can lead to the development of many diseases, including cancer.

Prokaryotic versus Eukaryotic Gene Expression

To understand how gene expression is regulated, we must first understand how a gene codes for a functional protein in a cell. The process occurs in both prokaryotic and eukaryotic cells, just in slightly different manners.

Prokaryotic organisms are single-celled organisms that lack a cell nucleus, and their DNA therefore floats freely in the cell cytoplasm. To synthesize a protein, the processes of transcription and translation occur almost simultaneously. When the resulting protein is no longer needed, transcription stops. As a result, the primary method to control what type of protein and how much of each protein is expressed in a prokaryotic cell is the regulation of DNA transcription. All of the subsequent steps occur automatically. When more protein is required, more transcription occurs. Therefore, in prokaryotic cells, the control of gene expression is mostly at the transcriptional level.

Eukaryotic cells, in contrast, have intracellular organelles that add to their complexity. In eukaryotic cells, the DNA is contained inside the cell's nucleus and there it is transcribed into RNA. The newly synthesized RNA is then transported out of the nucleus into the cytoplasm, where ribosomes translate the RNA into protein. The processes of transcription and translation are physically separated by the nuclear membrane; transcription occurs only within the nucleus, and translation occurs only outside the nucleus in the cytoplasm. The regulation of gene expression can occur at all stages of the process (Figure 3.6.2.1). Regulation may occur when the DNA is uncoiled and loosened from nucleosomes to bind transcription factors (epigenetic level), when the RNA is transcribed (transcriptional level), when the RNA is processed and exported to the cytoplasm after it is transcribed (post-transcriptional level), when the RNA is translated into protein (translational level), or after the protein has been made (post-translational level).

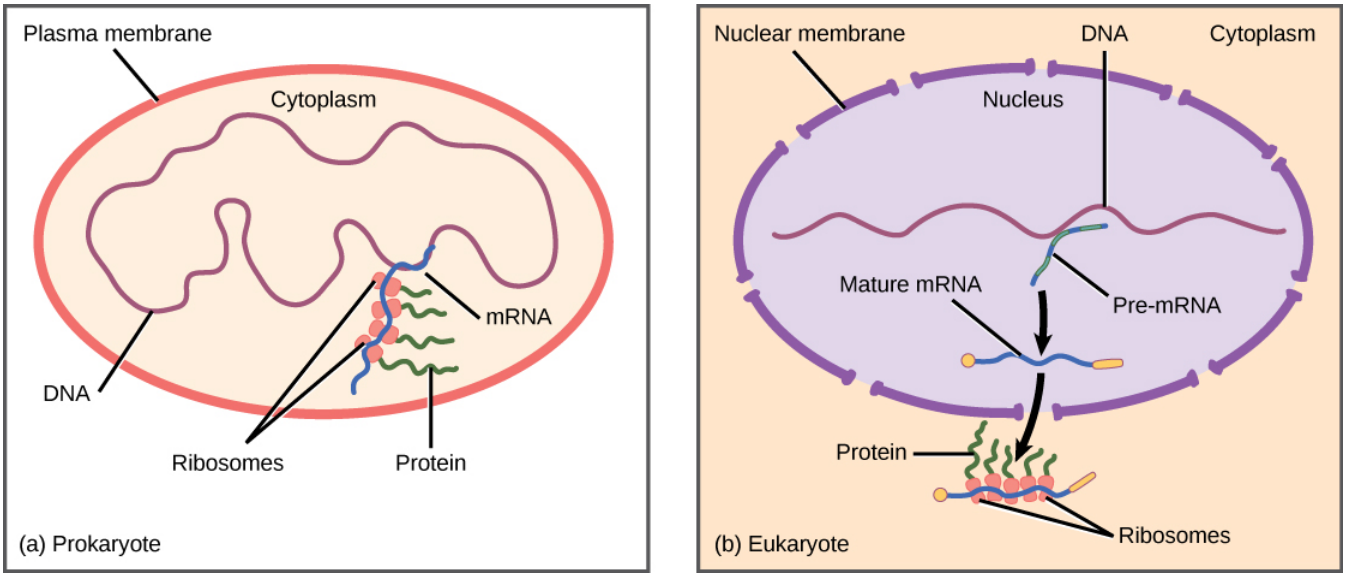


Figure 3.6.2.1: Prokaryotic transcription and translation occur simultaneously in the cytoplasm, and regulation occurs at the transcriptional level. Eukaryotic gene expression is regulated during transcription and RNA processing, which take place in the nucleus, and during protein translation, which takes place in the cytoplasm. Further regulation may occur through post-translational modifications of proteins.

The differences in the regulation of gene expression between prokaryotes and eukaryotes are summarized below. The regulation of gene expression is discussed in detail in subsequent modules.

Table 3.6.2.1: Differences in the Regulation of Gene Expression of Prokaryotic and Eukaryotic Organisms

Prokaryotic organisms	Eukaryotic organisms
Lack nucleus	Contain nucleus
DNA is found in the cytoplasm	DNA is confined to the nuclear compartment
RNA transcription and protein formation occur almost simultaneously	RNA transcription occurs prior to protein formation, and it takes place in the nucleus. Translation of RNA to protein occurs in the cytoplasm.
Gene expression is regulated primarily at the transcriptional level	Gene expression is regulated at many levels (epigenetic, transcriptional, nuclear shuttling, post-transcriptional, translational, and post-translational)

Evolution Connection: Evolution of Gene Regulation

Prokaryotic cells can only regulate gene expression by controlling the amount of transcription. As eukaryotic cells evolved, the complexity of the control of gene expression increased. For example, with the evolution of eukaryotic cells came compartmentalization of important cellular components and cellular processes. A nuclear region that contains the DNA was formed. Transcription and translation were physically separated into two different cellular compartments. It therefore became possible to control gene expression by regulating transcription in the nucleus, and also by controlling the RNA levels and protein translation present outside the nucleus.

Some cellular processes arose from the need of the organism to defend itself. Cellular processes such as gene silencing developed to protect the cell from viral or parasitic infections. If the cell could quickly shut off gene expression for a short period of time, it would be able to survive an infection when other organisms could not. Therefore, the organism evolved a new process that helped it survive, and it was able to pass this new development to offspring.

Summary

While all somatic cells within an organism contain the same DNA, not all cells within that organism express the same proteins. Prokaryotic organisms express the entire DNA they encode in every cell, but not necessarily all at the same time. Proteins are expressed only when they are needed. Eukaryotic organisms express a subset of the DNA that is encoded in any given cell. In each cell type, the type and amount of protein is regulated by controlling gene expression. To express a protein, the DNA is first transcribed into RNA, which is then translated into proteins. In prokaryotic cells, these processes occur almost simultaneously. In eukaryotic cells, transcription occurs in the nucleus and is separate from the translation that occurs in the cytoplasm. Gene expression in prokaryotes is regulated only at the transcriptional level, whereas in eukaryotic cells, gene expression is regulated at the epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels.

Glossary

epigenetic

heritable changes that do not involve changes in the DNA sequence

gene expression

processes that control the turning on or turning off of a gene

post-transcriptional

control of gene expression after the RNA molecule has been created but before it is translated into protein

post-translational

control of gene expression after a protein has been created

This page titled 3.6.2: Regulation of Gene Expression is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.1: Regulation of Gene Expression** by OpenStax is licensed CC BY 4.0.

3.6.3: Prokaryotic Gene Regulation

Skills to Develop

- Describe the steps involved in prokaryotic gene regulation
- Explain the roles of activators, inducers, and repressors in gene regulation

The DNA of prokaryotes is organized into a circular chromosome supercoiled in the nucleoid region of the cell cytoplasm. Proteins that are needed for a specific function, or that are involved in the same biochemical pathway, are encoded together in blocks called operons. For example, all of the genes needed to use lactose as an energy source are coded next to each other in the lactose (or *lac*) operon.

In prokaryotic cells, there are three types of regulatory molecules that can affect the expression of operons: repressors, activators, and inducers. Repressors are proteins that suppress transcription of a gene in response to an external stimulus, whereas activators are proteins that increase the transcription of a gene in response to an external stimulus. Finally, inducers are small molecules that either activate or repress transcription depending on the needs of the cell and the availability of substrate.

The *trp* Operon: A Repressor Operon

Bacteria such as *E. coli* need amino acids to survive. Tryptophan is one such amino acid that *E. coli* can ingest from the environment. *E. coli* can also synthesize tryptophan using enzymes that are encoded by five genes. These five genes are next to each other in what is called the tryptophan (*trp*) operon (Figure 3.6.3.1). If tryptophan is present in the environment, then *E. coli* does not need to synthesize it and the switch controlling the activation of the genes in the *trp* operon is switched off. However, when tryptophan availability is low, the switch controlling the operon is turned on, transcription is initiated, the genes are expressed, and tryptophan is synthesized.

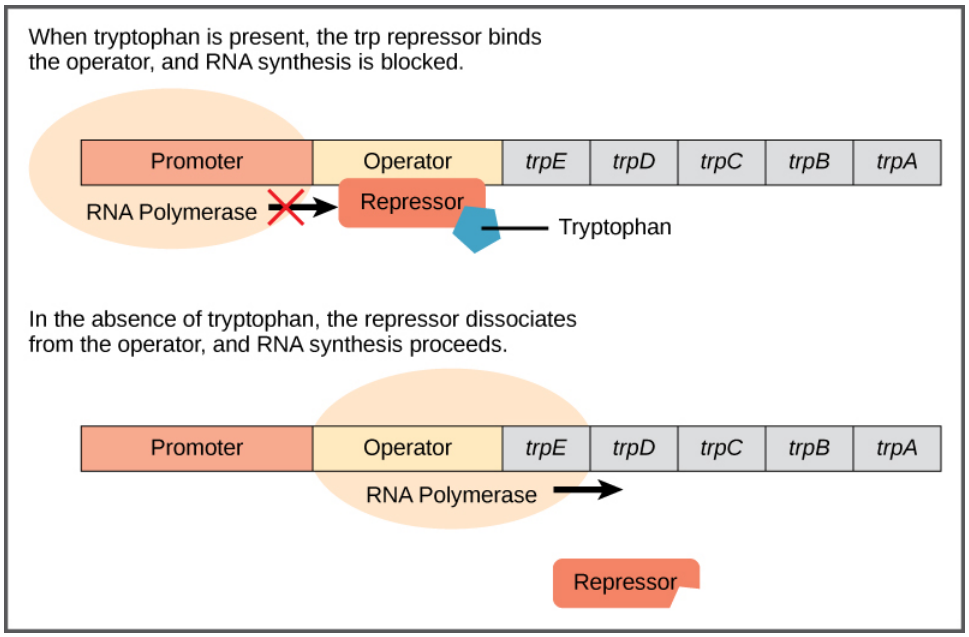


Figure 3.6.3.1: The five genes that are needed to synthesize tryptophan in *E. coli* are located next to each other in the *trp* operon. When tryptophan is plentiful, two tryptophan molecules bind the repressor protein at the operator sequence. This physically blocks the RNA polymerase from transcribing the tryptophan genes. When tryptophan is absent, the repressor protein does not bind to the operator and the genes are transcribed.

A DNA sequence that codes for proteins is referred to as the coding region. The five coding regions for the tryptophan biosynthesis enzymes are arranged sequentially on the chromosome in the operon. Just before the coding region is the transcriptional start site. This is the region of DNA to which RNA polymerase binds to initiate transcription. The promoter sequence is upstream of the transcriptional start site; each operon has a sequence within or near the promoter to which proteins (activators or repressors) can bind and regulate transcription.

A DNA sequence called the operator sequence is encoded between the promoter region and the first *trp* coding gene. This operator contains the DNA code to which the repressor protein can bind. When tryptophan is present in the cell, two tryptophan molecules bind to the *trp* repressor, which changes shape to bind to the *trp* operator. Binding of the tryptophan–repressor complex at the operator physically prevents the RNA polymerase from binding, and transcribing the downstream genes.

When tryptophan is not present in the cell, the repressor by itself does not bind to the operator; therefore, the operon is active and tryptophan is synthesized. Because the repressor protein actively binds to the operator to keep the genes turned off, the *trp* operon is negatively regulated and the proteins that bind to the operator to silence *trp* expression are negative regulators.

Link to Learning



Watch this video to learn more about the *trp* operon.

Catabolite Activator Protein (CAP): An Activator Regulator

Just as the *trp* operon is negatively regulated by tryptophan molecules, there are proteins that bind to the operator sequences that act as a positive regulator to turn genes on and activate them. For example, when glucose is scarce, *E. coli* bacteria can turn to other sugar sources for fuel. To do this, new genes to process these alternate genes must be transcribed. When glucose levels drop, cyclic AMP (cAMP) begins to accumulate in the cell. The cAMP molecule is a signaling molecule that is involved in glucose and energy metabolism in *E. coli*. When glucose levels decline in the cell, accumulating cAMP binds to the positive regulator catabolite activator protein (CAP), a protein that binds to the promoters of operons that control the processing of alternative sugars. When cAMP binds to CAP, the complex binds to the promoter region of the genes that are needed to use the alternate sugar sources (Figure 3.6.3.2). In these operons, a CAP binding site is located upstream of the RNA polymerase binding site in the promoter. This increases the binding ability of RNA polymerase to the promoter region and the transcription of the genes.

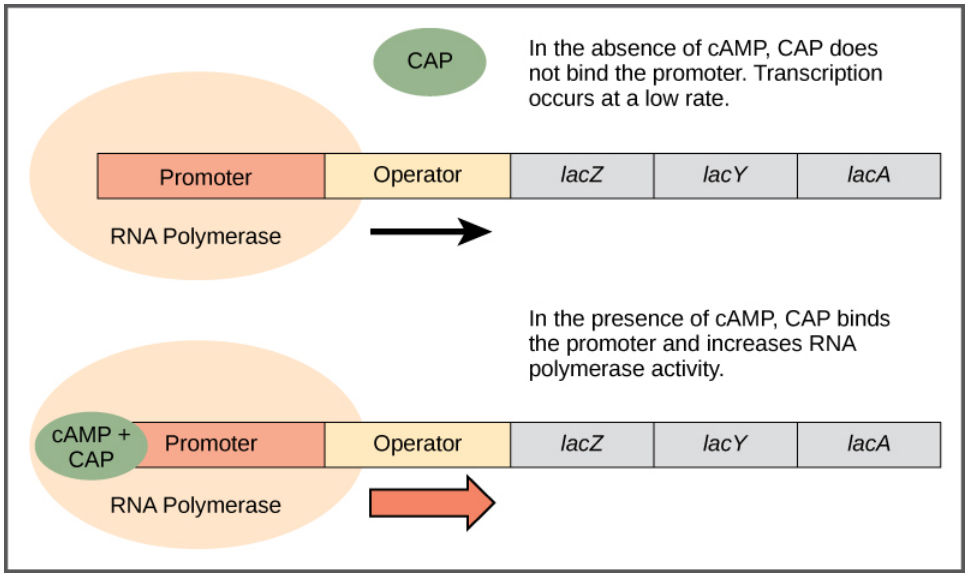


Figure 3.6.3.2: When glucose levels fall, *E. coli* may use other sugars for fuel but must transcribe new genes to do so. As glucose supplies become limited, cAMP levels increase. This cAMP binds to the CAP protein, a positive regulator that binds to an operator region upstream of the genes required to use other sugar sources.

The *lac* Operon: An Inducer Operon

The third type of gene regulation in prokaryotic cells occurs through inducible operons, which have proteins that bind to activate or repress transcription depending on the local environment and the needs of the cell. The *lac* operon is a typical inducible operon. As mentioned previously, *E. coli* is able to use other sugars as energy sources when glucose concentrations are low. To do so, the cAMP–CAP protein complex serves as a positive regulator to induce transcription. One such sugar source is lactose. The *lac* operon encodes the genes necessary to acquire and process the lactose from the local environment. CAP binds to the operator sequence upstream of the promoter that initiates transcription of the *lac* operon. However, for the *lac* operon to be activated, two conditions must be met. First, the level of glucose must be very low or non-existent. Second, lactose must be present. Only when glucose is absent and lactose is present will the *lac* operon be transcribed (Figure 3.6.3.3). This makes sense for the cell, because it would be energetically wasteful to create the proteins to process lactose if glucose was plentiful or lactose was not available.

Art Connection

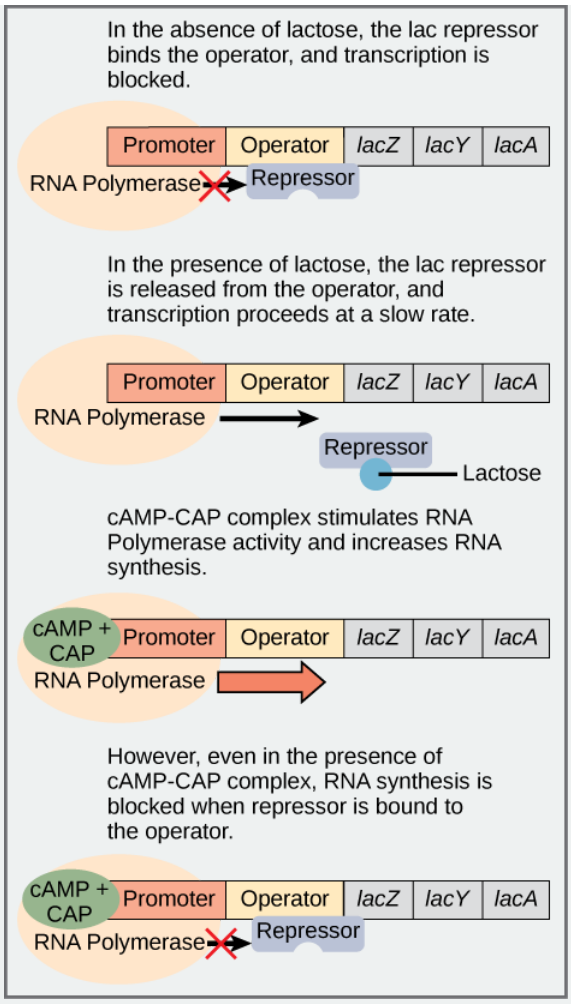


Figure 3.6.3.3: Transcription of the *lac* operon is carefully regulated so that its expression only occurs when glucose is limited and lactose is present to serve as an alternative fuel source.

In *E. coli*, the *trp* operon is on by default, while the *lac* operon is off. Why do you think this is the case?

If glucose is absent, then CAP can bind to the operator sequence to activate transcription. If lactose is absent, then the repressor binds to the operator to prevent transcription. If either of these requirements is met, then transcription remains off. Only when both conditions are satisfied is the *lac* operon transcribed (Table 3.6.3.1).

Table 3.6.3.1: Signals that Induce or Repress Transcription of the lac Operon

Glucose	CAP binds	Lactose	Repressor binds	Transcription
+	-	-	+	No
+	-	+	-	Some
-	+	-	+	No
-	+	+	-	Yes

Link to Learning



Watch an animated tutorial about the workings of *lac* operon here.

Summary

The regulation of gene expression in prokaryotic cells occurs at the transcriptional level. There are three ways to control the transcription of an operon: repressive control, activator control, and inducible control. Repressive control, typified by the *trp* operon, uses proteins bound to the operator sequence to physically prevent the binding of RNA polymerase and the activation of transcription. Therefore, if tryptophan is not needed, the repressor is bound to the operator and transcription remains off. Activator control, typified by the action of CAP, increases the binding ability of RNA polymerase to the promoter when CAP is bound. In this case, low levels of glucose result in the binding of cAMP to CAP. CAP then binds the promoter, which allows RNA polymerase to bind to the promoter better. In the last example—the *lac* operon—two conditions must be met to initiate transcription. Glucose must not be present, and lactose must be available for the *lac* operon to be transcribed. If glucose is absent, CAP binds to the operator. If lactose is present, the repressor protein does not bind to its operator. Only when both conditions are met will RNA polymerase bind to the promoter to induce transcription.

Art Connections

Figure 3.6.3.3: In *E. coli*, the *trp* operon is on by default, while the *lac* operon is off. Why do you think that this is the case?

Answer

Tryptophan is an amino acid essential for making proteins, so the cell always needs to have some on hand. However, if plenty of tryptophan is present, it is wasteful to make more, and the expression of the *trp* receptor is repressed. Lactose, a sugar found in milk, is not always available. It makes no sense to make the enzymes necessary to digest an energy source that is not available, so the *lac* operon is only turned on when lactose is present.

Glossary

activator
protein that binds to prokaryotic operators to increase transcription

catabolite activator protein (CAP)
protein that complexes with cAMP to bind to the promoter sequences of operons that control sugar processing when glucose is not available

inducible operon
operon that can be activated or repressed depending on cellular needs and the surrounding environment

lac operon
operon in prokaryotic cells that encodes genes required for processing and intake of lactose

negative regulator
protein that prevents transcription

operator
region of DNA outside of the promoter region that binds activators or repressors that control gene expression in prokaryotic cells

operon
collection of genes involved in a pathway that are transcribed together as a single mRNA in prokaryotic cells

positive regulator
protein that increases transcription

repressor
protein that binds to the operator of prokaryotic genes to prevent transcription

transcriptional start site
site at which transcription begins

trp operon
series of genes necessary to synthesize tryptophan in prokaryotic cells

tryptophan
amino acid that can be synthesized by prokaryotic cells when necessary

---

This page titled 3.6.3: Prokaryotic Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.2: Prokaryotic Gene Regulation** by OpenStax is licensed CC BY 4.0.

3.6.4: Eukaryotic Epigenetic Gene Regulation

Skills to Develop

- Explain the process of epigenetic regulation
- Describe how access to DNA is controlled by histone modification

Eukaryotic gene expression is more complex than prokaryotic gene expression because the processes of transcription and translation are physically separated. Unlike prokaryotic cells, eukaryotic cells can regulate gene expression at many different levels. Eukaryotic gene expression begins with control of access to the DNA. This form of regulation, called epigenetic regulation, occurs even before transcription is initiated.

Epigenetic Control: Regulating Access to Genes within the Chromosome

The human genome encodes over 20,000 genes; each of the 23 pairs of human chromosomes encodes thousands of genes. The DNA in the nucleus is precisely wound, folded, and compacted into chromosomes so that it will fit into the nucleus. It is also organized so that specific segments can be accessed as needed by a specific cell type.

The first level of organization, or packing, is the winding of DNA strands around histone proteins. Histones package and order DNA into structural units called nucleosome complexes, which can control the access of proteins to the DNA regions (Figure 3.6.4.1a). Under the electron microscope, this winding of DNA around histone proteins to form nucleosomes looks like small beads on a string (Figure 3.6.4.1b). These beads (histone proteins) can move along the string (DNA) and change the structure of the molecule.

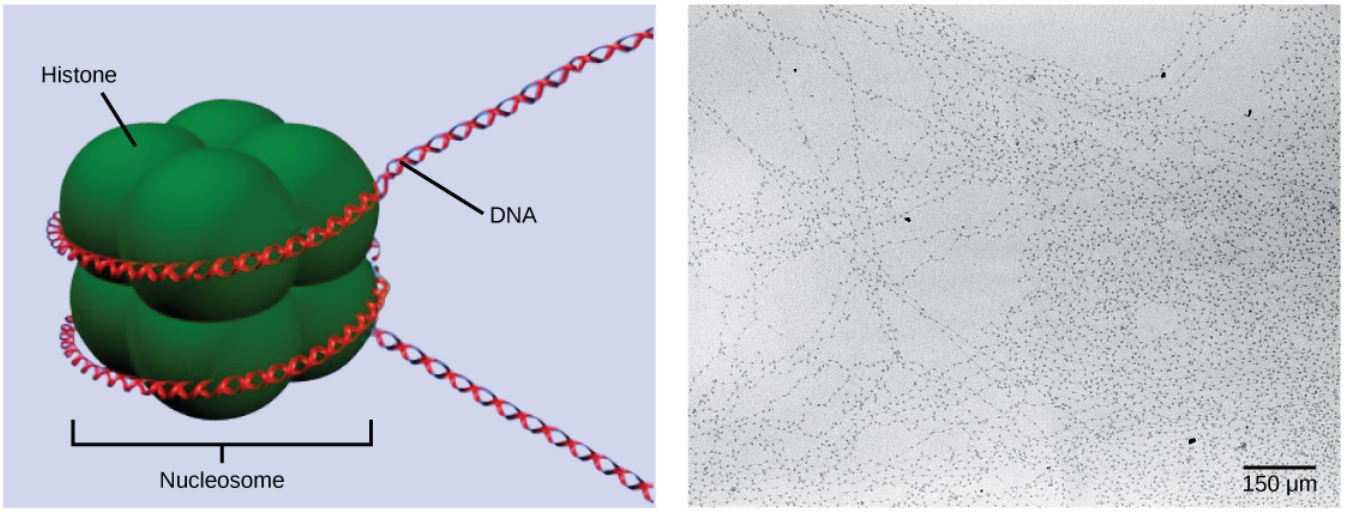
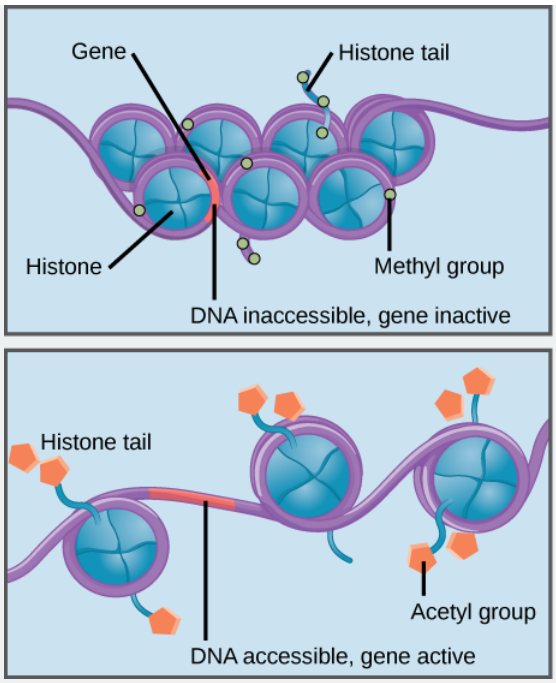


Figure 3.6.4.1: DNA is folded around histone proteins to create (a) nucleosome complexes. These nucleosomes control the access of proteins to the underlying DNA. When viewed through an electron microscope (b), the nucleosomes look like beads on a string. (credit “micrograph”: modification of work by Chris Woodcock)

If DNA encoding a specific gene is to be transcribed into RNA, the nucleosomes surrounding that region of DNA can slide down the DNA to open that specific chromosomal region and allow for the transcriptional machinery (RNA polymerase) to initiate transcription (Figure 3.6.4.2). Nucleosomes can move to open the chromosome structure to expose a segment of DNA, but do so in a very controlled manner.

Art Connection



Methylation of DNA and histones causes nucleosomes to pack tightly together. Transcription factors cannot bind the DNA, and genes are not expressed.

Histone acetylation results in loose packing of nucleosomes. Transcription factors can bind the DNA and genes are expressed.

Figure 3.6.4.2: Nucleosomes can slide along DNA. When nucleosomes are spaced closely together (top), transcription factors cannot bind and gene expression is turned off. When the nucleosomes are spaced far apart (bottom), the DNA is exposed. Transcription factors can bind, allowing gene expression to occur. Modifications to the histones and DNA affect nucleosome spacing.

In females, one of the two X chromosomes is inactivated during embryonic development because of epigenetic changes to the chromatin. What impact do you think these changes would have on nucleosome packing?

How the histone proteins move is dependent on signals found on both the histone proteins and on the DNA. These signals are tags added to histone proteins and DNA that tell the histones if a chromosomal region should be open or closed (Figure 3.6.4.3) depicts modifications to histone proteins and DNA). These tags are not permanent, but may be added or removed as needed. They are chemical modifications (phosphate, methyl, or acetyl groups) that are attached to specific amino acids in the protein or to the nucleotides of the DNA. The tags do not alter the DNA base sequence, but they do alter how tightly wound the DNA is around the histone proteins. DNA is a negatively charged molecule; therefore, changes in the charge of the histone will change how tightly wound the DNA molecule will be. When unmodified, the histone proteins have a large positive charge; by adding chemical modifications like acetyl groups, the charge becomes less positive.

The DNA molecule itself can also be modified. This occurs within very specific regions called CpG islands. These are stretches with a high frequency of cytosine and guanine dinucleotide DNA pairs (CG) found in the promoter regions of genes. When this configuration exists, the cytosine member of the pair can be methylated (a methyl group is added). This modification changes how the DNA interacts with proteins, including the histone proteins that control access to the region. Highly methylated (hypermethylated) DNA regions with deacetylated histones are tightly coiled and transcriptionally inactive.

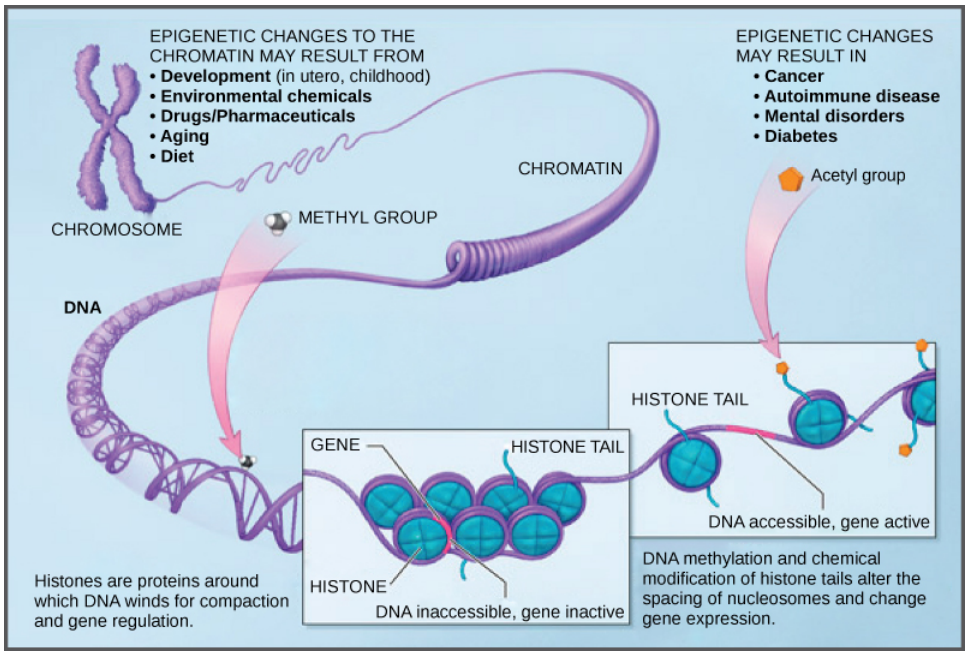


Figure 3.6.4.3: Histone proteins and DNA nucleotides can be modified chemically. Modifications affect nucleosome spacing and gene expression. (credit: modification of work by NIH)

This type of gene regulation is called epigenetic regulation. Epigenetic means “around genetics.” The changes that occur to the histone proteins and DNA do not alter the nucleotide sequence and are not permanent. Instead, these changes are temporary (although they often persist through multiple rounds of cell division) and alter the chromosomal structure (open or closed) as needed. A gene can be turned on or off depending upon the location and modifications to the histone proteins and DNA. If a gene is to be transcribed, the histone proteins and DNA are modified surrounding the chromosomal region encoding that gene. This opens the chromosomal region to allow access for RNA polymerase and other proteins, called transcription factors, to bind to the promoter region, located just upstream of the gene, and initiate transcription. If a gene is to remain turned off, or silenced, the histone proteins and DNA have different modifications that signal a closed chromosomal configuration. In this closed configuration, the RNA polymerase and transcription factors do not have access to the DNA and transcription cannot occur (Figure 3.6.4.3).

Link to Learning



View this video that describes how epigenetic regulation controls gene expression.

Summary

In eukaryotic cells, the first stage of gene expression control occurs at the epigenetic level. Epigenetic mechanisms control access to the chromosomal region to allow genes to be turned on or off. These mechanisms control how DNA is packed into the nucleus by regulating how tightly the DNA is wound around histone proteins. The addition or removal of chemical modifications (or flags) to histone proteins or DNA signals to the cell to open or close a chromosomal region. Therefore, eukaryotic cells can control whether a gene is expressed by controlling accessibility to transcription factors and the binding of RNA polymerase to initiate transcription.

Art Connections

Figure 3.6.4.2: In females, one of the two X chromosomes is inactivated during embryonic development because of epigenetic changes to the chromatin. What impact do you think these changes would have on nucleosome packing?

Answer

The nucleosomes would pack more tightly together.

Glossary

transcription factor

protein that binds to the DNA at the promoter or enhancer region and that influences transcription of a gene

This page titled 3.6.4: Eukaryotic Epigenetic Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.3: Eukaryotic Epigenetic Gene Regulation** by OpenStax is licensed CC BY 4.0.

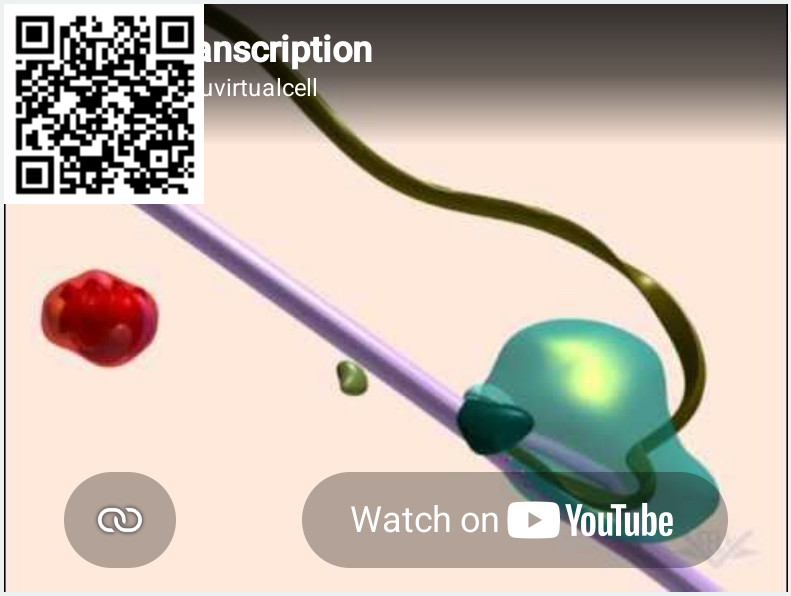
3.6.5: Eukaryotic Transcription Gene Regulation

Skills to Develop

- Discuss the role of transcription factors in gene regulation
- Explain how enhancers and repressors regulate gene expression

Like prokaryotic cells, the transcription of genes in eukaryotes requires the actions of an RNA polymerase to bind to a sequence upstream of a gene to initiate transcription. However, unlike prokaryotic cells, the eukaryotic RNA polymerase requires other proteins, or transcription factors, to facilitate transcription initiation. Transcription factors are proteins that bind to the promoter sequence and other regulatory sequences to control the transcription of the target gene. RNA polymerase by itself cannot initiate transcription in eukaryotic cells. Transcription factors must bind to the promoter region first and recruit RNA polymerase to the site for transcription to be established.

Link to Learning



View the process of transcription—the making of RNA from a DNA template—at this site.

The Promoter and the Transcription Machinery

Genes are organized to make the control of gene expression easier. The promoter region is immediately upstream of the coding sequence. This region can be short (only a few nucleotides in length) or quite long (hundreds of nucleotides long). The longer the promoter, the more available space for proteins to bind. This also adds more control to the transcription process. The length of the promoter is gene-specific and can differ dramatically between genes. Consequently, the level of control of gene expression can also differ quite dramatically between genes. The purpose of the promoter is to bind transcription factors that control the initiation of transcription.

Within the promoter region, just upstream of the transcriptional start site, resides the TATA box. This box is simply a repeat of thymine and adenine dinucleotides (literally, TATA repeats). RNA polymerase binds to the transcription initiation complex, allowing transcription to occur. To initiate transcription, a transcription factor (TFIID) is the first to bind to the TATA box. Binding of TFIID recruits other transcription factors, including TFIIB, TFIIE, TFIIF, and TFIIH to the TATA box. Once this complex is assembled, RNA polymerase can bind to its upstream sequence. When bound along with the transcription factors, RNA polymerase is phosphorylated. This releases part of the protein from the DNA to activate the transcription initiation complex and places RNA polymerase in the correct orientation to begin transcription; DNA-bending protein brings the enhancer, which can be quite a distance from the gene, in contact with transcription factors and mediator proteins (Figure 3.6.5.1).

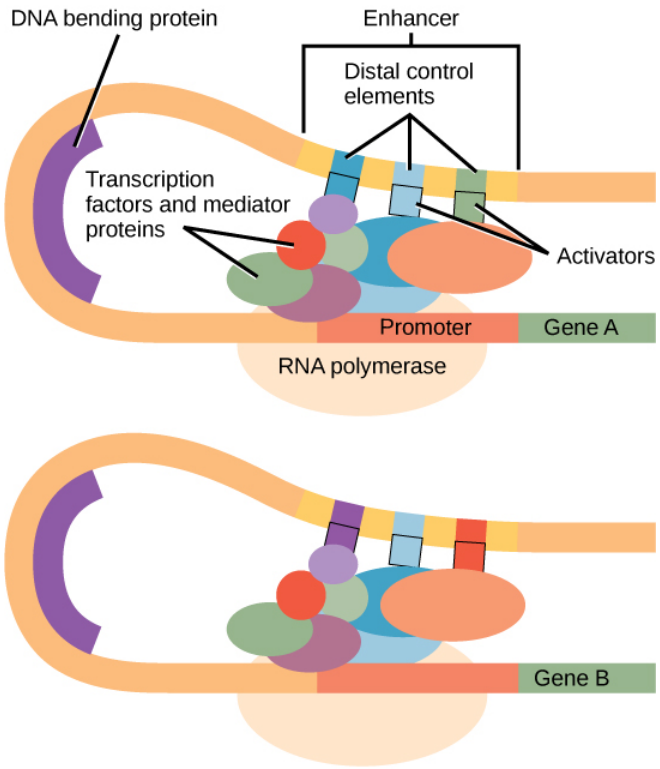


Figure 3.6.5.1: An enhancer is a DNA sequence that promotes transcription. Each enhancer is made up of short DNA sequences called distal control elements. Activators bound to the distal control elements interact with mediator proteins and transcription factors. Two different genes may have the same promoter but different distal control elements, enabling differential gene expression.

In addition to the general transcription factors, other transcription factors can bind to the promoter to regulate gene transcription. These transcription factors bind to the promoters of a specific set of genes. They are not general transcription factors that bind to every promoter complex, but are recruited to a specific sequence on the promoter of a specific gene. There are hundreds of transcription factors in a cell that each bind specifically to a particular DNA sequence motif. When transcription factors bind to the promoter just upstream of the encoded gene, it is referred to as a *cis*-acting element, because it is on the same chromosome just next to the gene. The region that a particular transcription factor binds to is called the transcription factor binding site. Transcription factors respond to environmental stimuli that cause the proteins to find their binding sites and initiate transcription of the gene that is needed.

Enhancers and Transcription

In some eukaryotic genes, there are regions that help increase or enhance transcription. These regions, called enhancers, are not necessarily close to the genes they enhance. They can be located upstream of a gene, within the coding region of the gene, downstream of a gene, or may be thousands of nucleotides away.

Enhancer regions are binding sequences, or sites, for transcription factors. When a DNA-bending protein binds, the shape of the DNA changes (Figure 3.6.5.1). This shape change allows for the interaction of the activators bound to the enhancers with the transcription factors bound to the promoter region and the RNA polymerase. Whereas DNA is generally depicted as a straight line in two dimensions, it is actually a three-dimensional object. Therefore, a nucleotide sequence thousands of nucleotides away can fold over and interact with a specific promoter.

Turning Genes Off: Transcriptional Repressors

Like prokaryotic cells, eukaryotic cells also have mechanisms to prevent transcription. Transcriptional repressors can bind to promoter or enhancer regions and block transcription. Like the transcriptional activators, repressors respond to external stimuli to prevent the binding of activating transcription factors.

Summary

To start transcription, general transcription factors, such as TFIID, TFIIH, and others, must first bind to the TATA box and recruit RNA polymerase to that location. The binding of additional regulatory transcription factors to *cis*-acting elements will either increase or prevent transcription. In addition to promoter sequences, enhancer regions help augment transcription. Enhancers can be upstream, downstream, within a gene itself, or on other chromosomes. Transcription factors bind to enhancer regions to increase or prevent transcription.

Glossary

***cis*-acting element**
: transcription factor binding sites within the promoter that regulate the transcription of a gene adjacent to it

enhancer
: segment of DNA that is upstream, downstream, perhaps thousands of nucleotides away, or on another chromosome that influence the transcription of a specific gene

***trans*-acting element**
: transcription factor binding site found outside the promoter or on another chromosome that influences the transcription of a particular gene

transcription factor binding site
: sequence of DNA to which a transcription factor binds

This page titled 3.6.5: Eukaryotic Transcription Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.4: Eukaryotic Transcription Gene Regulation** by OpenStax is licensed CC BY 4.0.

3.6.6: Eukaryotic Post-transcriptional Gene Regulation

Skills to Develop

- Understand RNA splicing and explain its role in regulating gene expression
- Describe the importance of RNA stability in gene regulation

RNA is transcribed, but must be processed into a mature form before translation can begin. This processing after an RNA molecule has been transcribed, but before it is translated into a protein, is called post-transcriptional modification. As with the epigenetic and transcriptional stages of processing, this post-transcriptional step can also be regulated to control gene expression in the cell. If the RNA is not processed, shuttled, or translated, then no protein will be synthesized.

RNA splicing, the first stage of post-transcriptional control

In eukaryotic cells, the RNA transcript often contains regions, called introns, that are removed prior to translation. The regions of RNA that code for protein are called exons (Figure 3.6.6.1). After an RNA molecule has been transcribed, but prior to its departure from the nucleus to be translated, the RNA is processed and the introns are removed by splicing.

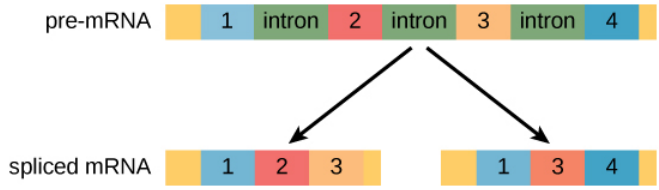


Figure 3.6.6.1: Pre-mRNA can be alternatively spliced to create different proteins.

Evolution Connection: Alternative RNA Splicing

In the 1970s, genes were first observed that exhibited alternative RNA splicing. Alternative RNA splicing is a mechanism that allows different protein products to be produced from one gene when different combinations of introns, and sometimes exons, are removed from the transcript (Figure 3.6.6.2). This alternative splicing can be haphazard, but more often it is controlled and acts as a mechanism of gene regulation, with the frequency of different splicing alternatives controlled by the cell as a way to control the production of different protein products in different cells or at different stages of development. Alternative splicing is now understood to be a common mechanism of gene regulation in eukaryotes; according to one estimate, 70 percent of genes in humans are expressed as multiple proteins through alternative splicing.

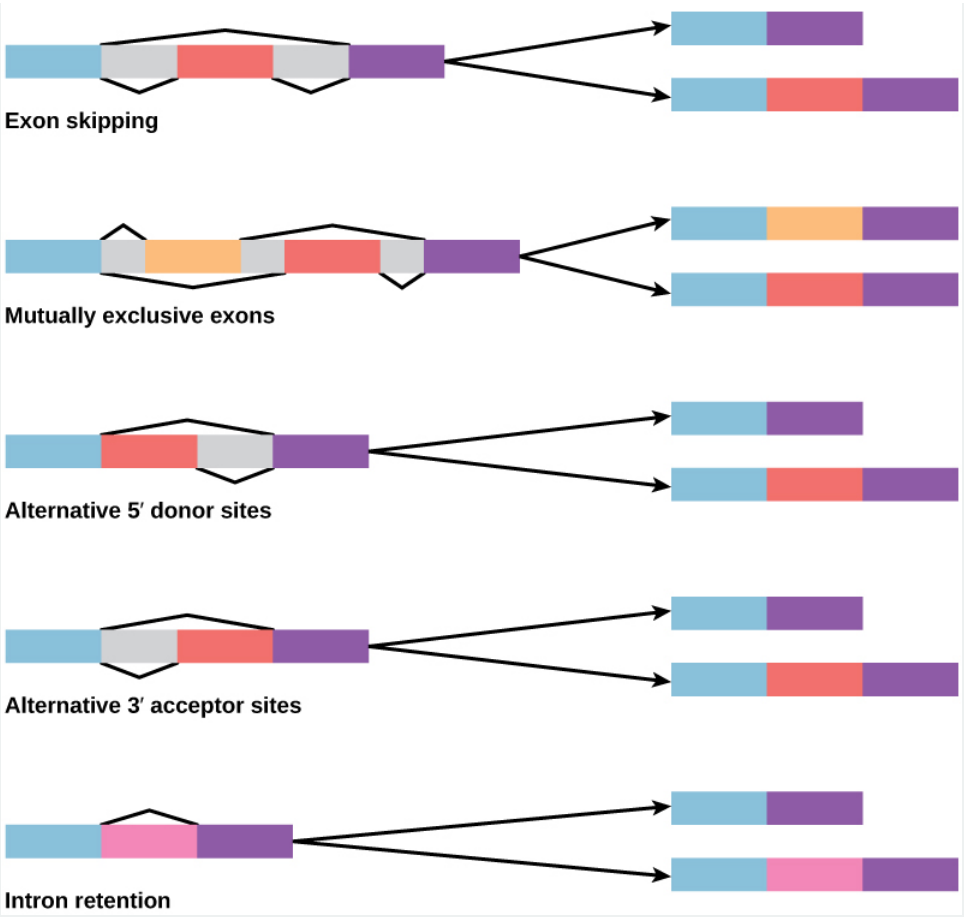


Figure 3.6.6.2: There are five basic modes of alternative splicing.

How could alternative splicing evolve? Introns have a beginning and ending recognition sequence; it is easy to imagine the failure of the splicing mechanism to identify the end of an intron and instead find the end of the next intron, thus removing two introns and the intervening exon. In fact, there are mechanisms in place to prevent such intron skipping, but mutations are likely to lead to their failure. Such “mistakes” would more than likely produce a nonfunctional protein. Indeed, the cause of many genetic diseases is alternative splicing rather than mutations in a sequence. However, alternative splicing would create a protein variant without the loss of the original protein, opening up possibilities for adaptation of the new variant to new functions. Gene duplication has played an important role in the evolution of new functions in a similar way by providing genes that may evolve without eliminating the original, functional protein.

Link to Learning



Visualize how mRNA splicing happens by watching the process in action in this video. NDSU Virtual Cell Animations Project animation 'mRNA Splicing'.

Control of RNA Stability

Before the mRNA leaves the nucleus, it is given two protective "caps" that prevent the end of the strand from degrading during its journey. The 5' cap, which is placed on the 5' end of the mRNA, is usually composed of a methylated guanosine triphosphate molecule (GTP). The poly-A tail, which is attached to the 3' end, is usually composed of a series of adenine nucleotides. Once the RNA is transported to the cytoplasm, the length of time that the RNA resides there can be controlled. Each RNA molecule has a defined lifespan and decays at a specific rate. This rate of decay can influence how much protein is in the cell. If the decay rate is increased, the RNA will not exist in the cytoplasm as long, shortening the time for translation to occur. Conversely, if the rate of decay is decreased, the RNA molecule will reside in the cytoplasm longer and more protein can be translated. This rate of decay is referred to as the RNA stability. If the RNA is stable, it will be detected for longer periods of time in the cytoplasm.

Binding of proteins to the RNA can influence its stability. Proteins, called RNA-binding proteins, or RBPs, can bind to the regions of the RNA just upstream or downstream of the protein-coding region. These regions in the RNA that are not translated into protein are called the untranslated regions, or UTRs. They are not introns (those have been removed in the nucleus). Rather, these are regions that regulate mRNA localization, stability, and protein translation. The region just before the protein-coding region is called the 5' UTR, whereas the region after the coding region is called the 3' UTR (Figure 3.6.6.3). The binding of RBPs to these regions can increase or decrease the stability of an RNA molecule, depending on the specific RBP that binds.

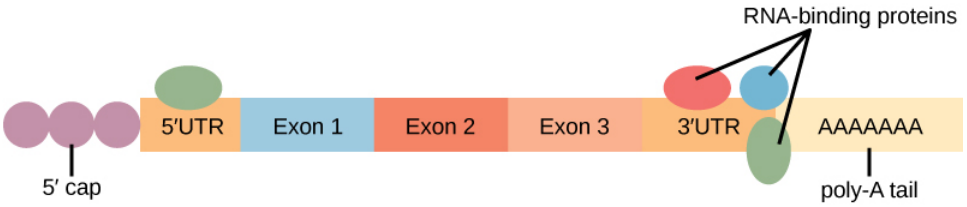


Figure 3.6.6.3: The protein-coding region of mRNA is flanked by 5' and 3' untranslated regions (UTRs). The presence of RNA-binding proteins at the 5' or 3' UTR influences the stability of the RNA molecule.

RNA Stability and microRNAs

In addition to RBPs that bind to and control (increase or decrease) RNA stability, other elements called microRNAs can bind to the RNA molecule. These microRNAs, or miRNAs, are short RNA molecules that are only 21–24 nucleotides in length. The miRNAs are made in the nucleus as longer pre-miRNAs. These pre-miRNAs are chopped into mature miRNAs by a protein called dicer. Like transcription factors and RBPs, mature miRNAs recognize a specific sequence and bind to the RNA; however, miRNAs also associate with a ribonucleoprotein complex called the RNA-induced silencing complex (RISC). RISC binds along with the miRNA to degrade the target mRNA. Together, miRNAs and the RISC complex rapidly destroy the RNA molecule.

Summary

Post-transcriptional control can occur at any stage after transcription, including RNA splicing, nuclear shuttling, and RNA stability. Once RNA is transcribed, it must be processed to create a mature RNA that is ready to be translated. This involves the removal of introns that do not code for protein. Spliceosomes bind to the signals that mark the exon/intron border to remove the introns and ligate the exons together. Once this occurs, the RNA is mature and can be translated. RNA is created and spliced in the nucleus, but needs to be transported to the cytoplasm to be translated. RNA is transported to the cytoplasm through the nuclear pore complex. Once the RNA is in the cytoplasm, the length of time it resides there before being degraded, called RNA stability, can also be altered to control the overall amount of protein that is synthesized. The RNA stability can be increased, leading to longer residency time in the cytoplasm, or decreased, leading to shortened time and less protein synthesis. RNA stability is controlled by RNA-binding proteins (RPBs) and microRNAs (miRNAs). These RPBs and miRNAs bind to the 5' UTR or the 3' UTR of the RNA to increase or decrease RNA stability. Depending on the RBP, the stability can be increased or decreased significantly; however, miRNAs always decrease stability and promote decay.

Glossary

3' UTR
: 3' untranslated region; region just downstream of the protein-coding region in an RNA molecule that is not translated

5' cap
: a methylated guanosine triphosphate (GTP) molecule that is attached to the 5' end of a messenger RNA to protect the end from degradation

5' UTR
: 5' untranslated region; region just upstream of the protein-coding region in an RNA molecule that is not translated

dicer
: enzyme that chops the pre-miRNA into the mature form of the miRNA

microRNA (miRNA)
: small RNA molecules (approximately 21 nucleotides in length) that bind to RNA molecules to degrade them

poly-A tail
: a series of adenine nucleotides that are attached to the 3' end of an mRNA to protect the end from degradation

RNA-binding protein (RBP)
: protein that binds to the 3' or 5' UTR to increase or decrease the RNA stability

RNA stability
: how long an RNA molecule will remain intact in the cytoplasm

untranslated region
: segment of the RNA molecule that are not translated into protein. These regions lie before (upstream or 5') and after (downstream or 3') the protein-coding region

RISC
: protein complex that binds along with the miRNA to the RNA to degrade it

---

This page titled 3.6.6: Eukaryotic Post-transcriptional Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.5: Eukaryotic Post-transcriptional Gene Regulation** by OpenStax is licensed CC BY 4.0.

3.6.7: Eukaryotic Translational and Post-translational Gene Regulation

Skills to Develop

- Understand the process of translation and discuss its key factors
- Describe how the initiation complex controls translation
- Explain the different ways in which the post-translational control of gene expression takes place

After the RNA has been transported to the cytoplasm, it is translated into protein. Control of this process is largely dependent on the RNA molecule. As previously discussed, the stability of the RNA will have a large impact on its translation into a protein. As the stability changes, the amount of time that it is available for translation also changes.

The Initiation Complex and Translation Rate

Like transcription, translation is controlled by proteins that bind and initiate the process. In translation, the complex that assembles to start the process is referred to as the initiation complex. The first protein to bind to the RNA to initiate translation is the eukaryotic initiation factor-2 (eIF-2). The eIF-2 protein is active when it binds to the high-energy molecule guanosine triphosphate (GTP). GTP provides the energy to start the reaction by giving up a phosphate and becoming guanosine diphosphate (GDP). The eIF-2 protein bound to GTP binds to the small 40S ribosomal subunit. When bound, the methionine initiator tRNA associates with the eIF-2/40S ribosome complex, bringing along with it the mRNA to be translated. At this point, when the initiator complex is assembled, the GTP is converted into GDP and energy is released. The phosphate and the eIF-2 protein are released from the complex and the large 60S ribosomal subunit binds to translate the RNA. The binding of eIF-2 to the RNA is controlled by phosphorylation. If eIF-2 is phosphorylated, it undergoes a conformational change and cannot bind to GTP. Therefore, the initiation complex cannot form properly and translation is impeded (Figure 3.6.7.1). When eIF-2 remains unphosphorylated, it binds the RNA and actively translates the protein.

Art Connection

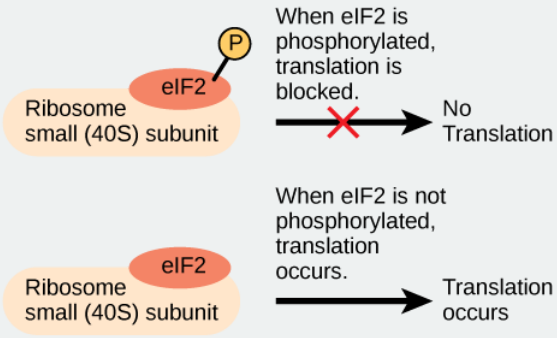


Figure 3.6.7.1: Gene expression can be controlled by factors that bind the translation initiation complex.

An increase in phosphorylation levels of eIF-2 has been observed in patients with neurodegenerative diseases such as Alzheimer's, Parkinson's, and Huntington's. What impact do you think this might have on protein synthesis?

Chemical Modifications, Protein Activity, and Longevity

Proteins can be chemically modified with the addition of groups including methyl, phosphate, acetyl, and ubiquitin groups. The addition or removal of these groups from proteins regulates their activity or the length of time they exist in the cell. Sometimes these modifications can regulate where a protein is found in the cell—for example, in the nucleus, the cytoplasm, or attached to the plasma membrane.

Chemical modifications occur in response to external stimuli such as stress, the lack of nutrients, heat, or ultraviolet light exposure. These changes can alter epigenetic accessibility, transcription, mRNA stability, or translation—all resulting in changes in expression of various genes. This is an efficient way for the cell to rapidly change the levels of specific proteins in response to the environment. Because proteins are involved in every stage of gene regulation, the phosphorylation of a protein (depending on the

protein that is modified) can alter accessibility to the chromosome, can alter translation (by altering transcription factor binding or function), can change nuclear shuttling (by influencing modifications to the nuclear pore complex), can alter RNA stability (by binding or not binding to the RNA to regulate its stability), can modify translation (increase or decrease), or can change post-translational modifications (add or remove phosphates or other chemical modifications).

The addition of an ubiquitin group to a protein marks that protein for degradation. Ubiquitin acts like a flag indicating that the protein lifespan is complete. These proteins are moved to the proteasome, an organelle that functions to remove proteins, to be degraded (Figure 3.6.7.2). One way to control gene expression, therefore, is to alter the longevity of the protein.

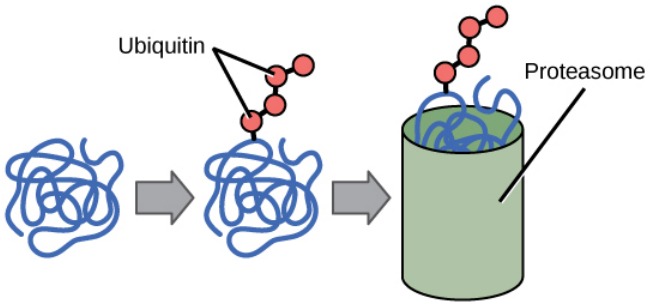


Figure 3.6.7.2: Proteins with ubiquitin tags are marked for degradation within the proteasome.

Summary

Changing the status of the RNA or the protein itself can affect the amount of protein, the function of the protein, or how long it is found in the cell. To translate the protein, a protein initiator complex must assemble on the RNA. Modifications (such as phosphorylation) of proteins in this complex can prevent proper translation from occurring. Once a protein has been synthesized, it can be modified (phosphorylated, acetylated, methylated, or ubiquitinated). These post-translational modifications can greatly impact the stability, degradation, or function of the protein.

Art Connections

Figure 3.6.7.1: An increase in phosphorylation levels of eIF-2 has been observed in patients with neurodegenerative diseases such as Alzheimer's, Parkinson's, and Huntington's. What impact do you think this might have on protein synthesis?

Answer

Protein synthesis would be inhibited.

Glossary

eukaryotic initiation factor-2 (eIF-2)
protein that binds first to an mRNA to initiate translation

guanine diphosphate (GDP)
molecule that is left after the energy is used to start translation

guanine triphosphate (GTP)
energy-providing molecule that binds to eIF-2 and is needed for translation

initiation complex
protein complex containing eIF2-2 that starts translation

large 60S ribosomal subunit
second, larger ribosomal subunit that binds to the RNA to translate it into protein

proteasome

organelle that degrades proteins

small 40S ribosomal subunit

ribosomal subunit that binds to the RNA to translate it into protein

---

This page titled 3.6.7: Eukaryotic Translational and Post-translational Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.6: Eukaryotic Translational and Post-translational Gene Regulation** by OpenStax is licensed CC BY 4.0.

3.6.8: Cancer and Gene Regulation

Skills to Develop

- Describe how changes to gene expression can cause cancer
- Explain how changes to gene expression at different levels can disrupt the cell cycle
- Discuss how understanding regulation of gene expression can lead to better drug design

Cancer is not a single disease but includes many different diseases. In cancer cells, mutations modify cell-cycle control and cells don't stop growing as they normally would. Mutations can also alter the growth rate or the progression of the cell through the cell cycle. One example of a gene modification that alters the growth rate is increased phosphorylation of cyclin B, a protein that controls the progression of a cell through the cell cycle and serves as a cell-cycle checkpoint protein.

For cells to move through each phase of the cell cycle, the cell must pass through checkpoints. This ensures that the cell has properly completed the step and has not encountered any mutation that will alter its function. Many proteins, including cyclin B, control these checkpoints. The phosphorylation of cyclin B, a post-translational event, alters its function. As a result, cells can progress through the cell cycle unimpeded, even if mutations exist in the cell and its growth should be terminated. This post-translational change of cyclin B prevents it from controlling the cell cycle and contributes to the development of cancer.

Cancer: Disease of Altered Gene Expression

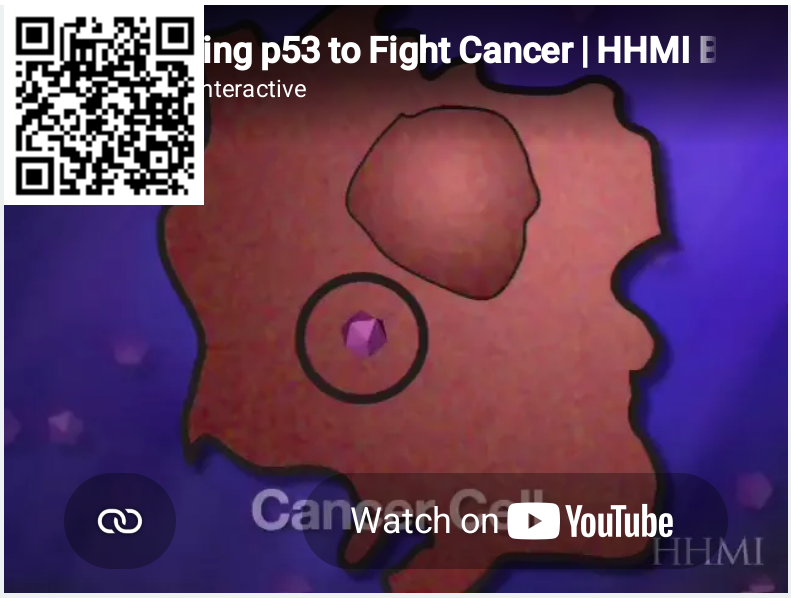
Cancer can be described as a disease of altered gene expression. There are many proteins that are turned on or off (gene activation or gene silencing) that dramatically alter the overall activity of the cell. A gene that is not normally expressed in that cell can be switched on and expressed at high levels. This can be the result of gene mutation or changes in gene regulation (epigenetic, transcription, post-transcription, translation, or post-translation).

Changes in epigenetic regulation, transcription, RNA stability, protein translation, and post-translational control can be detected in cancer. While these changes don't occur simultaneously in one cancer, changes at each of these levels can be detected when observing cancer at different sites in different individuals. Therefore, changes in histone acetylation (epigenetic modification that leads to gene silencing), activation of transcription factors by phosphorylation, increased RNA stability, increased translational control, and protein modification can all be detected at some point in various cancer cells. Scientists are working to understand the common changes that give rise to certain types of cancer or how a modification might be exploited to destroy a tumor cell.

Tumor Suppressor Genes, Oncogenes, and Cancer

In normal cells, some genes function to prevent excess, inappropriate cell growth. These are tumor suppressor genes, which are active in normal cells to prevent uncontrolled cell growth. There are many tumor suppressor genes in cells. The most studied tumor suppressor gene is p53, which is mutated in over 50 percent of all cancer types. The p53 protein itself functions as a transcription factor. It can bind to sites in the promoters of genes to initiate transcription. Therefore, the mutation of p53 in cancer will dramatically alter the transcriptional activity of its target genes.

Link to Learning



Watch this animation to learn more about the use of p53 in fighting cancer.

Proto-oncogenes are positive cell-cycle regulators. When mutated, proto-oncogenes can become oncogenes and cause cancer. Overexpression of the oncogene can lead to uncontrolled cell growth. This is because oncogenes can alter transcriptional activity, stability, or protein translation of another gene that directly or indirectly controls cell growth. An example of an oncogene involved in cancer is a protein called myc. Myc is a transcription factor that is aberrantly activated in Burkett's Lymphoma, a cancer of the lymph system. Overexpression of myc transforms normal B cells into cancerous cells that continue to grow uncontrollably. High B-cell numbers can result in tumors that can interfere with normal bodily function. Patients with Burkett's lymphoma can develop tumors on their jaw or in their mouth that interfere with the ability to eat.

Cancer and Epigenetic Alterations

Silencing genes through epigenetic mechanisms is also very common in cancer cells. There are characteristic modifications to histone proteins and DNA that are associated with silenced genes. In cancer cells, the DNA in the promoter region of silenced genes is methylated on cytosine DNA residues in CpG islands. Histone proteins that surround that region lack the acetylation modification that is present when the genes are expressed in normal cells. This combination of DNA methylation and histone deacetylation (epigenetic modifications that lead to gene silencing) is commonly found in cancer. When these modifications occur, the gene present in that chromosomal region is silenced. Increasingly, scientists understand how epigenetic changes are altered in cancer. Because these changes are temporary and can be reversed—for example, by preventing the action of the histone deacetylase protein that removes acetyl groups, or by DNA methyl transferase enzymes that add methyl groups to cytosines in DNA—it is possible to design new drugs and new therapies to take advantage of the reversible nature of these processes. Indeed, many researchers are testing how a silenced gene can be switched back on in a cancer cell to help re-establish normal growth patterns.

Genes involved in the development of many other illnesses, ranging from allergies to inflammation to autism, are thought to be regulated by epigenetic mechanisms. As our knowledge of how genes are controlled deepens, new ways to treat diseases like cancer will emerge.

Cancer and Transcriptional Control

Alterations in cells that give rise to cancer can affect the transcriptional control of gene expression. Mutations that activate transcription factors, such as increased phosphorylation, can increase the binding of a transcription factor to its binding site in a promoter. This could lead to increased transcriptional activation of that gene that results in modified cell growth. Alternatively, a mutation in the DNA of a promoter or enhancer region can increase the binding ability of a transcription factor. This could also lead to the increased transcription and aberrant gene expression that is seen in cancer cells.

Researchers have been investigating how to control the transcriptional activation of gene expression in cancer. Identifying how a transcription factor binds, or a pathway that activates where a gene can be turned off, has led to new drugs and new ways to treat cancer. In breast cancer, for example, many proteins are overexpressed. This can lead to increased phosphorylation of key transcription factors that increase transcription. One such example is the overexpression of the epidermal growth factor receptor (EGFR) in a subset of breast cancers. The EGFR pathway activates many protein kinases that, in turn, activate many transcription factors that control genes involved in cell growth. New drugs that prevent the activation of EGFR have been developed and are used to treat these cancers.

Cancer and Post-transcriptional Control

Changes in the post-transcriptional control of a gene can also result in cancer. Recently, several groups of researchers have shown that specific cancers have altered expression of miRNAs. Because miRNAs bind to the 3' UTR of RNA molecules to degrade them, overexpression of these miRNAs could be detrimental to normal cellular activity. Too many miRNAs could dramatically decrease the RNA population leading to a decrease in protein expression. Several studies have demonstrated a change in the miRNA population in specific cancer types. It appears that the subset of miRNAs expressed in breast cancer cells is quite different from the subset expressed in lung cancer cells or even from normal breast cells. This suggests that alterations in miRNA activity can contribute to the growth of breast cancer cells. These types of studies also suggest that if some miRNAs are specifically expressed only in cancer cells, they could be potential drug targets. It would, therefore, be conceivable that new drugs that turn off miRNA expression in cancer could be an effective method to treat cancer.

Cancer and Translational/Post-translational Control

There are many examples of how translational or post-translational modifications of proteins arise in cancer. Modifications are found in cancer cells from the increased translation of a protein to changes in protein phosphorylation to alternative splice variants of a protein. An example of how the expression of an alternative form of a protein can have dramatically different outcomes is seen in colon cancer cells. The c-Flip protein, a protein involved in mediating the cell death pathway, comes in two forms: long (c-FLIPL) and short (c-FLIPS). Both forms appear to be involved in initiating controlled cell death mechanisms in normal cells. However, in colon cancer cells, expression of the long form results in increased cell growth instead of cell death. Clearly, the expression of the wrong protein dramatically alters cell function and contributes to the development of cancer.

New Drugs to Combat Cancer: Targeted Therapies

Scientists are using what is known about the regulation of gene expression in disease states, including cancer, to develop new ways to treat and prevent disease development. Many scientists are designing drugs on the basis of the gene expression patterns within individual tumors. This idea, that therapy and medicines can be tailored to an individual, has given rise to the field of personalized medicine. With an increased understanding of gene regulation and gene function, medicines can be designed to specifically target diseased cells without harming healthy cells. Some new medicines, called targeted therapies, have exploited the overexpression of a specific protein or the mutation of a gene to develop a new medication to treat disease. One such example is the use of anti-EGF receptor medications to treat the subset of breast cancer tumors that have very high levels of the EGF protein. Undoubtedly, more targeted therapies will be developed as scientists learn more about how gene expression changes can cause cancer.

Career Connection: Clinical Trial Coordinator

A clinical trial coordinator is the person managing the proceedings of the clinical trial. This job includes coordinating patient schedules and appointments, maintaining detailed notes, building the database to track patients (especially for long-term follow-up studies), ensuring proper documentation has been acquired and accepted, and working with the nurses and doctors to facilitate the trial and publication of the results. A clinical trial coordinator may have a science background, like a nursing degree, or other certification. People who have worked in science labs or in clinical offices are also qualified to become a clinical trial coordinator. These jobs are generally in hospitals; however, some clinics and doctor’s offices also conduct clinical trials and may hire a coordinator.

Summary

Cancer can be described as a disease of altered gene expression. Changes at every level of eukaryotic gene expression can be detected in some form of cancer at some point in time. In order to understand how changes to gene expression can cause cancer, it is critical to understand how each stage of gene regulation works in normal cells. By understanding the mechanisms of control in normal, non-diseased cells, it will be easier for scientists to understand what goes wrong in disease states including complex ones like cancer.

Glossary

DNA methylation
: epigenetic modification that leads to gene silencing; commonly found in cancer cells

histone acetylation
: epigenetic modification that leads to gene silencing; commonly found in cancer cells found in cancer cells

myc
: oncogene that causes cancer in many cancer cells

This page titled 3.6.8: Cancer and Gene Regulation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.7: Cancer and Gene Regulation** by OpenStax is licensed CC BY 4.0.

3.6.E: Gene Expression (Exercises)

16.1: Regulation of Gene Expression

Review Questions

Control of gene expression in eukaryotic cells occurs at which level(s)?

A. only the transcriptional level
B. epigenetic and transcriptional levels
C. epigenetic, transcriptional, and translational levels
D. epigenetic, transcriptional, post-transcriptional, translational, and post-translational levels

Answer

D

Post-translational control refers to:

A. regulation of gene expression after transcription
B. regulation of gene expression after translation
C. control of epigenetic activation
D. period between transcription and translation

Answer

B

Free Response

Name two differences between prokaryotic and eukaryotic cells and how these differences benefit multicellular organisms.

Answer

Eukaryotic cells have a nucleus, whereas prokaryotic cells do not. In eukaryotic cells, DNA is confined within the nuclear region. Because of this, transcription and translation are physically separated. This creates a more complex mechanism for the control of gene expression that benefits multicellular organisms because it compartmentalizes gene regulation.

Gene expression occurs at many stages in eukaryotic cells, whereas in prokaryotic cells, control of gene expression only occurs at the transcriptional level. This allows for greater control of gene expression in eukaryotes and more complex systems to be developed. Because of this, different cell types can arise in an individual organism.

Describe how controlling gene expression will alter the overall protein levels in the cell.

Answer

The cell controls which proteins are expressed and to what level each protein is expressed in the cell. Prokaryotic cells alter the transcription rate to turn genes on or off. This method will increase or decrease protein levels in response to what is needed by the cell. Eukaryotic cells change the accessibility (epigenetic), transcription, or translation of a gene. This will alter the amount of RNA and the lifespan of the RNA to alter the amount of protein that exists. Eukaryotic cells also control protein translation to increase or decrease the overall levels. Eukaryotic organisms are much more complex and can manipulate protein levels by changing many stages in the process.

16.2: Prokaryotic Gene Regulation

Review Questions

If glucose is absent, but so is lactose, the *lac* operon will be _____.

A. activated
B. repressed
C. activated, but only partially
D. mutated

Answer

B

Prokaryotic cells lack a nucleus. Therefore, the genes in prokaryotic cells are:

A. all expressed, all of the time
B. transcribed and translated almost simultaneously
C. transcriptionally controlled because translation begins before transcription ends
D. b and c are both true

Answer

D

Free Response

Describe how transcription in prokaryotic cells can be altered by external stimulation such as excess lactose in the environment.

Answer

Environmental stimuli can increase or induce transcription in prokaryotic cells. In this example, lactose in the environment will induce the transcription of the *lac* operon, but only if glucose is not available in the environment.

What is the difference between a repressible and an inducible operon?

Answer

A repressible operon uses a protein bound to the promoter region of a gene to keep the gene repressed or silent. This repressor must be actively removed in order to transcribe the gene. An inducible operon is either activated or repressed depending on the needs of the cell and what is available in the local environment.

16.3: Eukaryotic Epigenetic Gene Regulation

Review Questions

What are epigenetic modifications?

A. the addition of reversible changes to histone proteins and DNA
B. the removal of nucleosomes from the DNA
C. the addition of more nucleosomes to the DNA
D. mutation of the DNA sequence

Answer

A

Which of the following are true of epigenetic changes?

A. allow DNA to be transcribed
B. move histones to open or close a chromosomal region
C. are temporary
D. all of the above

Answer

D

Free Response

In cancer cells, alteration to epigenetic modifications turns off genes that are normally expressed. Hypothetically, how could you reverse this process to turn these genes back on?

Answer

You can create medications that reverse the epigenetic processes (to add histone acetylation marks or to remove DNA methylation) and create an open chromosomal configuration.

16.4: Eukaryotic Transcription Gene Regulation

Review Questions

The binding of _____ is required for transcription to start.

A. a protein
B. DNA polymerase
C. RNA polymerase
D. a transcription factor

Answer

C

What will result from the binding of a transcription factor to an enhancer region?

A. decreased transcription of an adjacent gene
B. increased transcription of a distant gene
C. alteration of the translation of an adjacent gene
D. initiation of the recruitment of RNA polymerase

Answer

B

Free Response

A mutation within the promoter region can alter transcription of a gene. Describe how this can happen.

Answer

A mutation in the promoter region can change the binding site for a transcription factor that normally binds to increase transcription. The mutation could either decrease the ability of the transcription factor to bind, thereby decreasing transcription, or it can increase the ability of the transcription factor to bind, thus increasing transcription.

What could happen if a cell had too much of an activating transcription factor present?

Answer

If too much of an activating transcription factor were present, then transcription would be increased in the cell. This could lead to dramatic alterations in cell function.

16.5: Eukaryotic Post-transcriptional Gene Regulation

Review Questions

Which of the following are involved in post-transcriptional control?

A. control of RNA splicing
B. control of RNA shuttling
C. control of RNA stability
D. all of the above

Answer

D

Binding of an RNA binding protein will _____ the stability of the RNA molecule.

A. increase
B. decrease
C. neither increase nor decrease
D. either increase or decrease

Answer

D

Free Response

Describe how RBPs can prevent miRNAs from degrading an RNA molecule.

Answer

RNA binding proteins (RBP) bind to the RNA and can either increase or decrease the stability of the RNA. If they increase the stability of the RNA molecule, the RNA will remain intact in the cell for a longer period of time than normal. Since both RBPs and miRNAs bind to the RNA molecule, RBP can potentially bind first to the RNA and prevent the binding of the miRNA that will degrade it.

How can external stimuli alter post-transcriptional control of gene expression?

Answer

External stimuli can modify RNA-binding proteins (i.e., through phosphorylation of proteins) to alter their activity.

16.6: Eukaryotic Translational and Post-translational Gene Regulation

Review Questions

Post-translational modifications of proteins can affect which of the following?

A. protein function
B. transcriptional regulation
C. chromatin modification
D. all of the above

Answer

A

Free Response

Protein modification can alter gene expression in many ways. Describe how phosphorylation of proteins can alter gene expression.

Answer

Because proteins are involved in every stage of gene regulation, phosphorylation of a protein (depending on the protein that is modified) can alter accessibility to the chromosome, can alter translation (by altering the transcription factor binding or function), can change nuclear shuttling (by influencing modifications to the nuclear pore complex), can alter RNA stability (by binding or not binding to the RNA to regulate its stability), can modify translation (increase or decrease), or can change post-translational modifications (add or remove phosphates or other chemical modifications).

Alternative forms of a protein can be beneficial or harmful to a cell. What do you think would happen if too much of an alternative protein bound to the 3' UTR of an RNA and caused it to degrade?

Answer

If the RNA degraded, then less of the protein that the RNA encodes would be translated. This could have dramatic implications for the cell.

Changes in epigenetic modifications alter the accessibility and transcription of DNA. Describe how environmental stimuli, such as ultraviolet light exposure, could modify gene expression.

Answer

Environmental stimuli, like ultraviolet light exposure, can alter the modifications to the histone proteins or DNA. Such stimuli may change an actively transcribed gene into a silenced gene by removing acetyl groups from histone proteins or by adding methyl groups to DNA.

16.7: Cancer and Gene Regulation

Review Questions

Cancer causing genes are called _____.

A. transformation genes
B. tumor suppressor genes
C. oncogenes
D. mutated genes

Answer

C

Targeted therapies are used in patients with a set gene expression pattern. A targeted therapy that prevents the activation of the estrogen receptor in breast cancer would be beneficial to which type of patient?

A. patients who express the EGFR receptor in normal cells
B. patients with a mutation that inactivates the estrogen receptor
C. patients with lots of the estrogen receptor expressed in their tumor
D. patients that have no estrogen receptor expressed in their tumor

Answer

C

Free Response

New drugs are being developed that decrease DNA methylation and prevent the removal of acetyl groups from histone proteins. Explain how these drugs could affect gene expression to help kill tumor cells.

Answer

These drugs will keep the histone proteins and the DNA methylation patterns in the open chromosomal configuration so that transcription is feasible. If a gene is silenced, these drugs could reverse the epigenetic configuration to re-express the gene.

How can understanding the gene expression pattern in a cancer cell tell you something about that specific form of cancer?

Answer

Understanding which genes are expressed in a cancer cell can help diagnose the specific form of cancer. It can also help identify treatment options for that patient. For example, if a breast cancer tumor expresses the EGFR in high numbers, it might respond to specific anti-EGFR therapy. If that receptor is not expressed, it would not respond to that therapy.

This page titled 3.6.E: Gene Expression (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **16.E: Gene Expression (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

3.7: Biotechnology and Genomics

3.7.1: Prelude
3.7.2: Biotechnology
3.7.3: Mapping Genomes
3.7.4: Whole-Genome Sequencing
3.7.5: Applying Genomics
3.7.6: Genomics and Proteomics
3.7.E: Biotechnology and Genomics (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 3.7: Biotechnology and Genomics is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

3.7.1: Prelude

The study of nucleic acids began with the discovery of DNA, progressed to the study of genes and small fragments, and has now exploded to the field of genomics. Genomics is the study of entire genomes, including the complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species. The advances in genomics have been made possible by DNA sequencing technology. Just as information technology has led to Google maps that enable people to get detailed information about locations around the globe, genomic information is used to create similar maps of the DNA of different organisms. These findings have helped anthropologists to better understand human migration and have aided the field of medicine through the mapping of human genetic diseases. The ways in which genomic information can contribute to scientific understanding are varied and quickly growing.

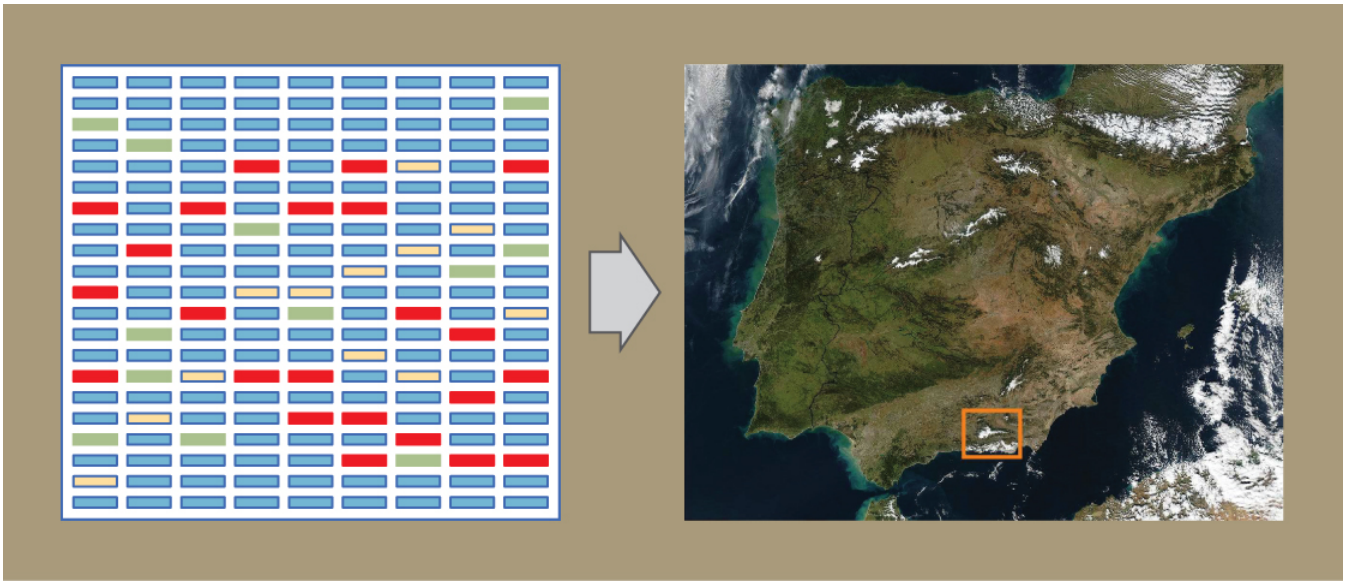


Figure 3.7.1.1: In genomics, the DNA of different organisms is compared, enabling scientists to create maps with which to navigate the DNA of different organisms. (credit "map": modification of photo by NASA)

This page titled 3.7.1: Prelude is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.0: Introduction** by OpenStax is licensed CC BY 4.0.

3.7.2: Biotechnology

Learning Objectives

- Describe gel electrophoresis
- Explain molecular and reproductive cloning
- Describe uses of biotechnology in medicine and agriculture

Biotechnology is the use of biological agents for technological advancement. Biotechnology was used for breeding livestock and crops long before the scientific basis of these techniques was understood. Since the discovery of the structure of DNA in 1953, the field of biotechnology has grown rapidly through both academic research and private companies. The primary applications of this technology are in medicine (production of vaccines and antibiotics) and agriculture (genetic modification of crops, such as to increase yields). Biotechnology also has many industrial applications, such as fermentation, the treatment of oil spills, and the production of biofuels (Figure 3.7.2.1).

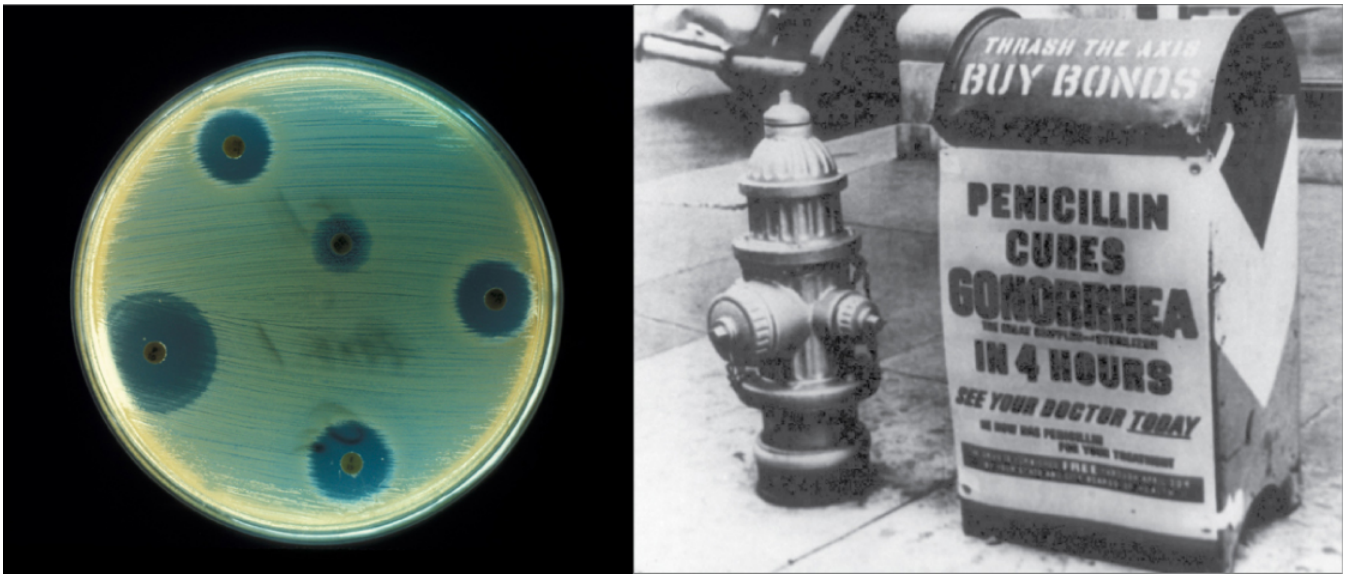
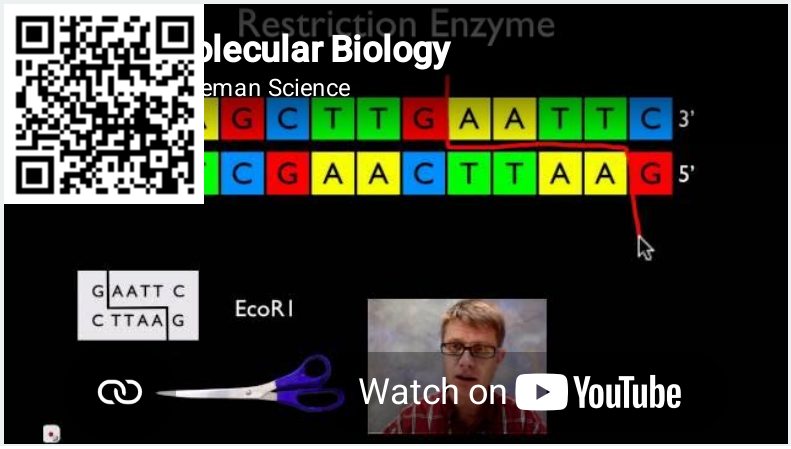


Figure 3.7.2.1: Antibiotics are chemicals produced by fungi, bacteria, and other organisms that have antimicrobial properties. The first antibiotic discovered was penicillin. Antibiotics are now commercially produced and tested for their potential to inhibit bacterial growth. (credit "advertisement": modification of work by NIH; credit "test plate": modification of work by Don Stalons/CDC; scale-bar data from Matt Russell)

Video



Basic Techniques to Manipulate Genetic Material (DNA and RNA)

To understand the basic techniques used to work with nucleic acids, remember that nucleic acids are macromolecules made of nucleotides (a sugar, a phosphate, and a nitrogenous base) linked by phosphodiester bonds. The phosphate groups on these molecules each have a net negative charge. An entire set of DNA molecules in the nucleus is called the genome. DNA has two complementary strands linked by hydrogen bonds between the paired bases. The two strands can be separated by exposure to high temperatures (DNA denaturation) and can be reannealed by cooling. The DNA can be replicated by the DNA polymerase enzyme. Unlike DNA, which is located in the nucleus of eukaryotic cells, RNA molecules leave the nucleus. The most common type of RNA that is analyzed is the messenger RNA (mRNA) because it represents the protein-coding genes that are actively expressed. However, RNA molecules present some other challenges to analysis, as they are often less stable than DNA.

DNA and RNA Extraction

To study or manipulate nucleic acids, the DNA or RNA must first be isolated or extracted from the cells. Various techniques are used to extract different types of DNA (Figure 3.7.2.2). Most nucleic acid extraction techniques involve steps to break open the cell and use enzymatic reactions to destroy all macromolecules that are not desired (such as degradation of unwanted molecules and separation from the DNA sample). Cells are broken using a lysis buffer (a solution which is mostly a detergent); lysis means “to split.” These enzymes break apart lipid molecules in the cell membranes and nuclear membranes. Macromolecules are inactivated using enzymes such as proteases that break down proteins, and ribonucleases (RNAses) that break down RNA. The DNA is then precipitated using alcohol. Human genomic DNA is usually visible as a gelatinous, white mass. The DNA samples can be stored frozen at –80°C for several years.

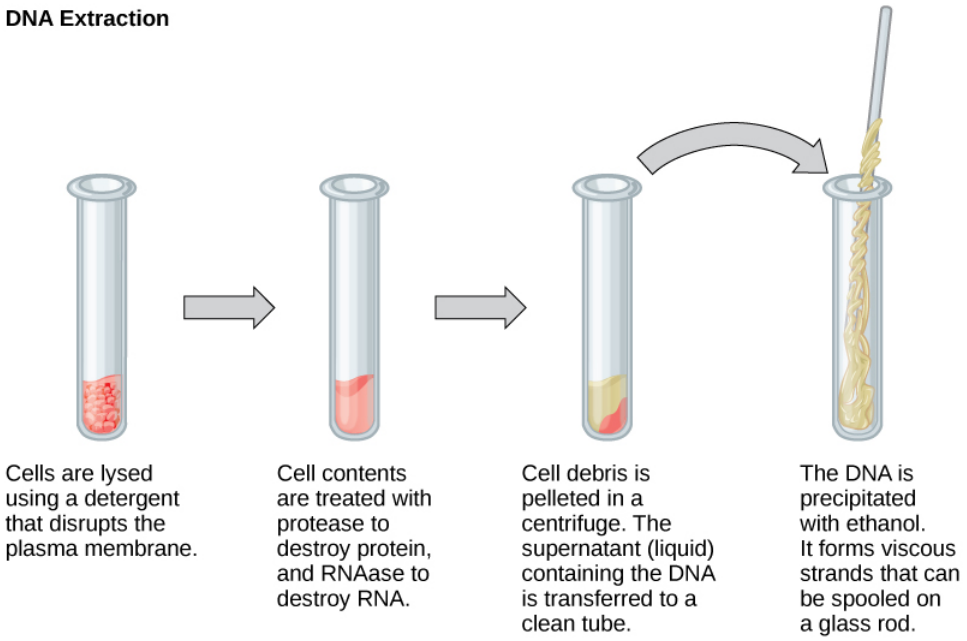


Figure 3.7.2.2: This diagram shows the basic method used for extraction of DNA.

RNA analysis is performed to study gene expression patterns in cells. RNA is naturally very unstable because RNAses are commonly present in nature and very difficult to inactivate. Similar to DNA, RNA extraction involves the use of various buffers and enzymes to inactivate macromolecules and preserve the RNA.

Gel Electrophoresis

Because nucleic acids are negatively charged ions at neutral or basic pH in an aqueous environment, they can be mobilized by an electric field. Gel electrophoresis is a technique used to separate molecules on the basis of size, using this charge. The nucleic acids can be separated as whole chromosomes or fragments. The nucleic acids are loaded into a slot near the negative electrode of a semisolid, porous gel matrix and pulled toward the positive electrode at the opposite end of the gel. Smaller molecules move through the pores in the gel faster than larger molecules; this difference in the rate of migration separates the fragments on the basis of size. There are molecular weight standard samples that can be run alongside the molecules to provide a size comparison. Nucleic

acids in a gel matrix can be observed using various fluorescent or colored dyes. Distinct nucleic acid fragments appear as bands at specific distances from the top of the gel (the negative electrode end) on the basis of their size (Figure 3.7.2.3). A mixture of genomic DNA fragments of varying sizes appear as a long smear, whereas uncut genomic DNA is usually too large to run through the gel and forms a single large band at the top of the gel.

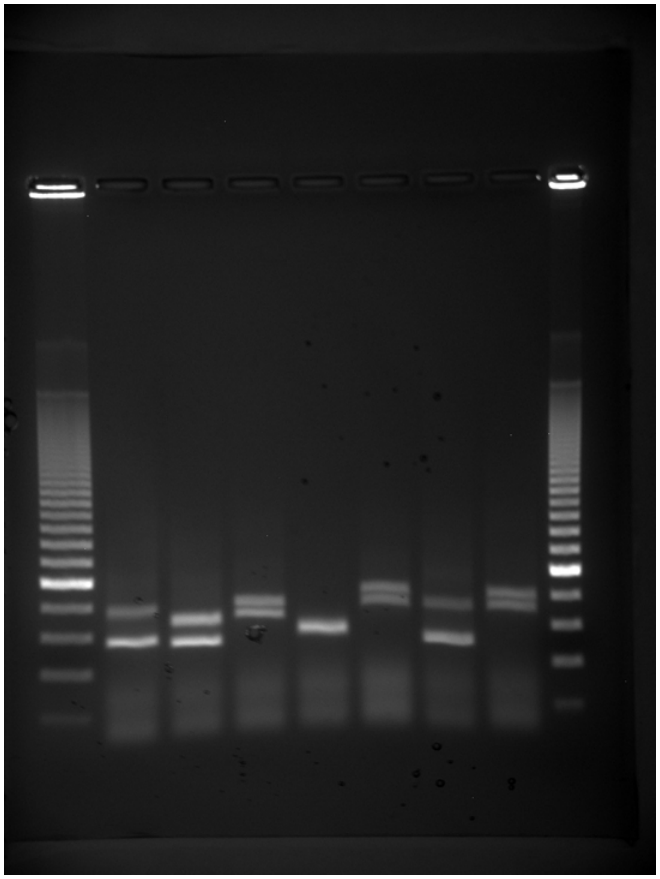


Figure 3.7.2.3: Shown are DNA fragments from seven samples run on a gel, stained with a fluorescent dye, and viewed under UV light. (credit: James Jacob, Tompkins Cortland Community College)

Video



Amplification of Nucleic Acid Fragments by Polymerase Chain Reaction

Although genomic DNA is visible to the naked eye when it is extracted in bulk, DNA analysis often requires focusing on one or more specific regions of the genome. **Polymerase chain reaction** (**PCR**) is a technique used to amplify specific regions of DNA for further analysis (Figure 3.7.2.4). PCR is used for many purposes in laboratories, such as the cloning of gene fragments to

analyze genetic diseases, identification of contaminant foreign DNA in a sample, and the amplification of DNA for sequencing. More practical applications include the determination of paternity and detection of genetic diseases.

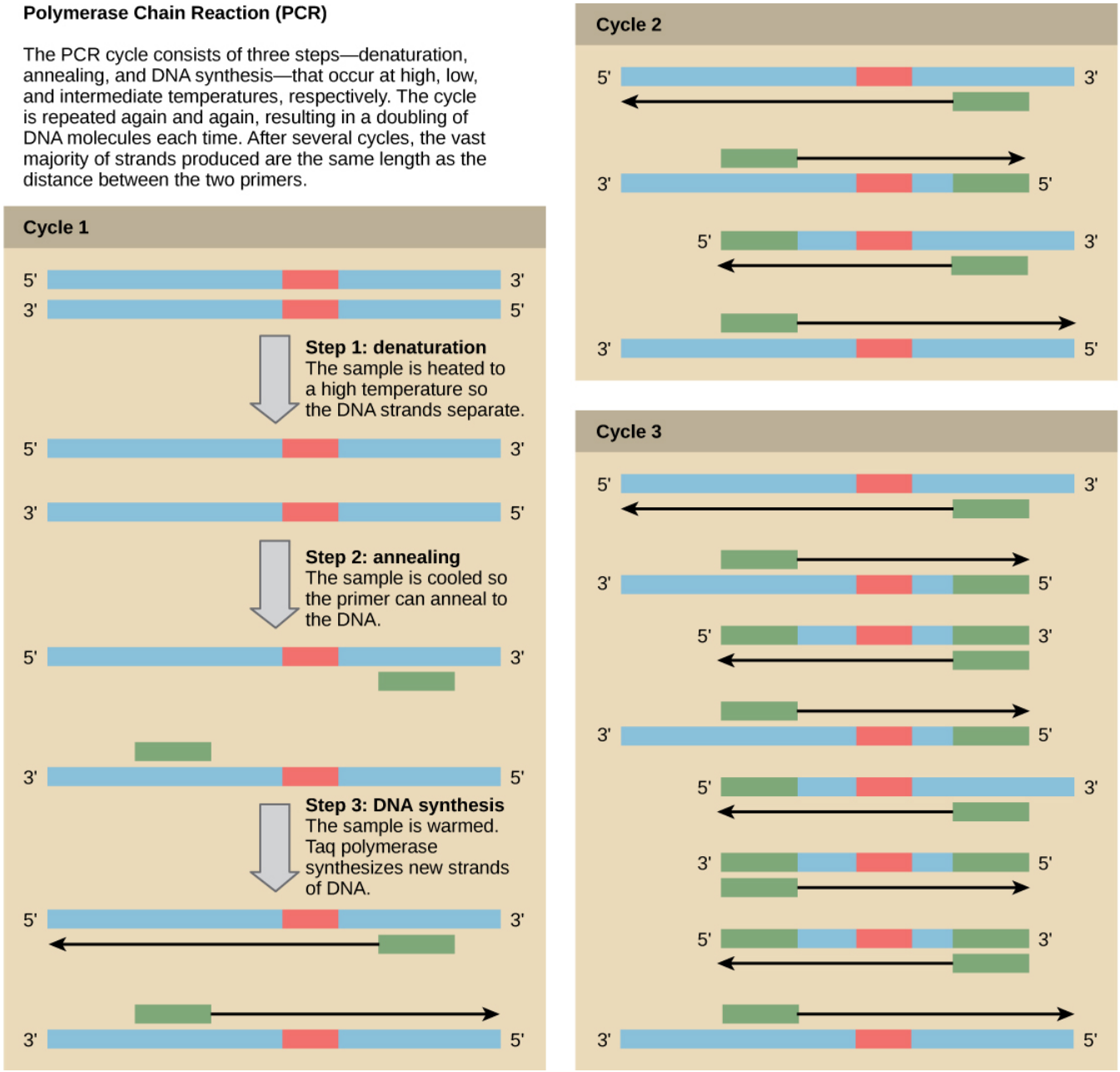


Figure 3.7.2.4: Polymerase chain reaction, or PCR, is used to amplify a specific sequence of DNA. Primers—short pieces of DNA complementary to each end of the target sequence—are combined with genomic DNA, Taq polymerase, and deoxynucleotides. Taq polymerase is a DNA polymerase isolated from the thermostable bacterium *Thermus aquaticus* that is able to withstand the high temperatures used in PCR. *Thermus aquaticus* grows in the Lower Geyser Basin of Yellowstone National Park. Reverse transcriptase PCR (RT-PCR) is similar to PCR, but cDNA is made from an RNA template before PCR begins.

DNA fragments can also be amplified from an RNA template in a process called reverse transcriptase PCR (RT-PCR). The first step is to recreate the original DNA template strand (called cDNA) by applying DNA nucleotides to the mRNA. This process is called reverse transcription. This requires the presence of an enzyme called reverse transcriptase. After the cDNA is made, regular PCR can be used to amplify it.

Link to Learning



Deepen your understanding of the polymerase chain reaction by clicking through this interactive exercise.

Hybridization, Southern Blotting, and Northern Blotting

Nucleic acid samples, such as fragmented genomic DNA and RNA extracts, can be probed for the presence of certain sequences. Short DNA fragments called probes are designed and labeled with radioactive or fluorescent dyes to aid detection. Gel electrophoresis separates the nucleic acid fragments according to their size. The fragments in the gel are then transferred onto a nylon membrane in a procedure called blotting (Figure 3.7.2.5). The nucleic acid fragments that are bound to the surface of the membrane can then be probed with specific radioactively or fluorescently labeled probe sequences. When DNA is transferred to a nylon membrane, the technique is called Southern blotting, and when RNA is transferred to a nylon membrane, it is called northern blotting. Southern blots are used to detect the presence of certain DNA sequences in a given genome, and northern blots are used to detect gene expression.

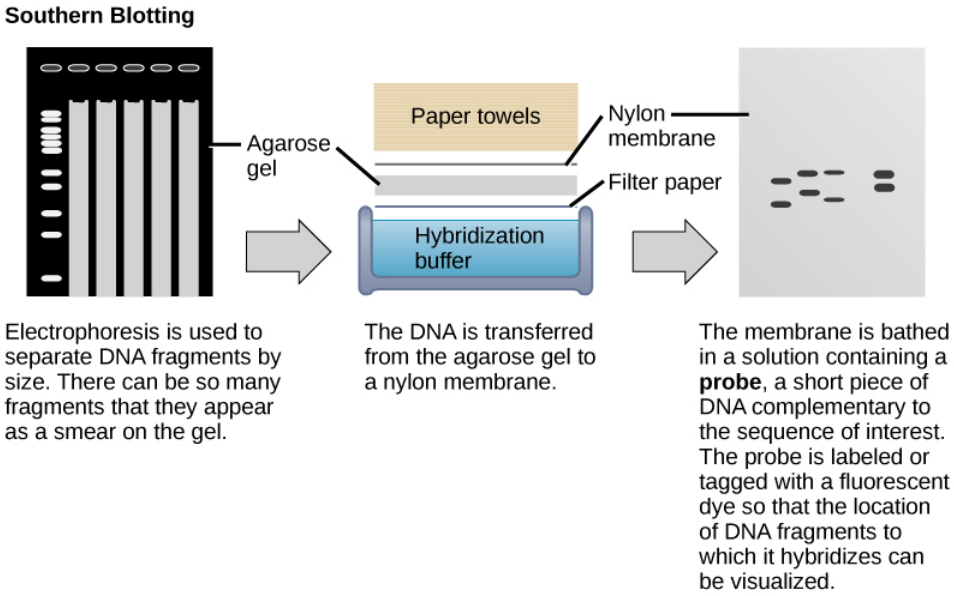


Figure 3.7.2.5: Southern blotting is used to find a particular sequence in a sample of DNA. DNA fragments are separated on a gel, transferred to a nylon membrane, and incubated with a DNA probe complementary to the sequence of interest. Northern blotting is similar to Southern blotting, but RNA is run on the gel instead of DNA. In western blotting, proteins are run on a gel and detected using antibodies.

Video



Molecular Cloning

In general, the word “cloning” means the creation of a perfect replica; however, in biology, the re-creation of a whole organism is referred to as “reproductive cloning.” Long before attempts were made to clone an entire organism, researchers learned how to reproduce desired regions or fragments of the genome, a process that is referred to as molecular cloning.

Cloning small fragments of the genome allows for the manipulation and study of specific genes (and their protein products), or noncoding regions in isolation. A plasmid (also called a vector) is a small circular DNA molecule that replicates independently of the chromosomal DNA. In cloning, the plasmid molecules can be used to provide a "folder" in which to insert a desired DNA fragment. Plasmids are usually introduced into a bacterial host for proliferation. In the bacterial context, the fragment of DNA from the human genome (or the genome of another organism that is being studied) is referred to as foreign DNA, or a transgene, to differentiate it from the DNA of the bacterium, which is called the host DNA.

Plasmids occur naturally in bacterial populations (such as *Escherichia coli*) and have genes that can contribute favorable traits to the organism, such as antibiotic resistance (the ability to be unaffected by antibiotics). Plasmids have been repurposed and engineered as vectors for molecular cloning and the large-scale production of important reagents, such as insulin and human growth hormone. An important feature of plasmid vectors is the ease with which a foreign DNA fragment can be introduced via the multiple cloning site (MCS). The MCS is a short DNA sequence containing multiple sites that can be cut with different commonly available restriction endonucleases. Restriction endonucleases recognize specific DNA sequences and cut them in a predictable manner; they are naturally produced by bacteria as a defense mechanism against foreign DNA. Many restriction endonucleases make staggered cuts in the two strands of DNA, such that the cut ends have a 2- or 4-base single-stranded overhang. Because these overhangs are capable of annealing with complementary overhangs, these are called “sticky ends.” Addition of an enzyme called DNA ligase permanently joins the DNA fragments via phosphodiester bonds. In this way, any DNA fragment generated by restriction endonuclease cleavage can be spliced between the two ends of a plasmid DNA that has been cut with the same restriction endonuclease (Figure 3.7.2.6).

Recombinant DNA Molecules

Plasmids with foreign DNA inserted into them are called recombinant DNA molecules because they are created artificially and do not occur in nature. They are also called chimeric molecules because the origin of different parts of the molecules can be traced back to different species of biological organisms or even to chemical synthesis. Proteins that are expressed from recombinant DNA molecules are called recombinant proteins. Not all recombinant plasmids are capable of expressing genes. The recombinant DNA may need to be moved into a different vector (or host) that is better designed for gene expression. Plasmids may also be engineered to express proteins only when stimulated by certain environmental factors, so that scientists can control the expression of the recombinant proteins.

Art Connection

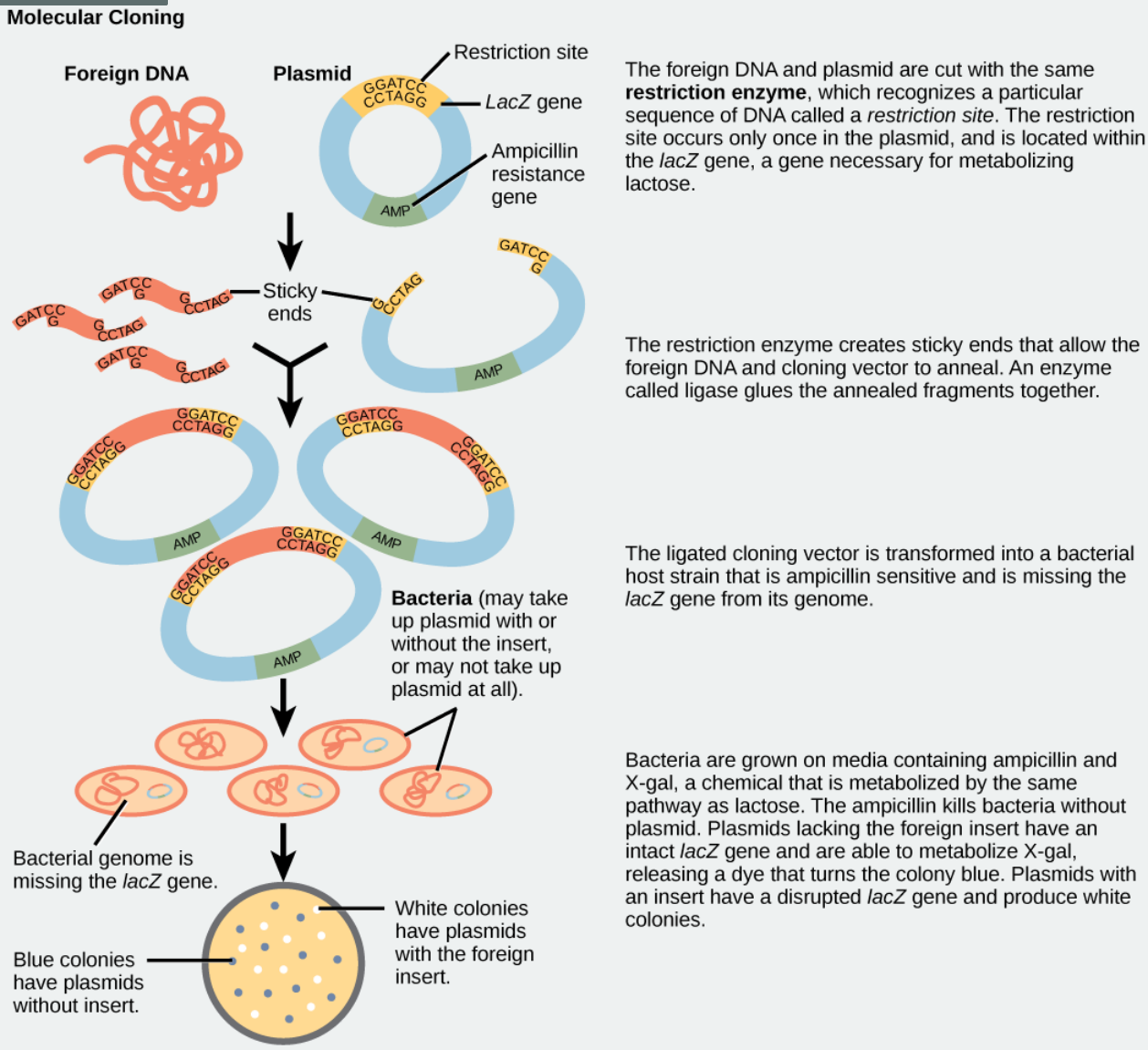


Figure 3.7.2.6: This diagram shows the steps involved in molecular cloning.

Figure 3.7.2.6: You are working in a molecular biology lab and, unbeknownst to you, your lab partner left the foreign genomic DNA that you are planning to clone on the lab bench overnight instead of storing it in the freezer. As a result, it was degraded by nucleases, but still used in the experiment. The plasmid, on the other hand, is fine. What results would you expect from your molecular cloning experiment?

A. There will be no colonies on the bacterial plate.
B. There will be blue colonies only.
C. There will be blue and white colonies.
D. The will be white colonies only.

Answer

B. The experiment would result in blue colonies only.

Link to Learning



View an animation of recombination in cloning from the DNA Learning Center.

Cellular Cloning

Unicellular organisms, such as bacteria and yeast, naturally produce clones of themselves when they replicate asexually by binary fission; this is known as cellular cloning. The nuclear DNA duplicates by the process of mitosis, which creates an exact replica of the genetic material.

Reproductive Cloning

Reproductive cloning is a method used to make a clone or an identical copy of an entire multicellular organism. Most multicellular organisms undergo reproduction by sexual means, which involves genetic hybridization of two individuals (parents), making it impossible for generation of an identical copy or a clone of either parent. Recent advances in biotechnology have made it possible to artificially induce asexual reproduction of mammals in the laboratory.

Parthenogenesis, or “virgin birth,” occurs when an embryo grows and develops without the fertilization of the egg occurring; this is a form of asexual reproduction. An example of parthenogenesis occurs in species in which the female lays an egg and if the egg is fertilized, it is a diploid egg and the individual develops into a female; if the egg is not fertilized, it remains a haploid egg and develops into a male. The unfertilized egg is called a parthenogenic, or virgin, egg. Some insects and reptiles lay parthenogenic eggs that can develop into adults.

Sexual reproduction requires two cells; when the haploid egg and sperm cells fuse, a diploid zygote results. The zygote nucleus contains the genetic information to produce a new individual. However, early embryonic development requires the cytoplasmic material contained in the egg cell. This idea forms the basis for reproductive cloning. Therefore, if the haploid nucleus of an egg cell is replaced with a diploid nucleus from the cell of any individual of the same species (called a donor), it will become a zygote that is genetically identical to the donor. Somatic cell nuclear transfer is the technique of transferring a diploid nucleus into an enucleated egg. It can be used for either therapeutic cloning or reproductive cloning.

The first cloned animal was Dolly, a sheep who was born in 1996. The success rate of reproductive cloning at the time was very low. Dolly lived for seven years and died of respiratory complications (Figure 17.1.7). There is speculation that because the cell DNA belongs to an older individual, the age of the DNA may affect the life expectancy of a cloned individual. Since Dolly, several animals such as horses, bulls, and goats have been successfully cloned, although these individuals often exhibit facial, limb, and cardiac abnormalities. There have been attempts at producing cloned human embryos as sources of embryonic stem cells, sometimes referred to as cloning for therapeutic purposes. Therapeutic cloning produces stem cells to attempt to remedy detrimental diseases or defects (unlike reproductive cloning, which aims to reproduce an organism). Still, therapeutic cloning efforts have met with resistance because of bioethical considerations.

Art Connection

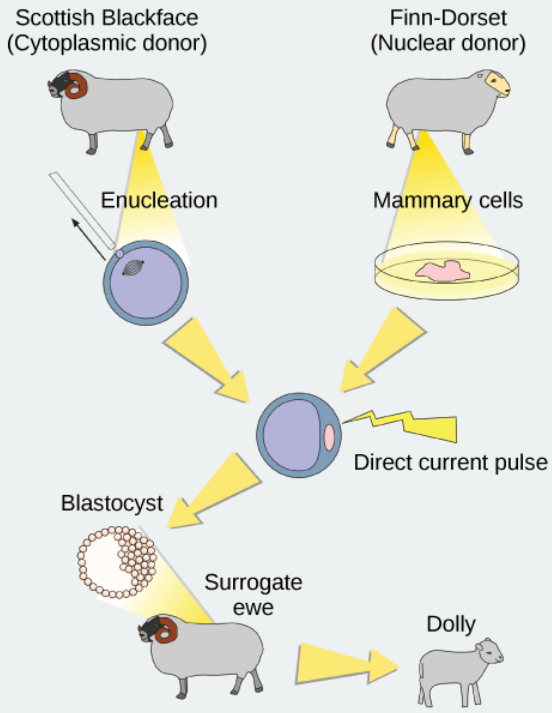


Figure 3.7.2.7: Dolly the sheep was the first mammal to be cloned. To create Dolly, the nucleus was removed from a donor egg cell. The nucleus from a second sheep was then introduced into the cell, which was allowed to divide to the blastocyst stage before being implanted in a surrogate mother. (credit: modification of work by "Squidonius"/Wikimedia Commons)

Figure 3.7.2.7: Do you think Dolly was a Finn-Dorset or a Scottish Blackface sheep?

Answer

Dolly was a Finn-Dorset sheep because even though the original cell came from a Scottish blackface sheep and the surrogate mother was a Scottish blackface, the DNA came from a Finn-Dorset.

Video



Genetic Engineering

Genetic engineering is the alteration of an organism's genotype using recombinant DNA technology to modify an organism's DNA to achieve desirable traits. The addition of foreign DNA in the form of recombinant DNA vectors generated by molecular cloning is the most common method of genetic engineering. The organism that receives the recombinant DNA is called a genetically modified

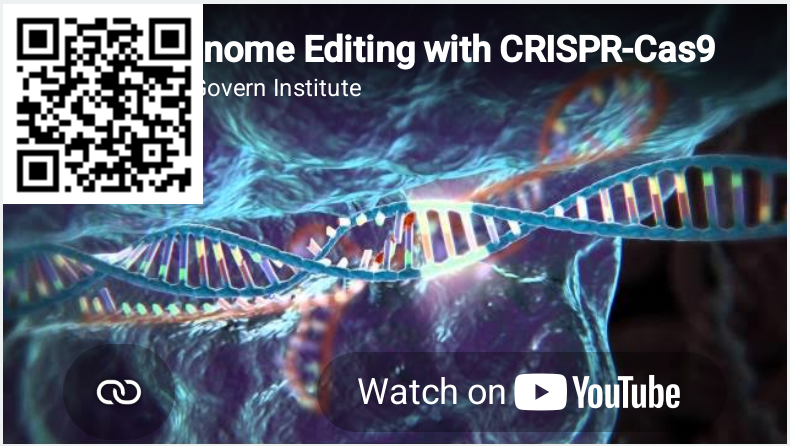
organism (GMO). If the foreign DNA that is introduced comes from a different species, the host organism is called transgenic. Bacteria, plants, and animals have been genetically modified since the early 1970s for academic, medical, agricultural, and industrial purposes. In the US, GMOs such as Roundup-ready soybeans and borer-resistant corn are part of many common processed foods.

Gene Targeting

Although classical methods of studying the function of genes began with a given phenotype and determined the genetic basis of that phenotype, modern techniques allow researchers to start at the DNA sequence level and ask: "What does this gene or DNA element do?" This technique, called reverse genetics, has resulted in reversing the classic genetic methodology. This method would be similar to damaging a body part to determine its function. An insect that loses a wing cannot fly, which means that the function of the wing is flight. The classical genetic method would compare insects that cannot fly with insects that can fly, and observe that the non-flying insects have lost wings. Similarly, mutating or deleting genes provides researchers with clues about gene function. The methods used to disable gene function are collectively called gene targeting. Gene targeting is the use of recombinant DNA vectors to alter the expression of a particular gene, either by introducing mutations in a gene, or by eliminating the expression of a certain gene by deleting a part or all of the gene sequence from the genome of an organism.

CRISPR-Cas9

Video



Biotechnology in Medicine and Agriculture

It is easy to see how biotechnology can be used for medicinal purposes. Knowledge of the genetic makeup of our species, the genetic basis of heritable diseases, and the invention of technology to manipulate and fix mutant genes provides methods to treat the disease. Biotechnology in agriculture can enhance resistance to disease, pest, and environmental stress, and improve both crop yield and quality.

Genetic Diagnosis and Gene Therapy

The process of testing for suspected genetic defects before administering treatment is called genetic diagnosis by genetic testing. Depending on the inheritance patterns of a disease-causing gene, family members are advised to undergo genetic testing. For example, women diagnosed with breast cancer are usually advised to have a biopsy so that the medical team can determine the genetic basis of cancer development. Treatment plans are based on the findings of genetic tests that determine the type of cancer. If the cancer is caused by inherited gene mutations, other female relatives are also advised to undergo genetic testing and periodic screening for breast cancer. Genetic testing is also offered for fetuses (or embryos with in vitro fertilization) to determine the presence or absence of disease-causing genes in families with specific debilitating diseases.

Gene therapy is a genetic engineering technique used to cure disease. In its simplest form, it involves the introduction of a good gene at a random location in the genome to aid the cure of a disease that is caused by a mutated gene. The good gene is usually introduced into diseased cells as part of a vector transmitted by a virus that can infect the host cell and deliver the foreign DNA

(Figure 3.7.2.8). More advanced forms of gene therapy try to correct the mutation at the original site in the genome, such as is the case with treatment of severe combined immunodeficiency (SCID).

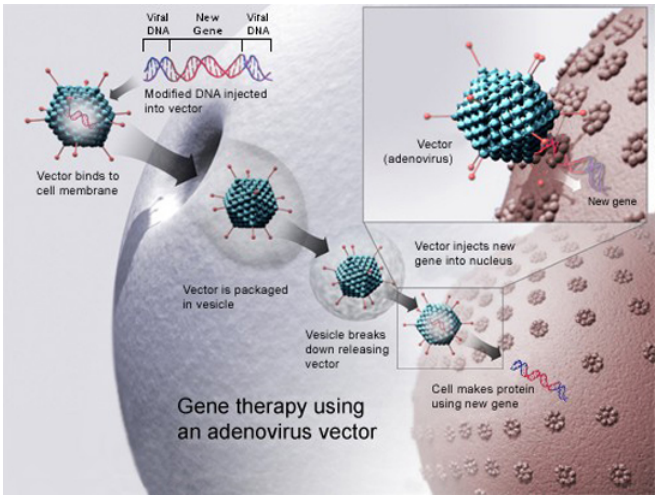
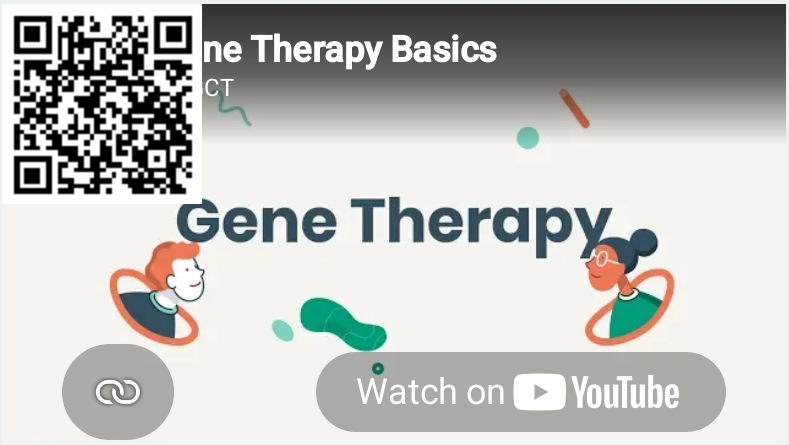


Figure 3.7.2.8: Gene therapy using an adenovirus vector can be used to cure certain genetic diseases in which a person has a defective gene. (credit: NIH)

Video



Production of Vaccines, Antibiotics, and Hormones

Traditional vaccination strategies use weakened or inactive forms of microorganisms to mount the initial immune response. Modern techniques use the genes of microorganisms cloned into vectors to mass produce the desired antigen. The antigen is then introduced into the body to stimulate the primary immune response and trigger immune memory. Genes cloned from the influenza virus have been used to combat the constantly changing strains of this virus.

Antibiotics are a biotechnological product. They are naturally produced by microorganisms, such as fungi, to attain an advantage over bacterial populations. Antibiotics are produced on a large scale by cultivating and manipulating fungal cells.

Recombinant DNA technology was used to produce large-scale quantities of human insulin in *E. coli* as early as 1978. Previously, it was only possible to treat diabetes with pig insulin, which caused allergic reactions in humans because of differences in the gene product. In addition, human growth hormone (HGH) is used to treat growth disorders in children. The HGH gene was cloned from a cDNA library and inserted into *E. coli* cells by cloning it into a bacterial vector.

Transgenic Animals

Although several recombinant proteins used in medicine are successfully produced in bacteria, some proteins require a eukaryotic animal host for proper processing. For this reason, the desired genes are cloned and expressed in animals, such as sheep, goats, chickens, and mice. Animals that have been modified to express recombinant DNA are called transgenic animals. Several human

proteins are expressed in the milk of transgenic sheep and goats, and some are expressed in the eggs of chickens. Mice have been used extensively for expressing and studying the effects of recombinant genes and mutations.

Transgenic Plants

Manipulating the DNA of plants (i.e., creating GMOs) has helped to create desirable traits, such as disease resistance, herbicide and pesticide resistance, better nutritional value, and better shelf-life (Figure 3.7.2.9). Plants are the most important source of food for the human population. Farmers developed ways to select for plant varieties with desirable traits long before modern-day biotechnology practices were established.



Figure 3.7.2.9: Corn, a major agricultural crop used to create products for a variety of industries, is often modified through plant biotechnology. (credit: Keith Weller, USDA)

Plants that have received recombinant DNA from other species are called transgenic plants. Because they are not natural, transgenic plants and other GMOs are closely monitored by government agencies to ensure that they are fit for human consumption and do not endanger other plant and animal life. Because foreign genes can spread to other species in the environment, extensive testing is required to ensure ecological stability. Staples like corn, potatoes, and tomatoes were the first crop plants to be genetically engineered.

Transformation of Plants Using *Agrobacterium tumefaciens*

Gene transfer occurs naturally between species in microbial populations. Many viruses that cause human diseases, such as cancer, act by incorporating their DNA into the human genome. In plants, tumors caused by the bacterium *Agrobacterium tumefaciens* occur by transfer of DNA from the bacterium to the plant. Although the tumors do not kill the plants, they make the plants stunted and more susceptible to harsh environmental conditions. Many plants, such as walnuts, grapes, nut trees, and beets, are affected by *A. tumefaciens*. The artificial introduction of DNA into plant cells is more challenging than in animal cells because of the thick plant cell wall.

Researchers used the natural transfer of DNA from *Agrobacterium* to a plant host to introduce DNA fragments of their choice into plant hosts. In nature, the disease-causing *A. tumefaciens* have a set of plasmids, called the Ti plasmids (tumor-inducing plasmids), that contain genes for the production of tumors in plants. DNA from the Ti plasmid integrates into the infected plant cell's genome.

Researchers manipulate the Ti plasmids to remove the tumor-causing genes and insert the desired DNA fragment for transfer into the plant genome. The Ti plasmids carry antibiotic resistance genes to aid selection and can be propagated in *E. coli* cells as well.

The Organic Insecticide *Bacillus thuringiensis*

Bacillus thuringiensis (Bt) is a bacterium that produces protein crystals during sporulation that are toxic to many insect species that affect plants. Bt toxin has to be ingested by insects for the toxin to be activated. Insects that have eaten Bt toxin stop feeding on the plants within a few hours. After the toxin is activated in the intestines of the insects, death occurs within a couple of days. Modern biotechnology has allowed plants to encode their own crystal Bt toxin that acts against insects. The crystal toxin genes have been cloned from Bt and introduced into plants. Bt toxin has been found to be safe for the environment, non-toxic to humans and other mammals, and is approved for use by organic farmers as a natural insecticide.

Flavr Savr Tomato

The first GM crop to be introduced into the market was the Flavr Savr Tomato produced in 1994. Antisense RNA technology was used to slow down the process of softening and rotting caused by fungal infections, which led to increased shelf life of the GM tomatoes. Additional genetic modification improved the flavor of this tomato. The Flavr Savr tomato did not successfully stay in the market because of problems maintaining and shipping the crop.

Summary

Nucleic acids can be isolated from cells for the purposes of further analysis by breaking open the cells and enzymatically destroying all other major macromolecules. Fragmented or whole chromosomes can be separated on the basis of size by gel electrophoresis. Short stretches of DNA or RNA can be amplified by PCR. Southern and northern blotting can be used to detect the presence of specific short sequences in a DNA or RNA sample. The term “cloning” may refer to cloning small DNA fragments (molecular cloning), cloning cell populations (cellular cloning), or cloning entire organisms (reproductive cloning). Genetic testing is performed to identify disease-causing genes, and gene therapy is used to cure an inheritable disease.

Transgenic organisms possess DNA from a different species, usually generated by molecular cloning techniques. Vaccines, antibiotics, and hormones are examples of products obtained by recombinant DNA technology. Transgenic plants are usually created to improve characteristics of crop plants.

Glossary

antibiotic resistance
: ability of an organism to be unaffected by the actions of an antibiotic

biotechnology
: use of biological agents for technological advancement

cellular cloning
: production of identical cell populations by binary fission

clone
: exact replica

foreign DNA
: DNA that belongs to a different species or DNA that is artificially synthesized

gel electrophoresis
: technique used to separate molecules on the basis of size using electric charge

gene targeting
: method for altering the sequence of a specific gene by introducing the modified version on a vector

gene therapy

technique used to cure inheritable diseases by replacing mutant genes with good genes

genetic diagnosis
diagnosis of the potential for disease development by analyzing disease-causing genes

genetic engineering
alteration of the genetic makeup of an organism

genetic testing
process of testing for the presence of disease-causing genes

genetically modified organism (GMO)
organism whose genome has been artificially changed

host DNA
DNA that is present in the genome of the organism of interest

lysis buffer
solution used to break the cell membrane and release cell contents

molecular cloning
cloning of DNA fragments

multiple cloning site (MCS)
site that can be recognized by multiple restriction endonucleases

northern blotting
transfer of RNA from a gel to a nylon membrane

polymerase chain reaction (PCR)
technique used to amplify DNA

probe
small DNA fragment used to determine if the complementary sequence is present in a DNA sample

protease
enzyme that breaks down proteins

recombinant DNA
combination of DNA fragments generated by molecular cloning that does not exist in nature; also known as a chimeric molecule

recombinant protein
protein product of a gene derived by molecular cloning

reproductive cloning
cloning of entire organisms

restriction endonuclease
enzyme that can recognize and cleave specific DNA sequences

reverse genetics
method of determining the function of a gene by starting with the gene itself instead of starting with the gene product

reverse transcriptase PCR (RT-PCR)
: PCR technique that involves converting RNA to DNA by reverse transcriptase

ribonuclease
: enzyme that breaks down RNA

Southern blotting
: transfer of DNA from a gel to a nylon membrane

Ti plasmid
: plasmid system derived from *Agrobacterium tumifaciens* that has been used by scientists to introduce foreign DNA into plant cells

transgenic
: organism that receives DNA from a different species

This page titled 3.7.2: Biotechnology is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.1: Biotechnology** by OpenStax is licensed CC BY 4.0.

3.7.3: Mapping Genomes

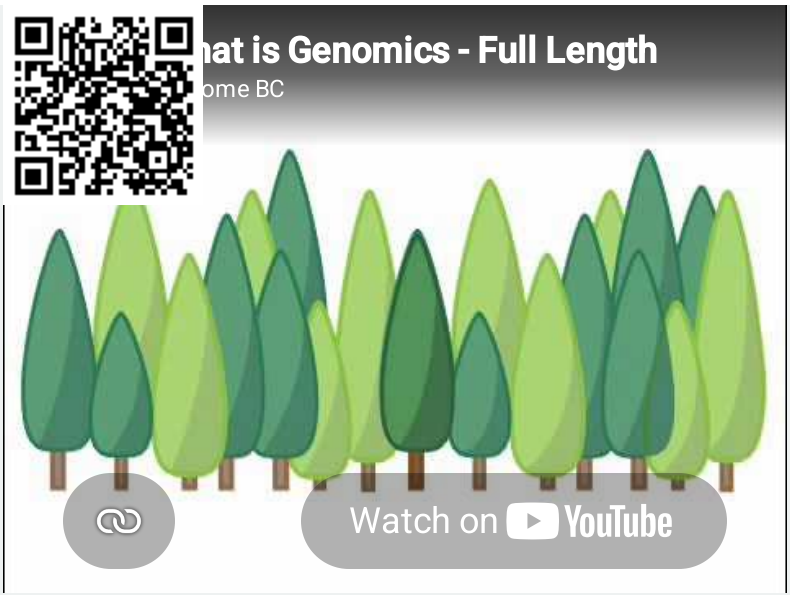
Learning Objectives

- Define genomics
- Describe genetic and physical maps
- Describe genomic mapping methods

Genomics is the study of entire genomes, including the complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species. Genome mapping is the process of finding the locations of genes on each chromosome. The maps created by genome mapping are comparable to the maps that we use to navigate streets. A genetic map is an illustration that lists genes and their location on a chromosome. Genetic maps provide the big picture (similar to a map of interstate highways) and use genetic markers (similar to landmarks). A genetic marker is a gene or sequence on a chromosome that co-segregates (shows genetic linkage) with a specific trait. Early geneticists called this linkage analysis. Physical maps present the intimate details of smaller regions of the chromosomes (similar to a detailed road map). A physical map is a representation of the physical distance, in nucleotides, between genes or genetic markers. Both genetic linkage maps and physical maps are required to build a complete picture of the genome. Having a complete map of the genome makes it easier for researchers to study individual genes. Human genome maps help researchers in their efforts to identify human disease-causing genes related to illnesses like cancer, heart disease, and cystic fibrosis. Genome mapping can be used in a variety of other applications, such as using live microbes to clean up pollutants or even prevent pollution. Research involving plant genome mapping may lead to producing higher crop yields or developing plants that better adapt to climate change.

Video





Genetic Maps

The study of genetic maps begins with linkage analysis, a procedure that analyzes the recombination frequency between genes to determine if they are linked or show independent assortment. The term *linkage* was used before the discovery of DNA. Early geneticists relied on the observation of phenotypic changes to understand the genotype of an organism. Shortly after Gregor Mendel (the father of modern genetics) proposed that traits were determined by what are now known as genes, other researchers observed that different traits were often inherited together, and thereby deduced that the genes were physically linked by being located on the same chromosome. The mapping of genes relative to each other based on linkage analysis led to the development of the first genetic maps.

Observations that certain traits were always linked and certain others were not linked came from studying the offspring of crosses between parents with different traits. For example, in experiments performed on the garden pea, it was discovered that the color of the flower and shape of the plant's pollen were linked traits, and therefore the genes encoding these traits were in close proximity on the same chromosome. The exchange of DNA between homologous pairs of chromosomes is called genetic recombination, which occurs by the crossing over of DNA between homologous strands of DNA, such as nonsister chromatids. Linkage analysis involves studying the recombination frequency between any two genes. The greater the distance between two genes, the higher the chance that a recombination event will occur between them, and the higher the recombination frequency between them. Two possibilities for recombination between two nonsister chromatids during meiosis are shown in Figure 3.7.3.1. If the recombination frequency between two genes is less than 50 percent, they are said to be linked.

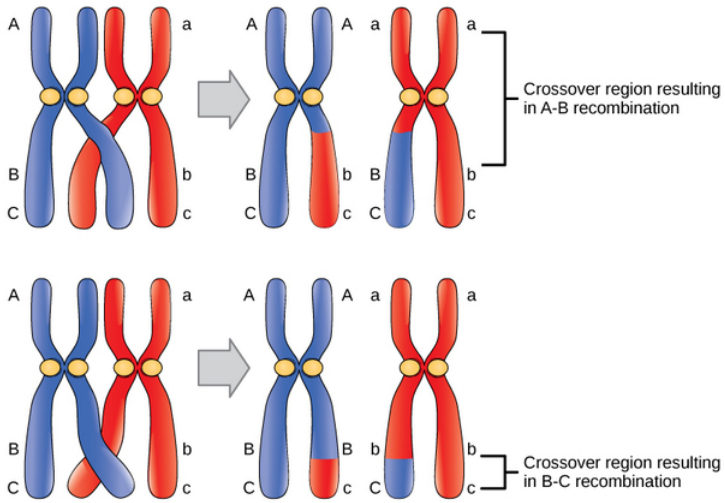


Figure 3.7.3.1: Crossover may occur at different locations on the chromosome. Recombination between genes *A* and *B* is more frequent than recombination between genes *B* and *C* because genes *A* and *B* are farther apart; a crossover is therefore more likely to occur between them.

The generation of genetic maps requires markers, just as a road map requires landmarks (such as rivers and mountains). Early genetic maps were based on the use of known genes as markers. More sophisticated markers, including those based on non-coding DNA, are now used to compare the genomes of individuals in a population. Although individuals of a given species are genetically similar, they are not identical; every individual has a unique set of traits. These minor differences in the genome between individuals in a population are useful for the purposes of genetic mapping. In general, a good genetic marker is a region on the chromosome that shows variability or polymorphism (multiple forms) in the population.

Some genetic markers used in generating genetic maps are restriction fragment length polymorphisms (RFLP), variable number of tandem repeats (VNTRs), microsatellite polymorphisms, and the single nucleotide polymorphisms (SNPs). RFLPs (sometimes pronounced “rif-lips”) are detected when the DNA of an individual is cut with a restriction endonuclease that recognizes specific sequences in the DNA to generate a series of DNA fragments, which are then analyzed by gel electrophoresis. The DNA of every individual will give rise to a unique pattern of bands when cut with a particular set of restriction endonucleases; this is sometimes referred to as an individual’s DNA “fingerprint.” Certain regions of the chromosome that are subject to polymorphism will lead to the generation of the unique banding pattern. VNTRs are repeated sets of nucleotides present in the non-coding regions of DNA. Non-coding, or “junk,” DNA has no known biological function; however, research shows that much of this DNA is actually transcribed. While its function is uncertain, it is certainly active, and it may be involved in the regulation of coding genes. The number of repeats may vary in individual organisms of a population. Microsatellite polymorphisms are similar to VNTRs, but the repeat unit is very small. SNPs are variations in a single nucleotide.

Because genetic maps rely completely on the natural process of recombination, mapping is affected by natural increases or decreases in the level of recombination in any given area of the genome. Some parts of the genome are recombination hotspots, whereas others do not show a propensity for recombination. For this reason, it is important to look at mapping information developed by multiple methods.

Physical Maps

A physical map provides detail of the actual physical distance between genetic markers, as well as the number of nucleotides. There are three methods used to create a physical map: cytogenetic mapping, radiation hybrid mapping, and sequence mapping. Cytogenetic mapping uses information obtained by microscopic analysis of stained sections of the chromosome. It is possible to determine the approximate distance between genetic markers using cytogenetic mapping, but not the exact distance (number of base pairs). Radiation hybrid mapping uses radiation, such as x-rays, to break the DNA into fragments. The amount of radiation can be adjusted to create smaller or larger fragments. This technique overcomes the limitation of genetic mapping and is not affected by increased or decreased recombination frequency. Sequence mapping resulted from DNA sequencing technology that allowed for the creation of detailed physical maps with distances measured in terms of the number of base pairs. The creation of genomic libraries and complementary DNA (cDNA) libraries (collections of cloned sequences or all DNA from a genome) has sped up the

process of physical mapping. A genetic site used to generate a physical map with sequencing technology (a sequence-tagged site, or STS) is a unique sequence in the genome with a known exact chromosomal location. An expressed sequence tag (EST) and a single sequence length polymorphism (SSLP) are common STSs. An EST is a short STS that is identified with cDNA libraries, while SSLPs are obtained from known genetic markers and provide a link between genetic maps and physical maps.

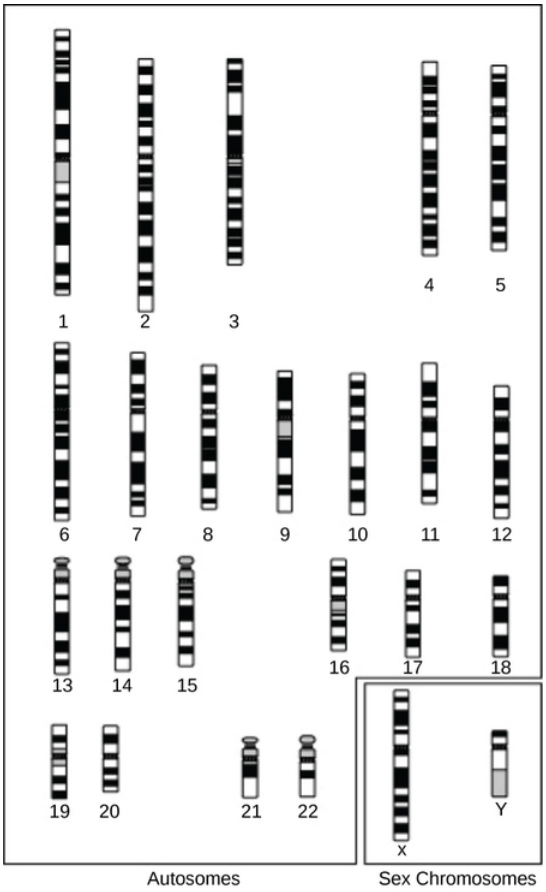


Figure 3.7.3.2: A cytogenetic map shows the appearance of a chromosome after it is stained and examined under a microscope. (credit: National Human Genome Research Institute)

Integration of Genetic and Physical Maps

Genetic maps provide the outline and physical maps provide the details. It is easy to understand why both types of genome mapping techniques are important to show the big picture. Information obtained from each technique is used in combination to study the genome. Genomic mapping is being used with different model organisms that are used for research. Genome mapping is still an ongoing process, and as more advanced techniques are developed, more advances are expected. Genome mapping is similar to completing a complicated puzzle using every piece of available data. Mapping information generated in laboratories all over the world is entered into central databases, such as GenBank at the National Center for Biotechnology Information (NCBI). Efforts are being made to make the information more easily accessible to researchers and the general public. Just as we use global positioning systems instead of paper maps to navigate through roadways, NCBI has created a genome viewer tool to simplify the data-mining process.

Scientific Method Connection: How to Use a Genome Map Viewer

Problem statement: Do the human, macaque, and mouse genomes contain common DNA sequences?

Develop a hypothesis.

To test the hypothesis, click here.

In Search box on the left panel, type any gene name or phenotypic characteristic, such as iris pigmentation (eye color). Select the species you want to study, and then press Enter. The genome map viewer will indicate which chromosome encodes the gene in your search. Click each hit in the genome viewer for more detailed information. This type of search is the most basic use of the genome viewer; it can also be used to compare sequences between species, as well as many other complicated tasks.

Is the hypothesis correct? Why or why not?

Link to Learning

Online Mendelian Inheritance in Man (OMIM) is a searchable online catalog of human genes and genetic disorders. This website shows genome mapping information, and also details the history and research of each trait and disorder. Click this link to search for traits (such as handedness) and genetic disorders (such as diabetes).

Summary

Genome mapping is similar to solving a big, complicated puzzle with pieces of information coming from laboratories all over the world. Genetic maps provide an outline for the location of genes within a genome, and they estimate the distance between genes and genetic markers on the basis of recombination frequencies during meiosis. Physical maps provide detailed information about the physical distance between the genes. The most detailed information is available through sequence mapping. Information from all mapping and sequencing sources is combined to study an entire genome.

Glossary

cytogenetic mapping
technique that uses a microscope to create a map from stained chromosomes

expressed sequence tag (EST)
short STS that is identified with cDNA

genetic map
outline of genes and their location on a chromosome

genetic marker
gene or sequence on a chromosome with a known location that is associated with a specific trait

genetic recombination
exchange of DNA between homologous pairs of chromosomes

genome mapping
process of finding the location of genes on each chromosome

cDNA library
collection of cloned cDNA sequences

genomic library
collection of cloned DNA which represents all of the sequences and fragments from a genome

genomics
study of entire genomes including the complete set of genes, their nucleotide sequence and organization, and their interactions within a species and with other species

linkage analysis
procedure that analyzes the recombination of genes to determine if they are linked

microsatellite polymorphism

variation between individuals in the sequence and number of repeats of microsatellite DNA

physical map
representation of the physical distance between genes or genetic markers

radiation hybrid mapping
information obtained by fragmenting the chromosome with x-rays

restriction fragment length polymorphism (RFLP)
variation between individuals in the length of DNA fragments generated by restriction endonucleases

sequence mapping
mapping information obtained after DNA sequencing

single nucleotide polymorphism (SNP)
variation between individuals in a single nucleotide

variable number of tandem repeats (VNTRs)
variation in the number of tandem repeats between individuals in the population

---

This page titled 3.7.3: Mapping Genomes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.2: Mapping Genomes** by OpenStax is licensed CC BY 4.0.

3.7.4: Whole-Genome Sequencing

Learning Objectives

- Describe three types of sequencing
- Define whole-genome sequencing

Although there have been significant advances in the medical sciences in recent years, doctors are still confounded by some diseases, and they are using whole-genome sequencing to get to the bottom of the problem. Whole-genome sequencing is a process that determines the DNA sequence of an entire genome. Whole-genome sequencing is a brute-force approach to problem solving when there is a genetic basis at the core of a disease. Several laboratories now provide services to sequence, analyze, and interpret entire genomes.

For example, whole-exome sequencing is a lower-cost alternative to whole genome sequencing. In exome sequencing, only the coding, exon-producing regions of the DNA are sequenced. In 2010, whole-exome sequencing was used to save a young boy whose intestines had multiple mysterious abscesses. The child had several colon operations with no relief. Finally, whole-exome sequencing was performed, which revealed a defect in a pathway that controls apoptosis (programmed cell death). A bone-marrow transplant was used to overcome this genetic disorder, leading to a cure for the boy. He was the first person to be successfully treated based on a diagnosis made by whole-exome sequencing. Today, human genome sequencing is more readily available and can be completed in a day or two for about $1000.

Strategies Used in Sequencing Projects

The basic sequencing technique used in all modern day sequencing projects is the chain termination method (also known as the dideoxy method), which was developed by Fred Sanger in the 1970s. The chain termination method involves DNA replication of a single-stranded template with the use of a primer and a regular deoxynucleotide (dNTP), which is a monomer, or a single unit, of DNA. The primer and dNTP are mixed with a small proportion of fluorescently labeled dideoxynucleotides (ddNTPs). The ddNTPs are monomers that are missing a hydroxyl group (–OH) at the site at which another nucleotide usually attaches to form a chain (Figure 3.7.4.1).

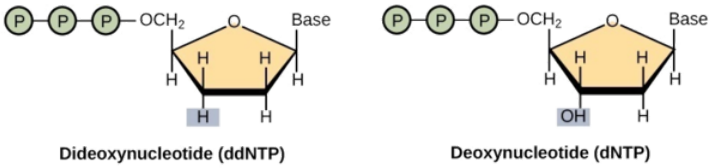


Figure 3.7.4.1: A dideoxynucleotide is similar in structure to a deoxynucleotide, but is missing the 3' hydroxyl group (indicated by the box). When a dideoxynucleotide is incorporated into a DNA strand, DNA synthesis stops.

Each ddNTP is labeled with a different color of fluorophore. Every time a ddNTP is incorporated in the growing complementary strand, it terminates the process of DNA replication, which results in multiple short strands of replicated DNA that are each terminated at a different point during replication. When the reaction mixture is processed by gel electrophoresis after being separated into single strands, the multiple newly replicated DNA strands form a ladder because of the differing sizes. Because the ddNTPs are fluorescently labeled, each band on the gel reflects the size of the DNA strand and the ddNTP that terminated the reaction. The different colors of the fluorophore-labeled ddNTPs help identify the ddNTP incorporated at that position. Reading the gel on the basis of the color of each band on the ladder produces the sequence of the template strand (Figure 3.7.4.2).

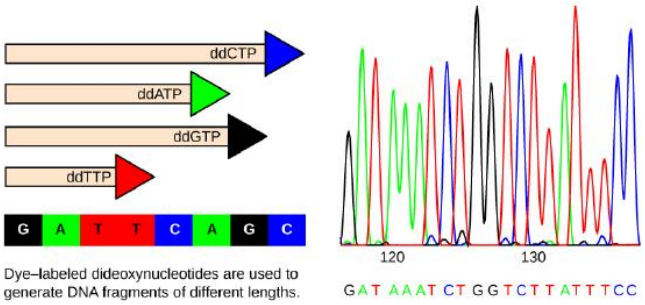


Figure 3.7.4.2: Frederick Sanger's dideoxy chain termination method is illustrated. Using dideoxynucleotides, the DNA fragment can be terminated at different points. The DNA is separated on the basis of size, and these bands, based on the size of the fragments, can be read.

Video



Early Strategies: Shotgun Sequencing and Pair-Wise End Sequencing

In shotgun sequencing method, several copies of a DNA fragment are cut randomly into many smaller pieces (somewhat like what happens to a round shot cartridge when fired from a shotgun). All of the segments are then sequenced using the chain-sequencing method. Then, with the help of a computer, the fragments are analyzed to see where their sequences overlap. By matching up overlapping sequences at the end of each fragment, the entire DNA sequence can be reformed. A larger sequence that is assembled from overlapping shorter sequences is called a contig. As an analogy, consider that someone has four copies of a landscape photograph that you have never seen before and know nothing about how it should appear. The person then rips up each photograph with their hands, so that different size pieces are present from each copy. The person then mixes all of the pieces together and asks you to reconstruct the photograph. In one of the smaller pieces you see a mountain. In a larger piece, you see that the same mountain is behind a lake. A third fragment shows only the lake, but it reveals that there is a cabin on the shore of the lake. Therefore, from looking at the overlapping information in these three fragments, you know that the picture contains a mountain behind a lake that has a cabin on its shore. This is the principle behind reconstructing entire DNA sequences using shotgun sequencing.

Originally, shotgun sequencing only analyzed one end of each fragment for overlaps. This was sufficient for sequencing small genomes. However, the desire to sequence larger genomes, such as that of a human, led to the development of double-barrel shotgun sequencing, more formally known as pairwise-end sequencing. In pairwise-end sequencing, both ends of each fragment are analyzed for overlap. Pairwise-end sequencing is, therefore, more cumbersome than shotgun sequencing, but it is easier to reconstruct the sequence because there is more available information.

Next-generation Sequencing

Since 2005, automated sequencing techniques used by laboratories are under the umbrella of next-generation sequencing, which is a group of automated techniques used for rapid DNA sequencing. These automated low-cost sequencers can generate sequences of

hundreds of thousands or millions of short fragments (25 to 500 base pairs) in the span of one day. These sequencers use sophisticated software to get through the cumbersome process of putting all the fragments in order.

Evolution Connection: Comparing Sequences

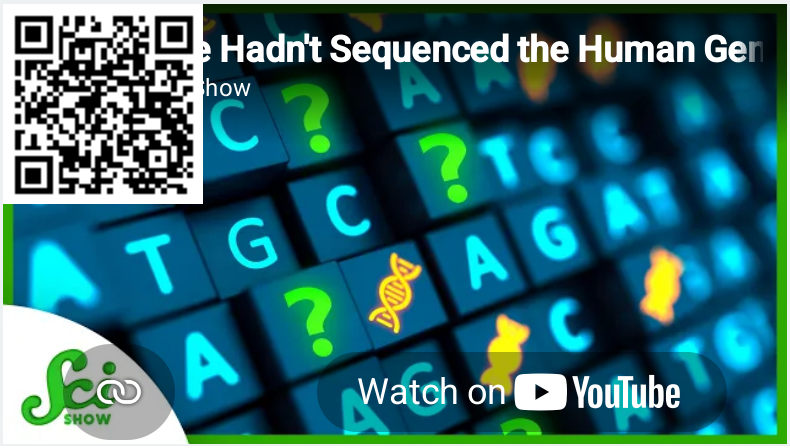
A sequence alignment is an arrangement of proteins, DNA, or RNA; it is used to identify regions of similarity between cell types or species, which may indicate conservation of function or structures. Sequence alignments may be used to construct phylogenetic trees. The following website uses a software program called BLAST (basic local alignment search tool).

Under “Basic Blast,” click “Nucleotide Blast.” Input the following sequence into the large "query sequence" box: ATTGCTTCGATTGCA. Below the box, locate the "Species" field and type "human" or "Homo sapiens". Then click “BLAST” to compare the inputted sequence against known sequences of the human genome. The result is that this sequence occurs in over a hundred places in the human genome. Scroll down below the graphic with the horizontal bars and you will see short description of each of the matching hits. Pick one of the hits near the top of the list and click on "Graphics". This will bring you to a page that shows where the sequence is found within the entire human genome. You can move the slider that looks like a green flag back and forth to view the sequences immediately around the selected gene. You can then return to your selected sequence by clicking the "ATG" button.

Use of Whole-Genome Sequences of Model Organisms

The first genome to be completely sequenced was of a bacterial virus, the bacteriophage fx174 (5368 base pairs); this was accomplished by Fred Sanger using shotgun sequencing. Several other organelle and viral genomes were later sequenced. The first organism whose genome was sequenced was the bacterium *Haemophilus influenzae*; this was accomplished by Craig Venter in the 1980s. Approximately 74 different laboratories collaborated on the sequencing of the genome of the yeast *Saccharomyces cerevisiae*, which began in 1989 and was completed in 1996, because it was 60 times bigger than any other genome that had been sequenced. By 1997, the genome sequences of two important model organisms were available: the bacterium *Escherichia coli* K12 and the yeast *Saccharomyces cerevisiae*. Genomes of other model organisms, such as the mouse *Mus musculus*, the fruit fly *Drosophila melanogaster*, the nematode *Caenorhabditis elegans*, and humans *Homo sapiens* are now known. A lot of basic research is performed in model organisms because the information can be applied to genetically similar organisms. A model organism is a species that is studied as a model to understand the biological processes in other species represented by the model organism. Having entire genomes sequenced helps with the research efforts in these model organisms. The process of attaching biological information to gene sequences is called genome annotation. Annotation of gene sequences helps with basic experiments in molecular biology, such as designing PCR primers and RNA targets.

Video



Uses of Genome Sequences

DNA microarrays are methods used to detect gene expression by analyzing an array of DNA fragments that are fixed to a glass slide or a silicon chip to identify active genes and identify sequences. Almost one million genotypic abnormalities can be

discovered using microarrays, whereas whole-genome sequencing can provide information about all six billion base pairs in the human genome. Although the study of medical applications of genome sequencing is interesting, this discipline tends to dwell on abnormal gene function. Knowledge of the entire genome will allow future onset diseases and other genetic disorders to be discovered early, which will allow for more informed decisions to be made about lifestyle, medication, and having children. Genomics is still in its infancy, although someday it may become routine to use whole-genome sequencing to screen every newborn to detect genetic abnormalities.

In addition to disease and medicine, genomics can contribute to the development of novel enzymes that convert biomass to biofuel, which results in higher crop and fuel production, and lower cost to the consumer. This knowledge should allow better methods of control over the microbes that are used in the production of biofuels. Genomics could also improve the methods used to monitor the impact of pollutants on ecosystems and help clean up environmental contaminants. Genomics has allowed for the development of agrochemicals and pharmaceuticals that could benefit medical science and agriculture.

It sounds great to have all the knowledge we can get from whole-genome sequencing; however, humans have a responsibility to use this knowledge wisely. Otherwise, it could be easy to misuse the power of such knowledge, leading to discrimination based on a person's genetics, human genetic engineering, and other ethical concerns. This information could also lead to legal issues regarding health and privacy.

Summary

Whole-genome sequencing is the latest available resource to treat genetic diseases. Some doctors are using whole-genome sequencing to save lives. Genomics has many industrial applications including biofuel development, agriculture, pharmaceuticals, and pollution control. The basic principle of all modern-day sequencing strategies involves the chain termination method of sequencing.

Although the human genome sequences provide key insights to medical professionals, researchers use whole-genome sequences of model organisms to better understand the genome of the species. Automation and the decreased cost of whole-genome sequencing may lead to personalized medicine in the future.

Glossary

chain termination method
: method of DNA sequencing using labeled dideoxynucleotides to terminate DNA replication; it is also called the dideoxy method or the Sanger method

contig
: larger sequence of DNA assembled from overlapping shorter sequences

deoxynucleotide
: individual monomer (single unit) of DNA

dideoxynucleotide
: individual monomer of DNA that is missing a hydroxyl group (–OH)

DNA microarray
: method used to detect gene expression by analyzing an array of DNA fragments that are fixed to a glass slide or a silicon chip to identify active genes and identify sequences

genome annotation
: process of attaching biological information to gene sequences

model organism
: species that is studied and used as a model to understand the biological processes in other species represented by the model organism

next-generation sequencing

group of automated techniques used for rapid DNA sequencing

shotgun sequencing

method used to sequence multiple DNA fragments to generate the sequence of a large piece of DNA

whole-genome sequencing

process that determines the DNA sequence of an entire genome

This page titled 3.7.4: Whole-Genome Sequencing is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.3: Whole-Genome Sequencing** by OpenStax is licensed CC BY 4.0.

3.7.5: Applying Genomics

Skills to Develop

- Explain pharmacogenomics
- Define polygenic

The introduction of DNA sequencing and whole genome sequencing projects, particularly the Human Genome project, has expanded the applicability of DNA sequence information. Genomics is now being used in a wide variety of fields, such as metagenomics, pharmacogenomics, and mitochondrial genomics. The most commonly known application of genomics is to understand and find cures for diseases.

Predicting Disease Risk at the Individual Level

Predicting the risk of disease involves screening currently healthy individuals by genome analysis at the individual level. Intervention with lifestyle changes and drugs can be recommended before disease onset. However, this approach is most applicable when the problem resides within a single gene defect. Such defects only account for approximately 5 percent of diseases in developed countries. Most of the common diseases, such as heart disease, are multi-factored or polygenic, which is a phenotypic characteristic that involves two or more genes, and also involve environmental factors such as diet. In April 2010, scientists at Stanford University published the genome analysis of a healthy individual (Stephen Quake, a scientist at Stanford University, who had his genome sequenced); the analysis predicted his propensity to acquire various diseases. A risk assessment was performed to analyze Quake's percentage of risk for 55 different medical conditions. A rare genetic mutation was found, which showed him to be at risk for sudden heart attack. He was also predicted to have a 23 percent risk of developing prostate cancer and a 1.4 percent risk of developing Alzheimer's. The scientists used databases and several publications to analyze the genomic data. Even though genomic sequencing is becoming more affordable and analytical tools are becoming more reliable, ethical issues surrounding genomic analysis at a population level remain to be addressed.

Art Connection

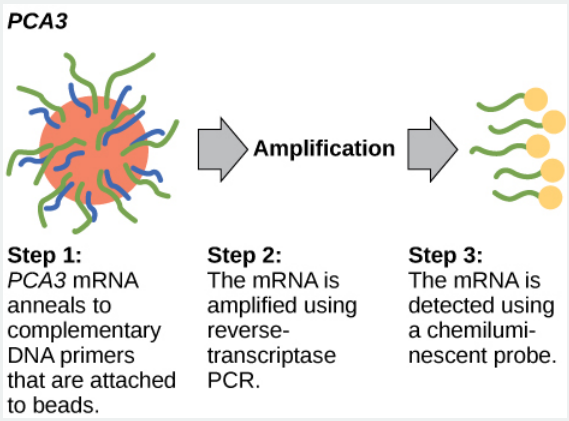


Figure 3.7.5.1: PCA3 is a gene that is expressed in prostate epithelial cells and overexpressed in cancerous cells. A high concentration of *PCA3* in urine is indicative of prostate cancer. The *PCA3* test is considered to be a better indicator of cancer than the more well know PSA test, which measures the level of PSA (prostate-specific antigen) in the blood.

In 2011, the United States Preventative Services Task Force recommended against using the PSA test to screen healthy men for prostate cancer. Their recommendation is based on evidence that screening does not reduce the risk of death from prostate cancer. Prostate cancer often develops very slowly and does not cause problems, while the cancer treatment can have severe side effects. The *PCA3* test is considered to be more accurate, but screening may still result in men who would not have been harmed by the cancer itself suffering side effects from treatment. What do you think? Should all healthy men be screened for prostate cancer using the *PCA3* or PSA test? Should people in general be screened to find out if they have a genetic risk for cancer or other diseases?

Pharmacogenomics and Toxicogenomics

Pharmacogenomics, also called toxicogenomics, involves evaluating the effectiveness and safety of drugs on the basis of information from an individual's genomic sequence. Genomic responses to drugs can be studied using experimental animals (such as laboratory rats or mice) or live cells in the laboratory before embarking on studies with humans. Studying changes in gene expression could provide information about the transcription profile in the presence of the drug, which can be used as an early indicator of the potential for toxic effects. For example, genes involved in cellular growth and controlled cell death, when disturbed, could lead to the growth of cancerous cells. Genome-wide studies can also help to find new genes involved in drug toxicity. Personal genome sequence information can be used to prescribe medications that will be most effective and least toxic on the basis of the individual patient's genotype. The gene signatures may not be completely accurate, but can be tested further before pathologic symptoms arise.

Video



Microbial Genomics: Metagenomics

Traditionally, microbiology has been taught with the view that microorganisms are best studied under pure culture conditions, which involves isolating a single type of cell and culturing it in the laboratory. Because microorganisms can go through several generations in a matter of hours, their gene expression profiles adapt to the new laboratory environment very quickly. In addition, the vast majority of bacterial species resist being cultured in isolation. Most microorganisms do not live as isolated entities, but in microbial communities known as biofilms. For all of these reasons, pure culture is not always the best way to study microorganisms. Metagenomics is the study of the collective genomes of multiple species that grow and interact in an environmental niche. Metagenomics can be used to identify new species more rapidly and to analyze the effect of pollutants on the environment (Figure 3.7.5.2).

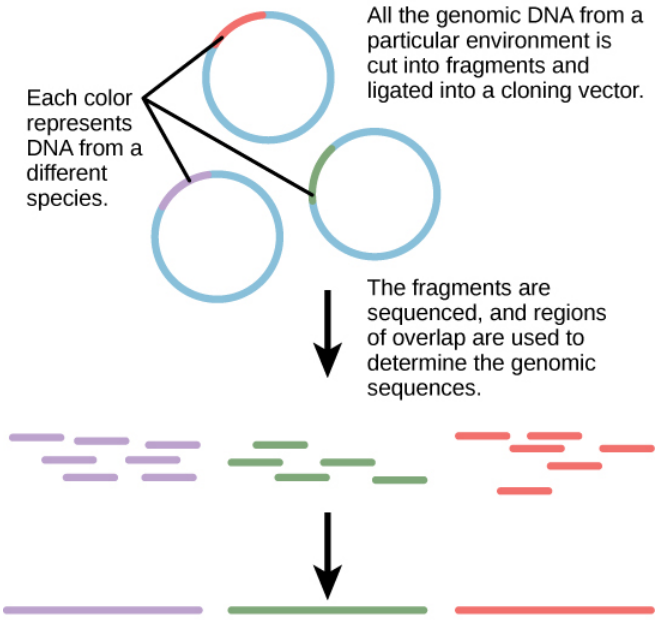


Figure 3.7.5.2: Metagenomics involves isolating DNA from multiple species within an environmental niche.

Microbial Genomics: Creation of New Biofuels

Knowledge of the genomics of microorganisms is being used to find better ways to harness biofuels from algae and cyanobacteria. The primary sources of fuel today are coal, oil, wood, and other plant products, such as ethanol. Although plants are renewable resources, there is still a need to find more alternative renewable sources of energy to meet our population's energy demands. The microbial world is one of the largest resources for genes that encode new enzymes and produce new organic compounds, and it remains largely untapped. Microorganisms are used to create products, such as enzymes that are used in research, antibiotics, and other anti-microbial mechanisms. Microbial genomics is helping to develop diagnostic tools, improved vaccines, new disease treatments, and advanced environmental cleanup techniques.

Mitochondrial Genomics

Mitochondria are intracellular organelles that contain their own DNA. Mitochondrial DNA mutates at a rapid rate and is often used to study evolutionary relationships. Another feature that makes studying the mitochondrial genome interesting is that the mitochondrial DNA in most multicellular organisms is passed on from the mother during the process of fertilization. For this reason, mitochondrial genomics is often used to trace genealogy.

Information and clues obtained from DNA samples found at crime scenes have been used as evidence in court cases, and genetic markers have been used in forensic analysis. Genomic analysis has also become useful in this field. In 2001, the first use of genomics in forensics was published. It was a collaborative attempt between academic research institutions and the FBI to solve the mysterious cases of anthrax communicated via the US Postal Service. Using microbial genomics, researchers determined that a specific strain of anthrax was used in all the mailings.

Genomics in Agriculture

Genomics can reduce the trials and failures involved in scientific research to a certain extent, which could improve the quality and quantity of crop yields in agriculture. Linking traits to genes or gene signatures helps to improve crop breeding to generate hybrids with the most desirable qualities. Scientists use genomic data to identify desirable traits, and then transfer those traits to a different organism. Scientists are discovering how genomics can improve the quality and quantity of agricultural production. For example, scientists could use desirable traits to create a useful product or enhance an existing product, such as making a drought-sensitive crop more tolerant of the dry season.

Summary

Imagination is the only barrier to the applicability of genomics. Genomics is being applied to most fields of biology; it is being used for personalized medicine, prediction of disease risks at an individual level, the study of drug interactions before the conduct of clinical trials, and the study of microorganisms in the environment as opposed to the laboratory. It is also being applied to developments such as the generation of new biofuels, genealogical assessment using mitochondria, advances in forensic science, and improvements in agriculture.

Art Connections

Figure 3.7.5.1: In 2011, the United States Preventative Services Task Force recommended against using the PSA test to screen healthy men for prostate cancer. Their recommendation is based on evidence that screening does not reduce the risk of death from prostate cancer. Prostate cancer often develops very slowly and does not cause problems, while the cancer treatment can have severe side effects. The *PCA3* test is considered to be more accurate, but screening may still result in men who would not have been harmed by the cancer itself suffering side effects from treatment. What do you think? Should all healthy men be screened for prostate cancer using the *PCA3* or PSA test? Should people in general be screened to find out if they have a genetic risk for cancer or other diseases?

Answer

There are no right or wrong answers to these questions. While it is true that prostate cancer treatment itself can be harmful, many men would rather be aware that they have cancer so they can monitor the disease and begin treatment if it progresses. And while genetic screening may be useful, it is expensive and may cause needless worry. People with certain risk factors may never develop the disease, and preventative treatments may do more harm than good.

Glossary

metagenomics

study of the collective genomes of multiple species that grow and interact in an environmental niche

pharmacogenomics

study of drug interactions with the genome or proteome; also called toxicogenomics

polygenic

phenotypic characteristic caused by two or more genes

pure culture

growth of a single type of cell in the laboratory

This page titled 3.7.5: Applying Genomics is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.4: Applying Genomics** by OpenStax is licensed CC BY 4.0.

3.7.6: Genomics and Proteomics

Learning Objectives

- Explain systems biology
- Describe a proteome
- Define protein signature

Proteins are the final products of genes, which help perform the function encoded by the gene. Proteins are composed of amino acids and play important roles in the cell. All enzymes (except ribozymes) are proteins that act as catalysts to affect the rate of reactions. Proteins are also regulatory molecules, and some are hormones. Transport proteins, such as hemoglobin, help transport oxygen to various organs. Antibodies that defend against foreign particles are also proteins. In the diseased state, protein function can be impaired because of changes at the genetic level or because of direct impact on a specific protein.

A proteome is the entire set of proteins produced by a cell type. Proteomes can be studied using the knowledge of genomes because genes code for mRNAs, and the mRNAs encode proteins. Although mRNA analysis is a step in the right direction, not all mRNAs are translated into proteins. The study of the function of proteomes is called proteomics. Proteomics complements genomics and is useful when scientists want to test their hypotheses that were based on genes. Even though all cells of a multicellular organism have the same set of genes, the set of proteins produced in different tissues is different and dependent on gene expression. Thus, the genome is constant, but the proteome varies and is dynamic within an organism. In addition, RNAs can be alternately spliced (cut and pasted to create novel combinations and novel proteins) and many proteins are modified after translation by processes such as proteolytic cleavage, phosphorylation, glycosylation, and ubiquitination. There are also protein-protein interactions, which complicate the study of proteomes. Although the genome provides a blueprint, the final architecture depends on several factors that can change the progression of events that generate the proteome.

Metabolomics is related to genomics and proteomics. Metabolomics involves the study of small molecule metabolites found in an organism. The metabolome is the complete set of metabolites that are related to the genetic makeup of an organism. Metabolomics offers an opportunity to compare genetic makeup and physical characteristics, as well as genetic makeup and environmental factors. The goal of metabolome research is to identify, quantify, and catalogue all of the metabolites that are found in the tissues and fluids of living organisms.

Video



Basic Techniques in Protein Analysis

The ultimate goal of proteomics is to identify or compare the proteins expressed from a given genome under specific conditions, study the interactions between the proteins, and use the information to predict cell behavior or develop drug targets. Just as the genome is analyzed using the basic technique of DNA sequencing, proteomics requires techniques for protein analysis. The basic technique for protein analysis, analogous to DNA sequencing, is mass spectrometry. Mass spectrometry is used to identify and determine the characteristics of a molecule. Advances in spectrometry have allowed researchers to analyze very small samples of

protein. X-ray crystallography, for example, enables scientists to determine the three-dimensional structure of a protein crystal at atomic resolution. Another protein imaging technique, nuclear magnetic resonance (NMR), uses the magnetic properties of atoms to determine the three-dimensional structure of proteins in aqueous solution. Protein microarrays have also been used to study interactions between proteins. Large-scale adaptations of the basic two-hybrid screen (Figure 3.7.6.1) have provided the basis for protein microarrays. Computer software is used to analyze the vast amount of data generated for proteomic analysis.

Genomic- and proteomic-scale analyses are part of systems biology. Systems biology is the study of whole biological systems (genomes and proteomes) based on interactions within the system. The European Bioinformatics Institute and the Human Proteome Organization (HUPO) are developing and establishing effective tools to sort through the enormous pile of systems biology data. Because proteins are the direct products of genes and reflect activity at the genomic level, it is natural to use proteomes to compare the protein profiles of different cells to identify proteins and genes involved in disease processes. Most pharmaceutical drug trials target proteins. Information obtained from proteomics is being used to identify novel drugs and understand their mechanisms of action.

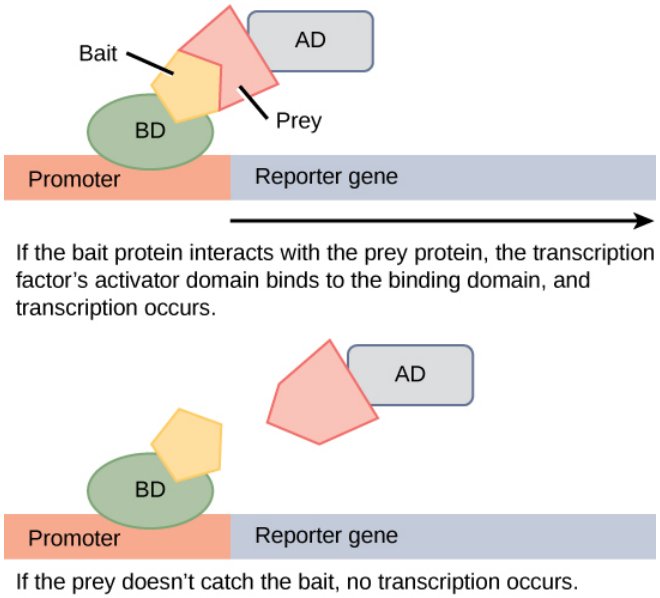


Figure 3.7.6.1: Two-hybrid screening is used to determine whether two proteins interact. In this method, a transcription factor is split into a DNA-binding domain (BD) and an activator domain (AD). The binding domain is able to bind the promoter in the absence of the activator domain, but it does not turn on transcription. A protein called the bait is attached to the BD, and a protein called the prey is attached to the AD. Transcription occurs only if the prey "catches" the bait.

The challenge of techniques used for proteomic analyses is the difficulty in detecting small quantities of proteins. Although mass spectrometry is good for detecting small amounts of proteins, variations in protein expression in diseased states can be difficult to discern. Proteins are naturally unstable molecules, which makes proteomic analysis much more difficult than genomic analysis.

Cancer Proteomics

Genomes and proteomes of patients suffering from specific diseases are being studied to understand the genetic basis of the disease. The most prominent disease being studied with proteomic approaches is cancer. Proteomic approaches are being used to improve screening and early detection of cancer; this is achieved by identifying proteins whose expression is affected by the disease process. An individual protein is called a biomarker, whereas a set of proteins with altered expression levels is called a protein signature. For a biomarker or protein signature to be useful as a candidate for early screening and detection of a cancer, it must be secreted in body fluids, such as sweat, blood, or urine, such that large-scale screenings can be performed in a non-invasive fashion. The current problem with using biomarkers for the early detection of cancer is the high rate of false-negative results. A false negative is an incorrect test result that should have been positive. In other words, many cases of cancer go undetected, which makes biomarkers unreliable. Some examples of protein biomarkers used in cancer detection are CA-125 for ovarian cancer and PSA for prostate cancer. Protein signatures may be more reliable than biomarkers to detect cancer cells. Proteomics is also being used to develop individualized treatment plans, which involves the prediction of whether or not an individual will respond to

specific drugs and the side effects that the individual may experience. Proteomics is also being used to predict the possibility of disease recurrence.

The National Cancer Institute has developed programs to improve the detection and treatment of cancer. The Clinical Proteomic Technologies for Cancer and the Early Detection Research Network are efforts to identify protein signatures specific to different types of cancers. The Biomedical Proteomics Program is designed to identify protein signatures and design effective therapies for cancer patients.

Summary

Proteomics is the study of the entire set of proteins expressed by a given type of cell under certain environmental conditions. In a multicellular organism, different cell types will have different proteomes, and these will vary with changes in the environment. Unlike a genome, a proteome is dynamic and in constant flux, which makes it both more complicated and more useful than the knowledge of genomes alone.

Proteomics approaches rely on protein analysis; these techniques are constantly being upgraded. Proteomics has been used to study different types of cancer. Different biomarkers and protein signatures are being used to analyze each type of cancer. The future goal is to have a personalized treatment plan for each individual.

Glossary

biomarker
: individual protein that is uniquely produced in a diseased state

false negative
: incorrect test result that should have been positive

metabolome
: complete set of metabolites which are related to the genetic makeup of an organism

metabolomics
: study of small molecule metabolites found in an organism

protein signature
: set of uniquely expressed proteins in the diseased state

proteome
: entire set of proteins produced by a cell type

proteomics
: study of the function of proteomes

systems biology
: study of whole biological systems (genomes and proteomes) based on interactions within the system

---

This page titled 3.7.6: Genomics and Proteomics is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.5: Genomics and Proteomics** by OpenStax is licensed CC BY 4.0.

3.7.E: Biotechnology and Genomics (Exercises)

17.1: Biotechnology

Biotechnology is the use of biological agents for technological advancement. Biotechnology was used for breeding livestock and crops long before the scientific basis of these techniques was understood. Biotechnology has grown rapidly through both academic research and private companies. The primary applications of this technology are in medicine (production of vaccines and antibiotics) and agriculture (genetic modification of crops, such as to increase yields).

Review Questions

GMOs are created by _____.

A. generating genomic DNA fragments with restriction endonucleases
B. introducing recombinant DNA into an organism by any means
C. overexpressing proteins in *E. coli.*
D. all of the above

Answer

B

Gene therapy can be used to introduce foreign DNA into cells _____.

A. for molecular cloning
B. by PCR
C. of tissues to cure inheritable disease
D. all of the above

Answer

C

Insulin produced by molecular cloning:

A. is of pig origin
B. is a recombinant protein
C. is made by the human pancreas
D. is recombinant DNA

Answer

B

Bt toxin is considered to be _____.

A. a gene for modifying insect DNA
B. an organic insecticide produced by bacteria
C. useful for humans to fight against insects
D. a recombinant protein

Answer

B

The Flavr Savr Tomato:

A. is a variety of vine-ripened tomato in the supermarket

A. is a variety of vine-ripened tomato in the supermarket
B. was created to have better flavor and shelf-life
C. does not undergo soft rot
D. all of the above

Answer

D

Free Response

Describe the process of Southern blotting.

Answer

Southern blotting is the transfer of DNA that has been enzymatically cut into fragments and run on an agarose gel onto a nylon membrane. The DNA fragments that are on the nylon membrane can be denatured to make them single-stranded, and then probed with small DNA fragments that are radioactively or fluorescently labeled, to detect the presence of specific sequences. An example of the use of Southern blotting would be in analyzing the presence, absence, or variation of a disease gene in genomic DNA from a group of patients.

A researcher wants to study cancer cells from a patient with breast cancer. Is cloning the cancer cells an option?

Answer

Cellular cloning of the breast cancer cells will establish a cell line, which can be used for further analysis

How would a scientist introduce a gene for herbicide resistance into a plant?

Answer

By identifying an herbicide resistance gene and cloning it into a plant expression vector system, like the Ti plasmid system from *Agrobacterium tumefaciens*. The scientist would then introduce it into the plant cells by transformation, and select cells that have taken up and integrated the herbicide-resistance gene into the genome.

If you had a chance to get your genome sequenced, what are some questions you might be able to have answered about yourself?

Answer

What diseases am I prone to and what precautions should I take? Am I a carrier for any disease-causing genes that may be passed on to children?

17.2: Mapping Genomes

Genome mapping is the process of finding the locations of genes on each chromosome. The maps created by genome mapping are comparable to the maps that we use to navigate streets. A genetic map is an illustration that lists genes and their location on a chromosome. Genetic maps provide the big picture and use genetic markers. A genetic marker is a gene or sequence on a chromosome that co-segregates (shows genetic linkage) with a specific trait.

Review Questions

ESTs are _____.

A. generated after a cDNA library is made
B. unique sequences in the genome
C. useful for mapping using sequence information

D. all of the above

Answer

D

Linkage analysis _____.

A. is used to create a physical map
B. is based on the natural recombination process
C. requires radiation hybrid mapping
D. involves breaking and re-joining of DNA artificially

Answer

B

Genetic recombination occurs by which process?

A. independent assortment
B. crossing over
C. chromosome segregation
D. sister chromatids

Answer

B

Individual genetic maps in a given species are:

A. genetically similar
B. genetically identical
C. genetically dissimilar
D. not useful in species analysis

Answer

A

Information obtained by microscopic analysis of stained chromosomes is used in:

A. radiation hybrid mapping
B. sequence mapping
C. RFLP mapping
D. cytogenetic mapping

Answer

D

Free Response

Why is so much effort being poured into genome mapping applications?

Answer

Genome mapping has many different applications and provides comprehensive information that can be used for predictive purposes.

How could a genetic map of the human genome help find a cure for cancer?

Answer

A human genetic map can help identify genetic markers and sequences associated with high cancer risk, which can help to screen and provide early detection of different types of cancer.

17.3: Whole-Genome Sequencing

Although there have been significant advances in the medical sciences in recent years, doctors are still confounded by some diseases, and they are using whole-genome sequencing to get to the bottom of the problem. Whole-genome sequencing is a process that determines the DNA sequence of an entire genome. Whole-genome sequencing is a brute-force approach to problem solving when there is a genetic basis at the core of a disease.

Review Questions

The chain termination method of sequencing:

A. uses labeled ddNTPs
B. uses only dideoxynucleotides
C. uses only deoxynucleotides
D. uses labeled dNTPs

Answer

A

Whole-genome sequencing can be used for advances in:

A. the medical field
B. agriculture
C. biofuels
D. all of the above

Answer

D

Sequencing an individual person’s genome

A. is currently possible
B. could lead to legal issues regarding discrimination and privacy
C. could help make informed choices about medical treatment
D. all of the above

Answer

D

What is the most challenging issue facing genome sequencing?

A. the inability to develop fast and accurate sequencing techniques
B. the ethics of using information from genomes at the individual level
C. the availability and stability of DNA

D. all of the above

Answer

B

17.4: Applying Genomics

The introduction of DNA sequencing and whole genome sequencing projects, particularly the Human Genome project, has expanded the applicability of DNA sequence information. Genomics is now being used in a wide variety of fields, such as metagenomics, pharmacogenomics, and mitochondrial genomics. The most commonly known application of genomics is to understand and find cures for diseases.

Review Questions

Genomics can be used in agriculture to:

A. generate new hybrid strains
B. improve disease resistance
C. improve yield
D. all of the above

Answer

D

Genomics can be used on a personal level to:

A. decrease transplant rejection
B. Predict genetic diseases that a person may have inherited
C. Determine the risks of genetic diseases for an individual's children
D. All the above

Answer

A

Free Response

Explain why metagenomics is probably the most revolutionary application of genomics.

Answer

Metagenomics is revolutionary because it replaced the practice of using pure cultures. Pure cultures were used to study individual species in the laboratory, but did not accurately represent what happens in the environment. Metagenomics studies the genomes of bacterial populations in their environmental niche.

How can genomics be used to predict disease risk and treatment options?

Answer

Genomics can provide the unique DNA sequence of an individual, which can be used for personalized medicine and treatment options.

17.5: Genomics and Proteomics

Proteins are the final products of genes, which help perform the function encoded by the gene. Proteins are composed of amino acids and play important roles in the cell. All enzymes (except ribozymes) are proteins that act as catalysts to affect the rate of reactions. Proteins are also regulatory molecules, and some are hormones. Transport proteins, such as hemoglobin, help transport oxygen to various organs. Antibodies that defend against foreign particles are also proteins.

Review Questions

What is a biomarker?

A. the color coding of different genes
B. a protein that is uniquely produced in a diseased state
C. a molecule in the genome or proteome
D. a marker that is genetically inherited

Answer

B

A protein signature is:

A. the path followed by a protein after it is synthesized in the nucleus
B. the path followed by a protein in the cytoplasm
C. a protein expressed on the cell surface
D. a unique set of proteins present in a diseased state

Answer

D

Free Response

How has proteomics been used in cancer detection and treatment?

Answer

Proteomics has provided a way to detect biomarkers and protein signatures, which have been used to screen for the early detection of cancer.

What is personalized medicine?

Answer

Personalized medicine is the use of an individual's genomic sequence to predict the risk for specific diseases. When a disease does occur, it can be used to develop a personalized treatment plan.

This page titled 3.7.E: Biotechnology and Genomics (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **17.E: Biotechnology and Genomics (Exercises)** is licensed CC BY 4.0.

SECTION OVERVIEW

4: Unit IV- Evolutionary Processes

Evolution is change in the heritable traits of biological populations over successive generations. Evolutionary processes give rise to diversity at every level of biological organization, including the levels of species, individual organisms, and molecules. In Unit 4, the core concepts of evolution are discussed in this unit with examples illustrating evolutionary processes. Additionally, the evolutionary basis of biology reappears throughout the textbook in general discussion and is reinforced through special call-out features highlighting specific evolution-based topics.

4.1: Evolution - History, Evidence, and Mechanisms

- 4.1.1: Understanding Evolution
- 4.1.2: Evidence of Evolution
- 4.1.3: Natural Selection and Adaptive Evolution
- 4.1.4: Additional Mechanisms of Evolution

4.2: The Origin of Species

- 4.2.1: Species Defined
- 4.2.2: Speciation
- 4.2.3: Rates of Speciation and Extinction

4.3: Genes Within Populations

- 4.3.1: Evolution of Genomes
- 4.3.2: Evolution in Populations

4.4: Systematics, Phylogeny and Comparative Biology

- 4.4.1: Systematics and Classification
- 4.4.2: Phylogeny and Cladistics

Contributors

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 4: Unit IV- Evolutionary Processes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

4.1: Evolution - History, Evidence, and Mechanisms

Learning Objectives

- Explain evolution as an underlying theme in biology
- Describe adaptations as a general concept
- Describe the wide range of adaptations of individual species use to interact with and adjust to variations in their environment
- Recognize misconceptions about the theory of evolution
- Identify the major requirements of natural selection
- Explain the relationships among adaptation, natural selection, and evolution
- Compare and contrast additional mechanisms of evolution: mutation, genetic drift, gene flow, and genetic recombination.

4.1.1: Understanding Evolution

4.1.2: Evidence of Evolution

4.1.3: Natural Selection and Adaptive Evolution

4.1.4: Additional Mechanisms of Evolution

This page titled 4.1: Evolution - History, Evidence, and Mechanisms is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

4.1.1: Understanding Evolution

Understanding Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe the historical influences on Darwin's and Wallace's theory of evolution
- Explain the requirements of evolution.
- Identify the major misconceptions of evolution and why they are incorrect.

Introduction: Evolution

Video





This 12-minute video summarizes much of the material below. You may want to revisit this video at the end of the Unit.

Question after watching: Darwin famously wrote that "endless forms most beautiful have been and are being evolved." In what way do we know that evolution is still taking place today?

The theory of evolution is the unifying theory of biology, meaning it is the framework within which biologists ask questions about the living world. The Ukrainian-born American geneticist Theodosius Dobzhansky famously wrote in 1964 that "nothing makes sense in biology except in the light of evolution." [1] The tenet that all species have evolved and diversified from a common ancestor is the foundation from which we approach all questions in biology. It provides a direction for predictions about living things and has been validated through extensive scientific experimentation. **Evolution** is simply a change in the gene pool of a species over time. More technically, evolution is the change in genetic composition of a population over time, specifically over generations, resulting from differential survival and reproduction of individuals. Evolution by natural selection describes one mechanism for this change. Natural selection is introduced here but is discussed in further detail in Section 2.2.3. Additional mechanisms are discussed in Section 2.2.4.

Adaptations

A heritable trait that aids the survival and reproduction of an organism in its present environment is called an **adaptation**. A population is adapted when a change in the range of genetic variation occurs over time that increases or maintains the survivability of that population in its current environmental conditions. The webbed feet of platypuses are an adaptation for swimming. The snow leopard's thick fur is an adaptation to living in the cold. The cheetah's fast speed is an adaptation for catching prey.



Figure 4.1.1.1: All organisms are products of evolution via adaptations to their environment. (a) Saguaro (*Carnegiea gigantea*) can soak up 750 liters of water in a single rain storm, enabling these cacti to survive the dry conditions of the Sonoran desert in Mexico and the Southwestern United States. (b) The Andean semiaquatic lizard (*Potamites montanicola*), discovered in Peru in 2010, lives between 1,570 to 2,100 meters in elevation and, unlike most lizards, is nocturnal and swims. Scientists still do not know how these cold-blood animals are able to move in the cold (10 to 15°C) temperatures of the Andean night.

Whether or not an individual trait is favorable depends on the environmental conditions at the time. The same traits are not always selected because environmental conditions can change. For example, consider a species of plant that grew in a moist climate and did not need to conserve water. Large leaves were selected because they allowed the plant to obtain more energy from the sun. Large leaves require more water to maintain than small leaves, and the moist environment provided favorable conditions to support large leaves. After thousands of years, the climate changed and the area no longer had excess water. The direction of natural selection shifted so that plants with small leaves were selected because those populations were able to conserve water to survive the new environmental conditions.

Video





This video identifies the three types of adaptations organisms may possess.
Questions after watching: What sorts of adaptations might you expect to arise in a plant species or a bacterial/unicellular species? Do you expect that the three types described in the video for animals will apply to these types of species?

History of the Theory of Evolution

Well before Darwin began to explore the concept of evolution, the idea that species change over time had already been suggested and debated. The view that species are static and unchanging was grounded in the writings of Plato more than 2000 years ago, yet there were also ancient Greeks who expressed ideas about evolution. During the eighteenth century, ideas about the evolution of animals were reintroduced by the naturalist Georges-Louis Leclerc Comte de Buffon who observed that various geographic regions have different plant and animal populations, even when the environments are similar. It was also accepted that there are extinct species.

During this time, a Scottish naturalist named James Hutton proposed that geological change occurs gradually by the accumulation of small changes over long periods of time. This theory contrasted with the predominant view of the time: that the geology of the planet is a consequence of catastrophic events that occurred during a relatively brief past. During the nineteenth century, Hutton's views were popularized by the geologist Charles Lyell, who was a friend of Charles Darwin. Lyell's ideas, in turn, influenced

Darwin's concept of evolution. The greater age of the earth proposed by Lyell supported the gradual evolution that Darwin proposed, and the slow process of geological change provided an analogy for the gradual change in species.

In the early nineteenth century, Jean-Baptiste Lamarck published a book that detailed a different mechanism for evolutionary change. This mechanism is now referred to as an inheritance of acquired characteristics. This idea states that modifications in an individual are caused by its environment, or the use or disuse of a structure during its lifetime. These changes can be inherited by its offspring, bringing about change in a species. While this mechanism for evolutionary change is now known to be incorrect, Lamarck's ideas were an important influence on the initial concepts of evolution, especially in regards to epigenetics, or the influence of the environment on genetic expression.

Charles Darwin and Alfred Russell Wallace

In the mid-nineteenth century, the mechanism for evolution was independently conceived of and described by two naturalists: Charles Darwin and Alfred Russel Wallace. Importantly, each naturalist spent time exploring the natural world on expeditions to the tropics. From 1831 to 1836, Darwin traveled around the world to places like South America, Australia, and the southern tip of Africa. Wallace traveled to Brazil to collect insects in the Amazon rainforest from 1848 to 1852 and to the Malay Archipelago from 1854 to 1862. Darwin's journey, as with Wallace's later journeys to the Malay Archipelago, included stops at several island chains, the last being the Galápagos Islands west of Ecuador.

On these islands, Darwin observed that species of organisms on different islands were clearly similar, yet had distinct differences. For example, the ground finches inhabiting the Galápagos Islands comprised several species with unique beak shapes. The species on the islands had a graded series of beak sizes and shapes with very small differences between the most similar. He observed that these finches closely resembled another finch species on the mainland of South America.

Darwin imagined that the island species might be modified from one of the original mainland species. Upon further study, he realized that the varied beaks of each finch helped the birds acquire a specific type of food. For example, seed-eating finches had stronger, thicker beaks for breaking seeds, while insect-eating finches had spear-like beaks for stabbing their prey. In 1860, he wrote, "seeing this gradation and diversity of structure in one small, intimately related group of birds, one might really fancy that from an original paucity of birds in this archipelago, one species had been taken and modified for different ends."

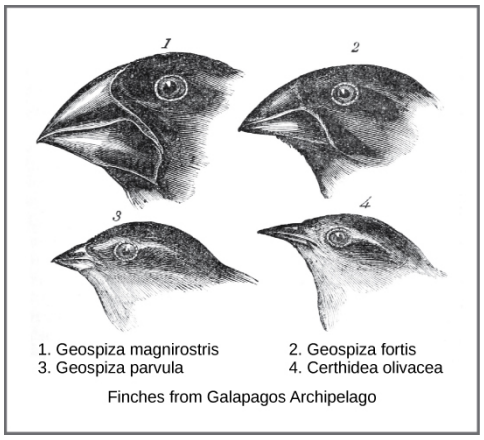


Figure 4.1.1.2: Darwin observed that beak shape varies among finch species. He postulated that the beak of an ancestral species had adapted over time to equip the finches to acquire different food sources.

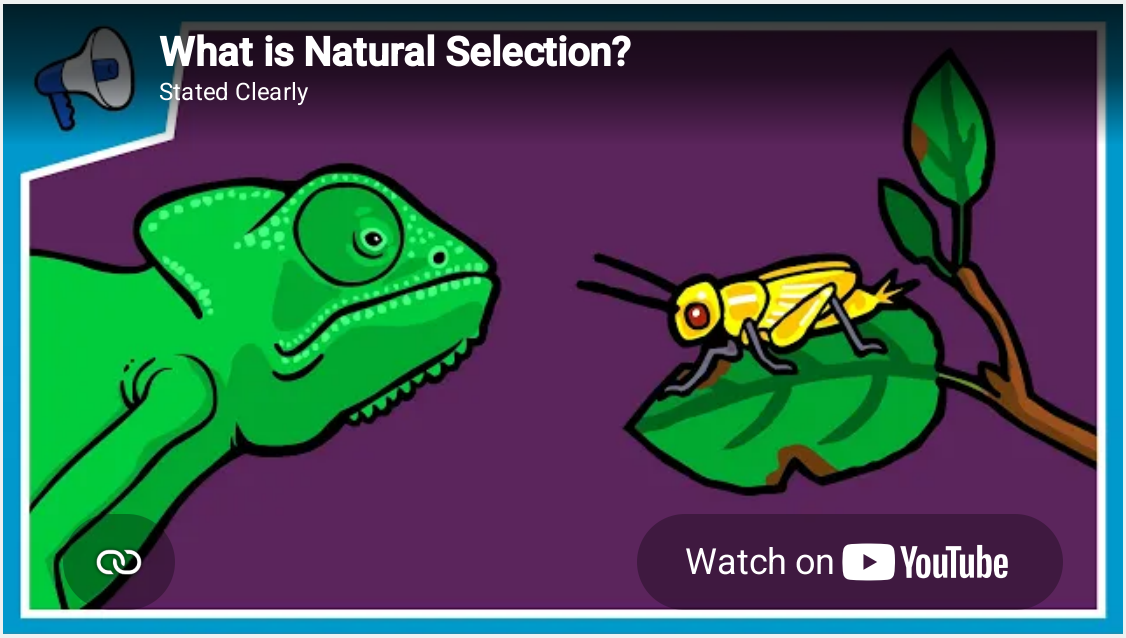
Origin of the Idea of Natural Selection

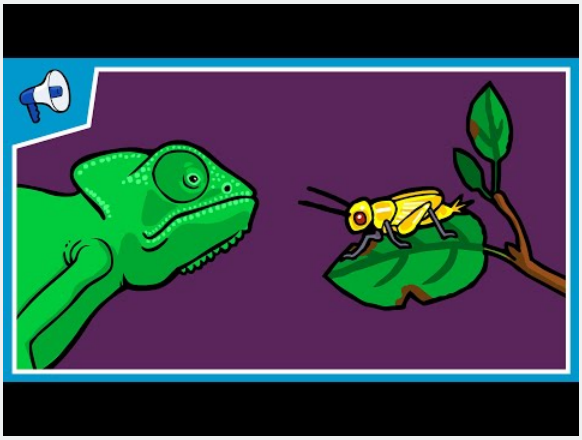
Wallace and Darwin observed similar patterns in other organisms and independently developed the same explanation for how and why such changes could take place. Darwin called this mechanism natural selection. **Natural selection**, also known as "survival of the fittest," is the more prolific reproduction of individuals with favorable traits that survive environmental change because of those traits. This leads to evolutionary change, the trait becoming predominant within a population. For example, Darwin observed that a population of giant tortoises found in the Galápagos Archipelago have longer necks than those that lived on other islands with dry lowlands. These tortoises were "selected" because they could reach more leaves and access more food than those with short necks. In times of drought, when fewer leaves would be available, those that could reach more leaves had a better chance to eat and

survive than those that could not reach the food source. Consequently, long-necked tortoises would more successfully reproduce and pass the long-necked trait to their offspring. Over time, only long-necked tortoises would be present in the population.

Natural selection, Darwin argued, was an inevitable outcome of three principles that operated in nature. First, *most characteristics of organisms are inherited*, or passed from parent to offspring, although *how* traits were inherited was unknown at the time. Second, *more offspring are produced than are able to survive*. The capacity for reproduction in all organisms outstrips the availability of resources to support their numbers. Thus, there is competition for those resources in each generation (note: when Darwin mentioned "survival of the fittest," he was referring to the competition between members of the same species for resources, not between different species, a common misconception). Both Darwin and Wallace were influenced by an essay written by economist Thomas Malthus who discussed this principle in relation to human populations. Third, Darwin and Wallace reasoned that *offspring with the inherited characteristics that allow them to best compete for limited resources will survive and have more offspring than those individuals with variations that are less able to compete*. Because characteristics are inherited, these traits will be better represented in the next generation. This will lead to change in populations over successive generations in a process that Darwin called descent with modification. Ultimately, natural selection leads to greater adaptation of the population to its local environment; it is the only mechanism known for adaptive evolution.

Video



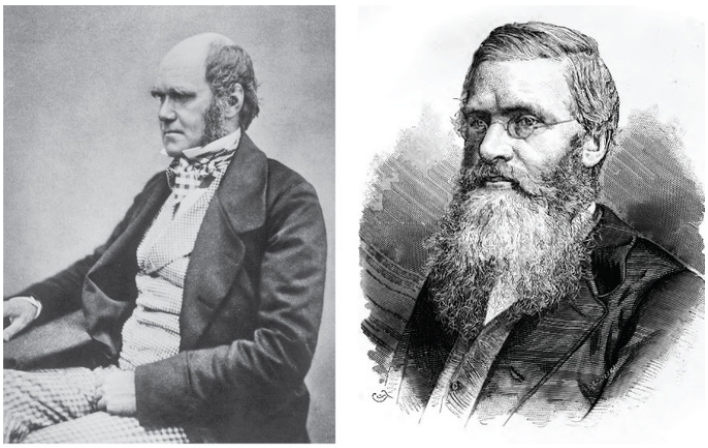


This 9-minute video is an overview of Darwin's concept of natural selection which is explained in a slightly different manner than the reading. Notably, it explains how evolution by natural selection has been harnessed in agriculture

and farming.

Question after watching: Which aspects of natural selection are random and which are not random?

Papers by Darwin and Wallace presenting the idea of natural selection were read together in 1858 before the Linnean Society in London. The following year, Darwin's book, *On the Origin of Species*, was published which outlined his arguments for evolution by natural selection.



(a) (b)

Figure 4.1.1.3: Both (a) Charles Darwin and (b) Alfred Wallace wrote scientific papers on natural selection that were presented together before the Linnean Society in 1858.

? Optional Activity 4.1.1.1

Which scientific concept did Charles Darwin and Alfred Russell Wallace independently discover?

a. mutation
b. natural selection
c. overbreeding
d. sexual reproduction

Answer

b. natural selection

Requirements for Evolution

All of the following are required for evolution to occur.

Variation

One of the hallmarks of Darwin and Wallace's theory of evolution via natural selection is that it can only take place if there is **variation**, or differences, among individuals in a population. Importantly, these differences must have a genetic basis (their **genotypes**); otherwise, selection will not lead to change in the next generation. This is critical because variation among individuals can be caused by non-genetic reasons, such as an individual losing a limb due to an accident. Variations of this type would not be inherited by the next generation.

Individuals of a population often display different **phenotypes**, or physical, metabolic, or behavioral expressions of their genotypes. Populations with two or more variations of particular characteristics, or trait, are called **polymorphic**. The distribution of phenotypes among individuals, known as the **population variation**, is influenced by a number of factors, including the population's genetic structure and the environment (Figure 4.1.1.4). Understanding the sources of a phenotypic variation in a population is important for determining how a population will evolve in response to different evolutionary pressures.



Figure 4.1.1.4: The distribution of phenotypes in this litter of kittens illustrates population variation. (credit: Pieter Lanser)

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 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 incase in frequency in the population, leading to a greater percentage of larger gorillas in the population. As a consequence, the average size of a gorilla in this population will increase. 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. In addition to natural selection, below are the details of five other agents of evolutionary change that are all acting in concert with natural selection.

This variation, or **genetic diversity,** within a population comes from two main mechanisms: mutation and, in those species that reproduce sexually, sexual reproduction. **Mutation**, a change in the DNA sequence, is the ultimate source of new alleles, or new genetic variation in any population. The genetic changes caused by mutation can have one of three outcomes:

- Many mutations will have no effect on the genetic contribution of an individual to future generations; these are called neutral mutations.
- A mutation may affect the phenotype of the organism in a way that gives it a lower likelihood of survival or fewer offspring.
- A mutation may produce a phenotype with a beneficial effect on survival or its genetic contribution to future generations.

Different mutations will have a range of above effects on an organism that expresses them in their phenotype, from a small to great.

Sexual reproduction also leads to genetic diversity: when two individuals of a sexually-reproducing species reproduce, unique combinations of alleles assemble to produce the unique genotypes and thus phenotypes in each of the offspring. However, sexual reproduction does not lead to *new* genes, but rather provides a new combination of genes in a given individual.

Inheritance

The trait or adaptation being selected for or against must be heritable.

Differential Reproduction and Survival

Individuals with a certain version of the trait are more likely to survive and reproduce than individuals with a different version of the trait

Time

The version of the trait that helps individuals survive and reproduce becomes more common in the population over multiple generations. Individuals do not evolve.

? Optional Activity 4.1.1.2

Which of the following situations may lead to natural selection?

a. The seeds of two plants land near each other and one grows larger faster.
b. Two types of fish eat the same kind of food but one is better able to gather food than the other.

c. In a species of fungi, one colony spreads faster through the soil to reach nutrients than another colony of the same species.
d. All of the above may lead to natural selection.

Answer

d. All of the above may lead to natural selection.

Patterns of Evolution

The evolution of species has resulted in enormous variation in form and function. Sometimes, evolution gives rise to groups of organisms that become tremendously different from each other. We call two species that evolve in diverse directions from a common point **divergent evolution**. We can see such divergent evolution in the forms of the reproductive organs of flowering plants which share the same basic anatomies (Figure 4.1.1.5); however, they can look very different as a result of selection in different physical environments and adaptation to different kinds of pollinators.



Figure 4.1.1.5: Flowering plants evolved from a common ancestor. Notice that the (a) dense blazing star (Liatrus spicata) and the (b) purple coneflower (Echinacea purpurea) vary in appearance, yet both share a similar basic morphology.

In other cases, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have structures we refer to as wings, which are adaptations to flight. However, bat and insect wings have evolved from very different original structures. We call this phenomenon **convergent evolution**, where similar traits evolve independently in species that do not share a common ancestry. The two species came to the same function, flying, but did so separately from each other.

These physical changes occur over enormous time spans and help explain how evolution occurs. Natural selection acts on individual organisms, which can then shape an entire species. Although natural selection may work in a single generation on an individual, it can take thousands or even millions of years for an entire species' genotype to evolve. It is over these large time spans that life on earth has changed and continues to change.

? Optional Activity 4.1.1.3

Which situation is most likely an example of convergent evolution?

a. Squid and humans have eyes similar in structure.
b. Worms and snakes both move without legs.
c. Some bats and birds have wings that allow them to fly.
d. All of the above are examples of convergent evolution.

Answer

D. All of the above are examples of convergent evolution.

The Modern Synthesis: Natural Selection and Genetics

The mechanisms of inheritance, **genetics**, were not understood at the time Darwin and Wallace were developing their idea of natural selection. This lack of understanding was a stumbling block to comprehending many aspects of evolution. In fact, blending inheritance was the incorrect, but predominant, genetic theory of the time. This made it difficult to understand how natural selection might operate. Darwin and Wallace were unaware of the genetics work by Austrian monk Gregor Mendel, which was published in 1866, not long after the publication of *On the Origin of Species*. Mendel's work was rediscovered in the early twentieth century at which time geneticists were rapidly coming to an understanding of the basics of inheritance. Initially, the newly discovered particulate nature of genes made it difficult for biologists to understand how gradual evolution could occur. But over the next few decades, genetics and evolution were integrated into what became known as the **modern synthesis**—the coherent understanding of the relationship between natural selection and genetics that took shape by the 1940s and is generally accepted today. In sum, the modern synthesis describes how evolutionary pressures, such as natural selection, can affect a population's genetic makeup, and, in turn, how this can result in the gradual evolution of populations and species. The theory also connects this gradual change of a population over time, called **microevolution**, with the processes that gave rise to new species and higher taxonomic groups with widely divergent characters, called **macroevolution**.

Misconceptions about Evolution

The theory of evolution has been amply tested by researchers over the past 200 years. From this work, confidence in the theory's basic tenants has been bolstered. Today, the vast majority of scientists accept the theory of evolution by natural selection as the most plausible, supported mechanism to explain how organisms change over time.

However, certain groups, led by values other than the scientific search for evidence, have objected to the theory of evolution including as an explanation for the diversity of life. This has led to the spread of some misinformation and misconception about the theory. Below, these misconceptions are explicitly addressed.

Concept in Action

This website addresses some of the main misconceptions associated with the theory of evolution.

Misconception #1: 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 concept that has been extensively tested and supported over time. We have a theory of the atom, a theory of gravity, and the theory of relativity, each of which describes the strong evidence that scientists have to support our understanding of nature and the universe. In the same way, the theory of evolution describes our scientific understanding about life. As such, a theory in science has survived significant efforts to discredit it by scientists, who are naturally skeptical. While theories can sometimes be overturned or revised, this does not lessen their weight but simply reflects the constantly growing state of scientific understanding. In contrast, a "theory" in common vernacular means a guess or suggested explanation for something. This meaning is more along the lines of the concept of a scientific **hypothesis**, which is a tentative explanation for something that is proposed to either be supported or disproved. When critics of evolution say evolution is "just a theory," they are mischaracterizing the science and inferring that there is little evidence supporting it. This is far from accurate. Evolution is widely accepted, extensively tested, heavily supported, and can be monitored in real-time, such as with Darwin's finches.

Misconception #2: Individuals Evolve

An individual is born with the genes it has—these do not change as the individual ages. Therefore, an individual cannot evolve or adapt through natural selection. Individuals do change over their lifetime, but this is called development; it 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 the change in the average value of the characteristic in the population over time. For example, when natural selection leads to a bill-size change 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 after there has been a strong

selective pressure, this average value may be different as a result of evolution. Although some individuals may survive from the first time to the second, those individuals will still have the same bill size. However, there may be enough new individuals with different bill sizes to change the average bill size.

Misconception #3: 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 complain that it cannot 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, over a very long time, and presumably 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. The early stages of life included the use or formation of organic molecules such as carbohydrates, amino acids, or nucleotides. If these were formed from inorganic precursors today, they would simply be broken down by living things. The early stages of life also probably included more complex aggregations of molecules into enclosed structures with an internal environment, a boundary layer of some form, and an external environment. Such structures, if they were formed now, would be quickly consumed or broken down by living organisms.

However, once a mechanism of inheritance was in place in the form of a molecule like DNA or RNA, either within a cell or within a 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.

Misconception #4: Organisms Evolve on Purpose

Statements such as "organisms evolve in response to a change in an environment," are quite common. There are two easy misunderstandings possible with such a statement. First of all, the statement must not be understood to mean that individual organisms evolve, as was discussed above. 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 characters 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 for 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 for individuals that are resistant, since these would be the only ones that survived and divided. Experiments have demonstrated that mutations for antibiotic resistance do not arise as a result of the antibiotic application.

In a larger sense, evolution is also 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. This kind of language is common in popular literature. Certain organisms, ourselves included, are described as the "pinnacle" of evolution, or "perfected" by evolution. 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 holds equally well for a species of insect as it does for the human species.

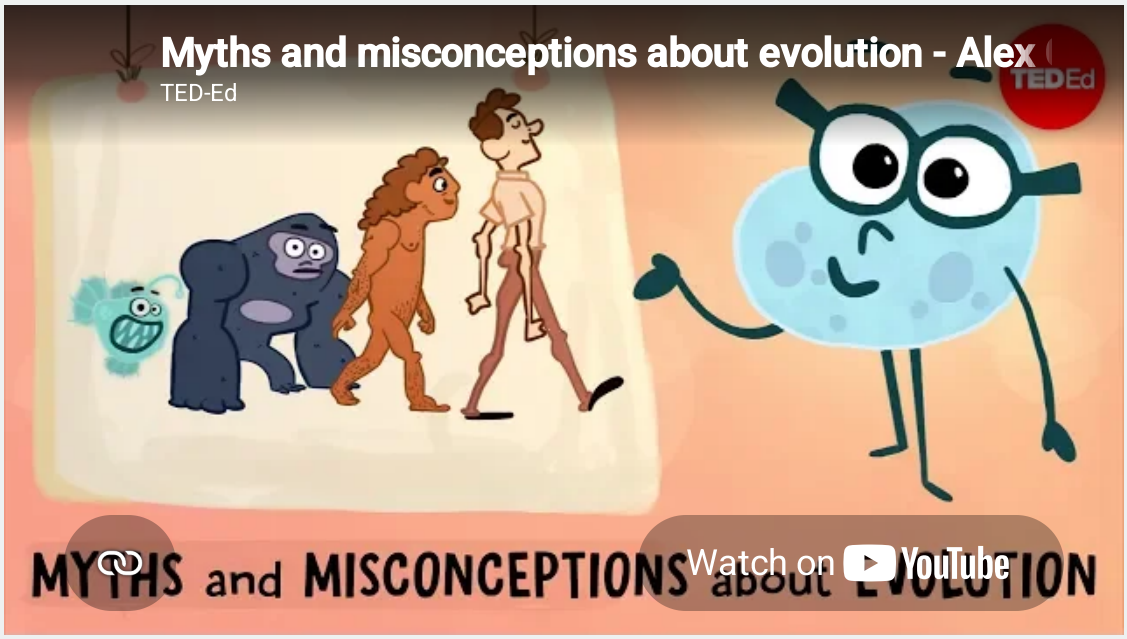
Misconception #5: Evolution Is Controversial among Scientists

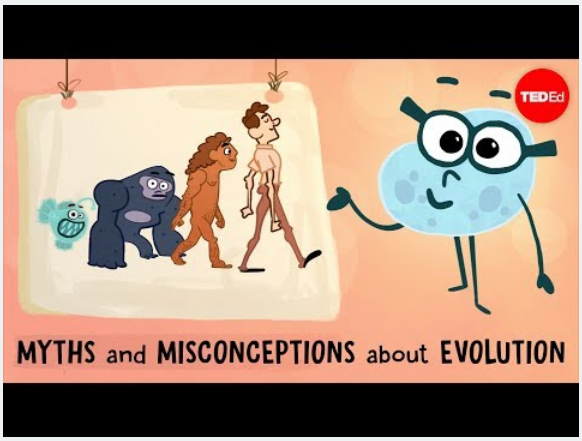
The theory of evolution was controversial when it was first proposed in 1859, yet within 20 years virtually every working biologist had accepted evolution as the explanation for the diversity of life. The rate of acceptance was extraordinarily rapid, partly because Darwin had amassed an impressive body of evidence. The early controversies involved both scientific arguments against the theory

and the arguments of religious leaders. It was the arguments of the biologists that were resolved after a short time, while the arguments of religious leaders have persisted to this day.

The number of working scientists who reject the theory of evolution, or question its validity and say so, is small. A Pew Research poll in 2009 found that 97 percent of the 2500 scientists polled believe species evolve.[2] The support for the theory is reflected in signed statements from many scientific societies such as the American Association for the Advancement of Science, which includes working scientists as members. Many of the scientists who reject or question the theory of evolution are non-biologists, such as engineers, physicians, and chemists. There are no experimental results or research programs that contradict the theory. There are no papers published in peer-reviewed scientific journals that appear to refute the theory. The latter observation might be considered a consequence of the suppression of dissent, but it must be remembered that scientists are skeptics and that there is a long history of published reports that challenged scientific orthodoxy in unpopular ways. Examples include the endosymbiotic theory of eukaryotic origins, the theory of group selection, the microbial cause of stomach ulcers, the asteroid-impact theory of the Cretaceous extinction, and the theory of plate tectonics. Research with evidence and ideas with scientific merit are considered by the scientific community. Research that does not meet these standards is rejected.

Video





This 4-minute video provides an overview of the main misconceptions about evolution, how they came to be, and what the accurate interpretation should be.

Question after watching: How can the expression "survival of the fittest" be misunderstood? Explain how it can be misunderstood and the accurate concept.

Footnotes

1. 1 Theodosius Dobzhansky. "Biology, Molecular and Organismic." *American Zoologist* 4, no. 4 (1964): 449.
2. 2 Pew Research Center for the People & the Press, *Public Praises Science; Scientists Fault Public, Media* (Washington, DC, 2009), 37.Contributors

This page titled 4.1.1: Understanding Evolution is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **19.2: Population Genetics** by OpenStax is licensed CC BY 4.0.
- **11.1: Discovering How Populations Change** by OpenStax is licensed CC BY 4.0.
- **11.5: Common Misconceptions about Evolution** by OpenStax is licensed CC BY 4.0.
- **1.2: Themes and Concepts of Biology** is licensed CC BY 4.0.

4.1.2: Evidence of Evolution

Evidence of Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2.5 hours.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain how a variety of forms of evidence support the theory of evolution.

Evolution - It's a Thing

Video



This 11-minute video describes the formation of fossils.
Question after watching: What were the forms of evidence highlighted that inform scientists about whale evolution?

Modern Studies of Darwin's Finches - Evidence of Natural Selection

Scientific studies of evolution by natural selection can be time-consuming. One of the best demonstrations has been in the very birds that helped to inspire the theory, the Galápagos finches. Peter and Rosemary Grant and their colleagues have studied Galápagos finch populations every year since 1976 and have provided important demonstrations of the operation of natural selection. The Grants found changes from one generation to the next in the beak shapes of the medium ground finches on the Galápagos island of Daphne Major. The medium-ground finch feeds on seeds. The birds have inherited variations in the bill shape with some individuals having wide, deep bills and others having thinner bills. Large-billed birds feed more efficiently on large, hard seeds, whereas smaller-billed birds feed more efficiently on small, soft seeds.

During 1977, a drought period altered vegetation on the island. After this period, the number of seeds declined dramatically: the decline in small, soft seeds was greater than the decline in large, hard seeds. The large-billed birds were able to survive better than the small-billed birds the following year. The year following the drought when the Grants measured beak sizes in the much-reduced population, they found that the average bill size was larger (Figure 4.1.2.3). This was clear evidence for natural selection (differences in survival) of bill size caused by the availability of seeds.

The Grants had studied the inheritance of bill sizes and knew that the surviving large-billed birds would tend to produce offspring with larger bills, so the selection would lead to evolution of bill size. Subsequent studies by the Grants have demonstrated selection

on, and evolution of, bill size in this species in response to changing conditions on the island. The evolution has occurred both to larger bills, as in this case, and to smaller bills when large seeds became rare.

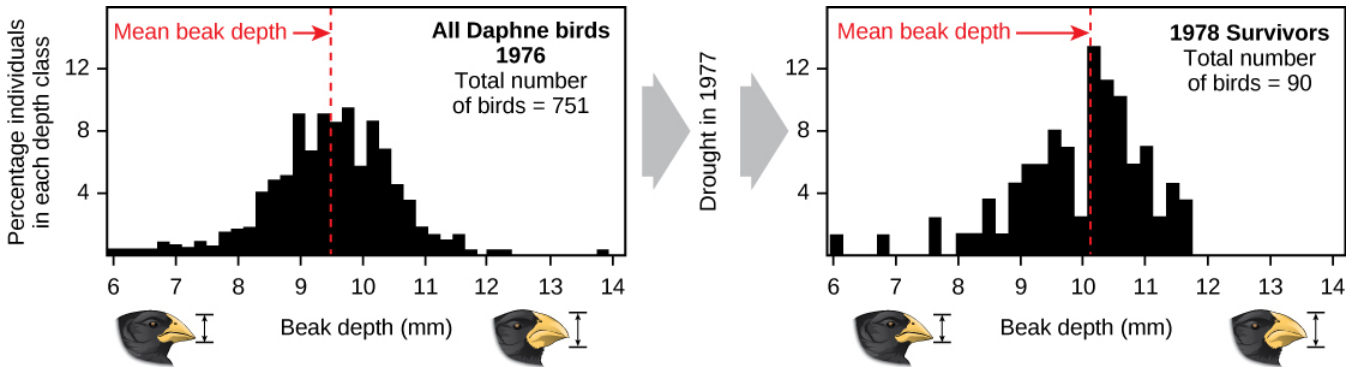


Figure 4.1.2.1: A drought on the Galápagos island of Daphne Major in 1977 reduced the number of small seeds available to finches, causing many of the small-beaked finches to die. This caused an increase in the finches' average beak size between 1976 and 1978.

The Fossil Record as Evidence for Evolution

Fossils tell us when organisms lived, as well as provide evidence for the progression and evolution of life on earth over millions of years.

Fossils are preserved remains or traces of animals, plants, and other organisms from the past. Fossils range in age from 10,000 to 3.48 billion years old. The observation that certain fossils were associated with certain rock strata led 19th-century geologists to recognize a geological timescale. Like extant organisms, fossils vary in size from microscopic, like single-celled bacteria, to gigantic, like dinosaurs and trees.



Figure 4.1.2.2: "Sue": The bones of this *Tyrannosaurus rex* were preserved through the process of permineralization, which suggests that this organism was covered by sediment soon after death.

Permineralization

Permineralization is a process of fossilization that occurs when an organism is buried. Small-scale permineralization can produce very detailed fossils. For permineralization to occur, the organism must be covered by sediment soon after death, or soon after the initial decay process.

It would not be an exaggeration to say that the typical vertebrate fossil consists of a single bone, or tooth, or fish scale. The preservation of an intact skeleton with the bones in the relative positions they had in life requires remarkable circumstances. The mineralization of soft parts is even less common and is seen only in exceptionally rare chemical and biological conditions.

Some of the best fossil beds in the world are located in Canada, due to the vast age of the rocks in the shield formations there. Alberta is well known for its *T. rex*, *Albertasaurus*, and *Edmontonsaurus* specimens. Fossils in the Burgess Shale, located between Alberta and British Columbia, date back even further to before the Cambrian Explosion more than 550 million years ago.



a b

Figure 4.1.2.3: Dinosaur National Park in Alberta. (a) Scientists must be careful with their footing as small fossils abound.(b) A trilobite fossil. (Copyright; CC-BY-SA 4.0 Annie Prud'homme Genereux)

Video





This 4-minute video humorously describes the formation of fossils.
Question after watching: If you were a paleontologist, where would you go to look for a fossil?

Trace Fossils

Fossils may also consist of the marks left behind by the organism while it was alive, such as footprints or feces. These types of fossils are called **trace fossils**, or ichnofossils, as opposed to body fossils. Past life may also leave some markers that cannot be seen but can be detected in the form of biochemical signals; these are known as chemofossils or biomarkers.



Figure 4.1.2.4: These dinosaur footprints, examples of trace fossils, are located in Denver, Colorado's Dino Ridge. Similar footprints can be seen in Grande Prarie in Northern Alberta and Northern British Columbia (CC-BY-SA 4.0 Annie Prud'homme Genereux).

The Fossil Record

The totality of fossils, both discovered and undiscovered, and their placement in fossiliferous (fossil-containing) rock formations and sedimentary layers (strata) is known as the **fossil record**. The fossil record was one of the early sources of data underlying the study of evolution and continues to be relevant to the history of life on Earth. The development of radiometric dating techniques in the early 20th-century allowed geologists to determine the numerical or “absolute” age of various strata and their included fossils.

Each fossil discovery represents a snapshot of the process of evolution. Because of the specialized and rare conditions required for a biological structure to fossilize, many important species or groups may never leave fossils at all. Even if they do leave fossils, humans may never find them—for example, if they are buried under hundreds of feet of ice in Antarctica. The number of species discovered through the fossil record is less than 5% of the number of species alive today. Fossilized species may represent less than 1% of all the species that have ever lived.

The fossil record is very uneven and is mostly comprised of fossils of organisms with hard body parts, leaving most groups of soft-bodied organisms with little to no fossil record. Groups considered to have a good fossil record, including transitional fossils between these groups, are the vertebrates, the echinoderms, the brachiopods, and some groups of arthropods. Their hard bones and shells fossilize easily, unlike the bodies of organisms like cephalopods or jellyfish.

Romer’s gap is an example of an apparent gap in the tetrapod fossil record used in the study of evolutionary biology. These gaps represent periods from which no relevant fossils have been found. Romer’s gap is named after paleontologist Alfred Romer, who first recognized it. Romer’s gap spanned from approximately 360 to 345 million years ago, corresponding to the first 15 million years of the Carboniferous Period. There has been much debate over why there are so few fossils from this time period. Some scientists have suggested that the geochemistry of the time period caused bad conditions for fossil formation, so few organisms were fossilized. Another hypothesis suggests that scientists have simply not yet discovered an excavation site for these fossils, due to inaccessibility or random chance.



Figure 4.1.2.5: The bank of the Whiteadder Water in Scotland is one of the few known localities bearing fossils of tetrapods from Romer's gap.

Determining Fossil Ages

Paleontology seeks to map out how life evolved across geologic time. A substantial hurdle is in the difficulty of working out fossil ages. There are several different methods for estimating the ages of fossils, including:

1. stratigraphy
2. biostratigraphy
3. carbon dating

Stratigraphy

Paleontologists rely on stratigraphy to date fossils. **Stratigraphy** is the science of understanding the strata, or layers, that form the sedimentary record. Strata are differentiated from each other by their different colors or compositions and are exposed in cliffs, quarries, and river banks. These rocks normally form relatively horizontal, parallel layers, with younger layers forming on top.

If a fossil is found between two layers of rock whose ages are known, the fossil's age is thought to be between those two known ages. Because rock sequences are not continuous but may be broken up by faults or periods of erosion, it is difficult to match up rock beds that are not directly adjacent.



Figure 4.1.2.6: The layers of sedimentary rock, or strata, can be seen as horizontal bands of differently colored or differently structured materials exposed in this cliff. The deeper layers are older than the layers found at the top, which aids in determining the relative age of fossils found within the strata.

Biostratigraphy

Fossils of species that survived for a relatively short time can be used to match isolated rocks: this technique is called **biostratigraphy**. For instance, the extinct chordate *Eoplacognathus pseudoplanus* is thought to have existed for a short time in the Middle Ordovician period. If rocks of unknown age have traces of *E. pseudoplanus*, they have a mid-Ordovician age. Such index fossils must be distinctive, globally distributed, and occupy a short time range to be useful. Misleading results can occur if the index fossils are incorrectly dated.

Relative Dating

Stratigraphy and biostratigraphy can in general provide only relative dating (A was before B), which is often sufficient for studying evolution. This is difficult for some time periods, however, because of the barriers involved in matching rocks of the same age across continents. Family-tree relationships can help to narrow down the date when lineages first appeared. For example, if fossils of B date to X million years ago and the calculated "family tree" says A was an ancestor of B, then A must have evolved earlier.

It is also possible to estimate how long ago two living branches of a family tree diverged by assuming that DNA mutations accumulate at a constant rate. However, these "**molecular clocks**" are sometimes inaccurate and provide only approximate timing. For example, they are not sufficiently precise and reliable for estimating when the groups that feature in the Cambrian explosion first evolved, and estimates produced by different approaches to this method may vary as well.

Carbon Dating

Together with stratigraphic principles, radioactive elements are used in geochronology to establish the geological time scale. Beds that preserve fossils typically lack these traditional radioactive elements. Instead, **radiocarbon dating**, or simply "carbon dating", is used Figure 4.1.2.7. The principle of radiocarbon dating is simple: the rates at which various radioactive elements decay are known, and the ratio of the radioactive element to its decay products shows how long the radioactive element has existed in the rock. This rate is represented by the half-life, which is the time it takes for half of a sample to decay.

The half-life of carbon-14 is 5,730 years, so carbon dating is only relevant for dating fossils less than 60,000 years old. Radioactive elements are common only in rocks with a volcanic origin, so the only fossil-bearing rocks that can be dated using traditional elements are volcanic ash layers. Carbon dating uses the decay of carbon-14 to estimate the age of organic materials, such as wood and leather.

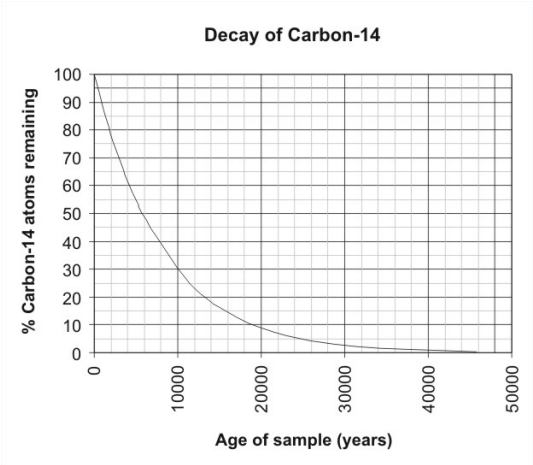


Figure 4.1.2.7: Radiocarbon dating is a technique used to date carbon in rocks or fossils usually based on a comparison between the observed abundance of a naturally occurring radioactive isotope (in this case, carbon-14) and its decay products, using known decay rates.

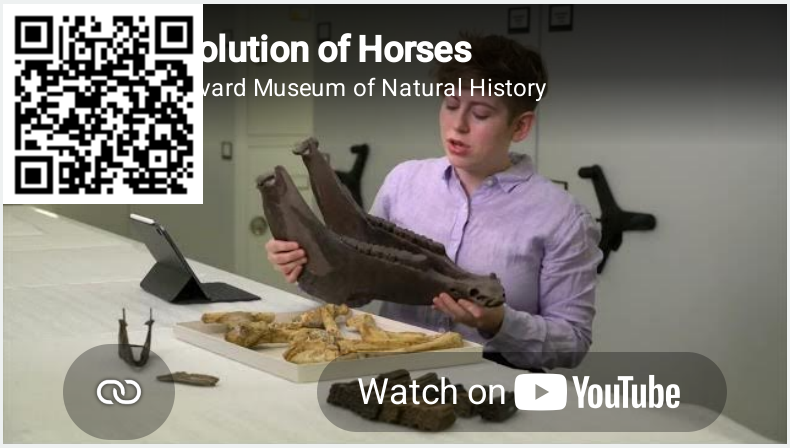
Case Study: The Fossil Record and the Evolution of the Modern Horse

Highly detailed fossil records have been recovered for sequences in the evolution of modern horses. The fossil record of horses in North America is especially rich and contains transition fossils: fossils that show intermediate stages between earlier and later forms. The fossil record extends back to a dog-like ancestor some 55 million years ago, which gave rise to the first horse-like species 55 to 42 million years ago in the genus *Eohippus*.

The first *Equid* fossil was found in the gypsum quarries in Montmartre, Paris in the 1820s. The tooth was sent to the Paris Conservatory, where Georges Cuvier identified it as browsing equine, related to the tapir. His sketch of the entire animal matched later skeletons found at the site. During the H.M.S. Beagle survey expedition, Charles Darwin had remarkable success with fossil hunting in Patagonia. In 1833 in Santa Fe, Argentina, he was "filled with astonishment" when he found a horse's tooth in the same stratum as fossils of giant armadillos and wondered if it might have been washed down from a later layer, but concluded this was "not very probable." In 1836, the anatomist Richard Owen confirmed the tooth was from an extinct species, which he subsequently named *Equus curvidens*.

The original sequence of species believed to have evolved into the horse was based on fossils discovered in North America in the 1870s by paleontologist Othniel Charles Marsh. The sequence, from *Eohippus* to the modern horse (*Equus*), was popularized by Thomas Huxley and became one of the most widely known examples of a clear evolutionary progression. The sequence of transitional fossils was assembled by the American Museum of Natural History into an exhibit that emphasized the gradual, "straight-line" evolution of the horse.

Video



This video explains how fossils show dramatic changes in horse morphology over nearly 60 million years of evolution.

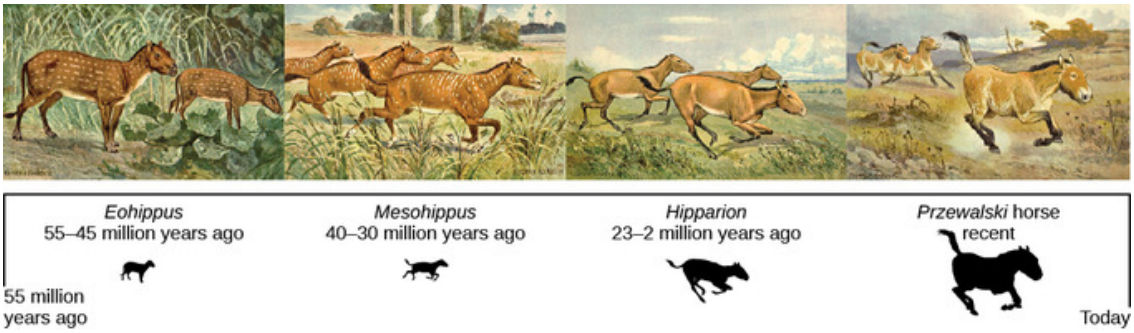


Figure 4.1.2.8: This illustration shows an artist's renderings of species derived from fossils of the evolutionary history of the horse and its ancestors. The species depicted are only four from a very diverse lineage that contains many branches, dead ends, and adaptive radiations. One of the trends, depicted here, is the evolutionary tracking of a drying climate and increase in prairie versus forest habitat reflected in forms that are more adapted to grazing and predator escape through running.

Since then, as the number of *Equid* fossils has increased, the actual evolutionary progression from *Eohippus* to *Equus* has been discovered to be much more complex and multi-branched than was initially supposed. Detailed fossil information on the rate and distribution of new *Equid* species has also revealed that the progression between species was not as smooth and consistent as was once believed.

Although some transitions were indeed gradual progressions, a number of others were relatively abrupt in geologic time, taking place over only a few million years. Both **anagenesis**, a gradual change in an entire population's gene frequency, and **cladogenesis**, a population "splitting" into two distinct evolutionary branches, occurred, and many species coexisted with "ancestor" species at various times.

Adaptation for Grazing

The series of fossils tracks the change in anatomy resulting from a gradual drying trend that changed the landscape from a forested habitat to a prairie habitat. Early horse ancestors were originally specialized for tropical forests, while modern horses are now adapted to life on drier land. Successive fossils show the evolution of teeth shapes and foot and leg anatomy to a grazing habit with adaptations for escaping predators.

The horse belongs to the order Perissodactyla (odd-toed ungulates), the members of which all share hoofed feet and an odd number of toes on each foot, as well as mobile upper lips and a similar tooth structure. This means that horses share a common ancestry with tapirs and rhinoceroses. Later species showed gains in size, such as those of *Hipparion*, which existed from about 23 to 2 million years ago. The fossil record shows several adaptive radiations, or periods of cladogenesis, in the horse lineage, which is now much reduced to only one genus, *Equus*, with several species. Paleozoologists have been able to piece together a more complete outline of the modern horse's evolutionary lineage than that of any other animal.

Additional Evidence for Evolution

Homologous Structures vs Analogous Structures

Homology is the relationship between structures or DNA derived from the most recent common ancestor. A common example of **homologous structures** in evolutionary biology is the wings of bats and the arms of primates. Although these two structures do not look similar or have the same function, genetically, they come from the same structure from the last common ancestor. Homologous traits of organisms are therefore explained by descent from a common ancestor. In genetics, homology is measured by comparing protein or DNA sequences. Homologous gene sequences share a high similarity, supporting the hypothesis that they share a common ancestor. It's important to note that defining two structures or sequences as homologous depends on what ancestor is being described as the common ancestor.

Homology can also be partial: new structures can evolve through the combination of developmental pathways or parts of them. As a result, hybrid or mosaic structures can evolve that exhibit partial homologies. For example, certain compound leaves of flowering plants are partially homologous both to leaves and shoots because they combine some traits of leaves and some of shoots.

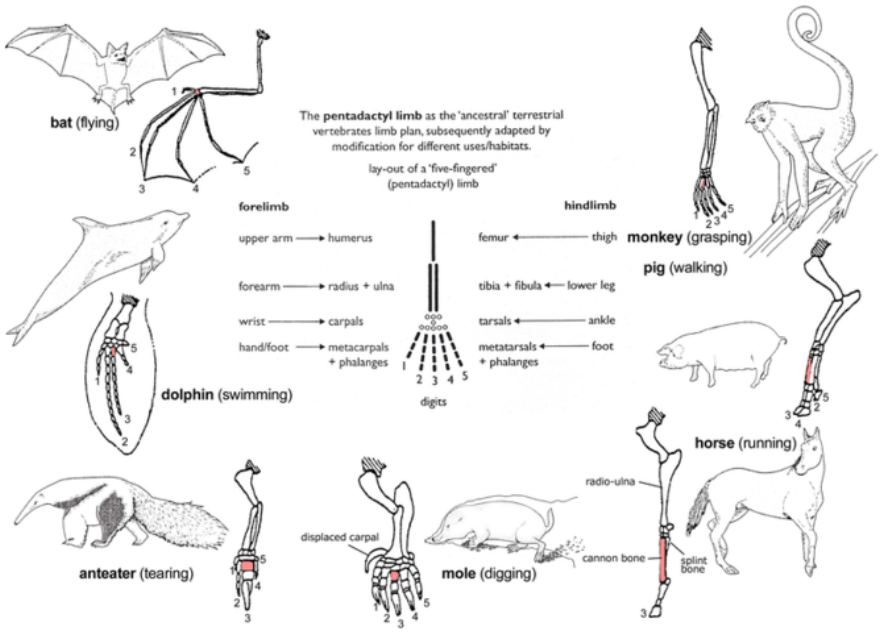


Figure 4.1.2.9: The principle of homology illustrated by the adaptive radiation of the forelimb of mammals. All conform to the basic pentadactyl pattern but are modified for different usages. The third metacarpal is shaded throughout; the shoulder is crossed-hatched.

The opposite of homologous structures is **analogous structures**, which are physically similar structures between two taxa that evolved separately (rather than being present in the last common ancestor). Bat wings and bird wings evolved independently and are considered analogous structures. Genetically, a bat wing and a bird wing have very little in common; the last common ancestor of bats and birds did not have wings like either bats or birds. Wings evolved independently in each lineage after diverging from ancestors with forelimbs that were not used as wings (terrestrial mammals and theropod dinosaurs, respectively).

It is important to distinguish between different hierarchical levels of homology in order to make informative biological comparisons. In the above example, the bird and bat wings are analogous as wings, but homologous as forelimbs because the organ served as a forearm (not a wing) in the last common ancestor of tetrapods.

Analogy is different than homology. Although analogous characteristics are superficially similar, they are not homologous because they are phylogenetically independent. The wings of a maple seed and the wings of an albatross are analogous but not homologous (they both allow the organism to travel on the wind, but they did not both develop from the same structure).

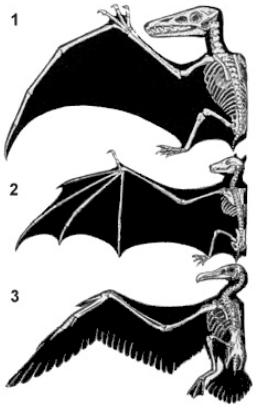


Figure 4.1.2.10: The wings of pterosaurs (1), bats (2), and birds (3) are analogous as wings, but homologous as forelimbs. This is because they are similar characteristically and even functionally, but evolved from different ancestral roots.

Vestigial Structures

Some organisms possess structures with no apparent function which appear to be residual parts from a past ancestor. For example, some snakes have pelvic bones despite having no legs because they descended from reptiles that did have legs. Another example of a structure with no function is the human vermiform appendix. These unused structures without function are called **vestigial structures**. Other examples of vestigial structures are wings (which may have other functions) on flightless birds like the ostrich, leaves on some cacti, traces of pelvic bones in whales, and the sightless eyes of cave animals.

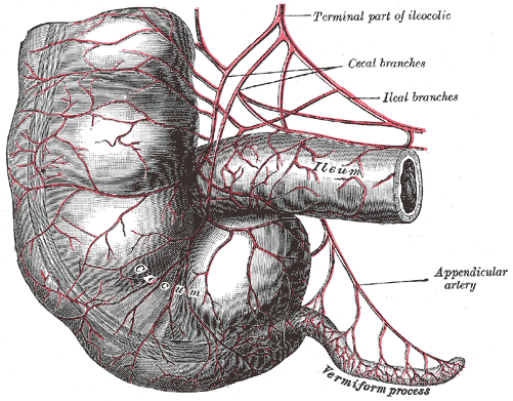


Figure 4.1.2.11: In humans, the appendix is a vestigial structure; it has lost much of its ancestral function.

There are also several reflexes and behaviors that are considered to be vestigial. The formation of goosebumps in humans under stress is a vestigial reflex its function in human ancestors was to raise the body's hair, making the ancestor appear larger and scaring off predators. The arrector pili muscle, which is a band of smooth muscle that connects the hair follicle to connective tissue. When it contracts it creates goosebumps on the skin.

Vestigial Structures in Evolution

Vestigial structures are often homologous to structures that function normally in other species. Therefore, vestigial structures can be considered evidence for evolution, the process by which beneficial heritable traits arise in populations over an extended period of time. The existence of vestigial traits can be attributed to changes in the environment and behavior patterns of the organism in question. As the function of the trait is no longer beneficial for survival, the likelihood that future offspring will inherit the "normal" form of it decreases. If there are no selection pressures actively lowering the fitness of the individual, the trait will persist in future generations unless the trait is eliminated through genetic drift or other random events.

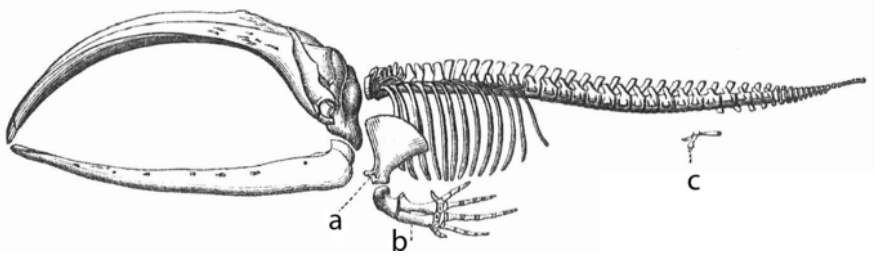
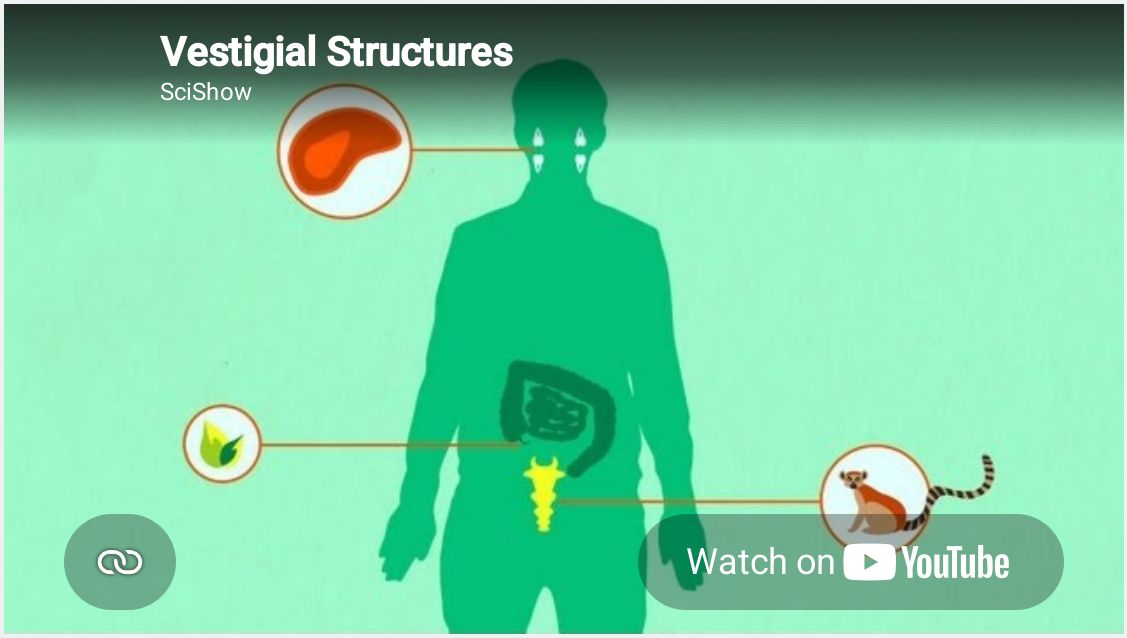


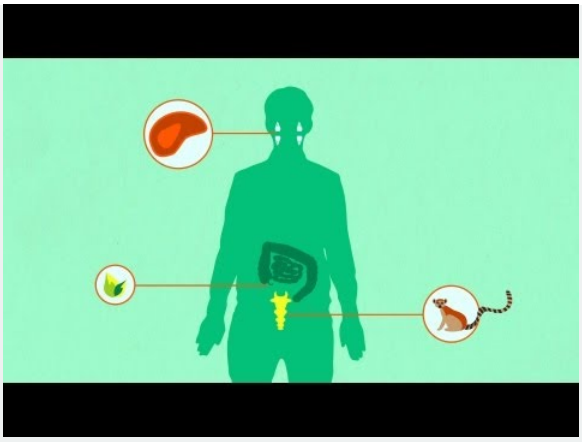
Figure 4.1.2.12: The pelvic bones in whales are also a good example of vestigial evolution (whales evolved from four-legged land mammals and secondarily lost their hind legs). Letter c in the picture indicates the undeveloped hind legs of a baleen whale.

In some cases, the structure becomes detrimental to the organism. Although in many cases the vestigial structure is of no direct harm, all structures require extra energy in terms of development, maintenance, and weight and are also a risk in terms of disease (e.g., infection, cancer). This provides some selective pressure for the removal of parts that do not contribute to an organism's fitness, but a structure that is not directly harmful will take longer to be 'phased out' than one that is. Some vestigial structures persist due to limitations in development, such that complete loss of the structure could not occur without major alterations of the organism's developmental pattern, and such alterations would likely produce numerous negative side effects.

The vestigial versions of a structure can be compared to the original version of the structure in other species in order to determine the homology of the structure. Homologous structures indicate common ancestry with those organisms that have a functional version of the structure. Vestigial traits can still be considered adaptations because an adaptation is often defined as a trait that has been favored by natural selection. Adaptations, therefore, need not be adaptive, as long as they were at some point.

Video





This 4-minute video takes you on a tour of vestigial structures in the human body.
Question after watching: We say that vestigial structures are evidence for evolution. Why is that? What could account for these structures if evolution was not the reason?

Convergent Evolution

Sometimes, similar phenotypes evolve independently in distantly related species. For example, flight has evolved in both bats and insects, and they both have wings, which are adaptations to flight. However, the wings of bats and insects have evolved from very different original structures. This phenomenon is called **convergent evolution**, where similar traits evolve independently in species that do not share a recent common ancestry.

Examples of Convergent Evolution

Convergent evolution describes the independent evolution of similar features in species of different lineages. The two species came to the same function, flying, but did so separately from each other. They have "converged" on this useful trait. Both sharks and dolphins have similar body forms, yet are only distantly related: sharks are fish and dolphins are mammals. Such similarities are a result of both populations being exposed to the same selective pressures. Within both groups, changes that aid swimming have been favored. Thus, over time, they developed similar appearances (morphology), even though they are not closely related.

One of the most well-known examples of convergent evolution is the camera eye of cephalopods (e.g., octopus), vertebrates (e.g., mammals), and cnidaria (e.g., box jellies). Their last common ancestor had at most a very simple photoreceptive spot, but a range of processes led to the progressive refinement of this structure to the advanced camera eye. There is, however, one subtle difference: the cephalopod eye is "wired" in the opposite direction, with blood and nerve vessels entering from the back of the retina, rather than the front as in vertebrates.

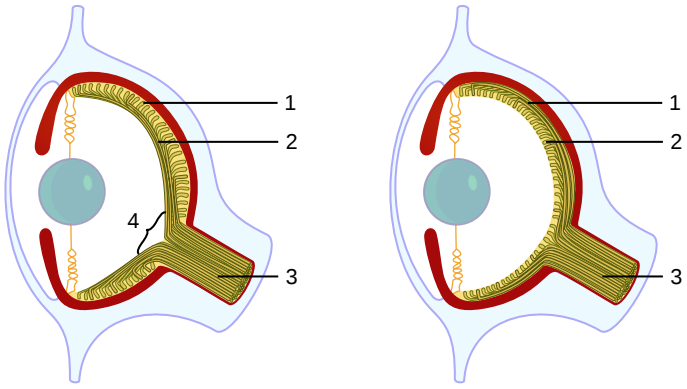


Figure 4.1.2.13: Vertebrates and octopuses developed the camera eye independently. In the vertebrate version (left), the nerve fibers pass in front of the retina, and there is a blind spot (4) where the nerves pass through the retina. In the octopus version (right), the eye is constructed the "right way out," with the nerves attached to the rear of the retina. This means that octopuses do not have a blind spot.

The opposite of convergent evolution is **divergent evolution**, whereby related species evolve different traits. On a molecular level, this can happen due to random mutation unrelated to adaptive changes. More will be discussed on divergent evolution in Unit 2.3.

Biogeography and the Modern Distribution of Species

Biogeography is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors, such as temperature and rainfall, vary based on latitude and elevation, primarily. As these abiotic factors change, the composition of plant and animal communities also changes.

Patterns of Species Distribution

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An **endemic species** is one that is naturally found only in a specific geographic area that is usually restricted in size. Other species are **cosmopolitan**: species that live in a wide variety of geographic areas. The raccoon, for example, is native to most of North and Central America.

Since species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia.



Figure 4.1.2.14: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal.

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 *Glossopteris* in Australia, Antarctica, India, Africa, and South America is best explained by the plant family's presence there prior to the southern supercontinent Gondwana breaking up.

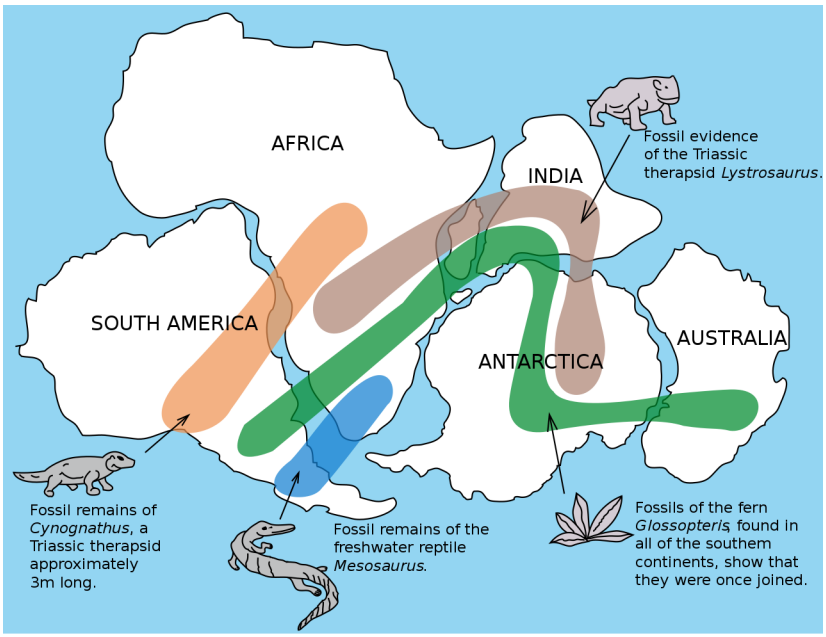


Figure 4.1.2.15: The *Glossopteris* genus of ferns evolved before the supercontinent Gondwana broke up. Today, members of this plant family are found throughout the southern hemisphere (shown in green).

Artificial Selection: Human-Initiated Change

Most contemporary evolutionary biologists study evolution experimentally using laboratory organisms such as *Drosophila* or natural systems in the wild. However, 18th- and 19th-century evolutionary biologists, including Darwin, emphasized the similarities between natural evolution and artificial ‘ improvement’ of livestock under domestication. They believed that studying domesticated animals and plants could illuminate the mechanisms of natural evolution. Indeed, Chapter 1 of *On the Origin of Species…* is entitled ‘Variation under domestication’. Recent discoveries reveal the relationship between natural evolutionary mechanisms and the practical technologies used to breed plants, animals, yeasts, and microbes, to produce food, clothing, transport, companionship, decoration, entertainment, and medicines.

Artificial selection is any selective breeding intentionally practiced by humans leading to the evolution of domesticated organisms. Artificial selection may oppose or amplify or be neutral in relation to natural selection. Most livestock, including dogs, cats, goats, pigs, cattle, sheep, guinea pigs, horses, geese, poultry, and scores of crop plants were domesticated more than 5000 years ago. Estimates of dates of domestication based upon the archeological record differ enormously from those based on genetic analysis for almost all crops and livestock. However, experts agree that dogs were among the first mammalian species to become domesticated, followed by sheep. During the last few hundred years, people have domesticated a wide range of other animals such as guppies, hamsters, mice, and budgerigars, mostly for use as pets, together with thousands of culinary, medicinal, and ornamental plants.

Domesticated animals are usually held in small, isolated populations with limited opportunities for interbreeding. For centuries, drovers herded large numbers of non-breeding pigs, cattle, sheep, geese, and poultry to market for slaughter, often over hundreds of kilometers. However, the breeding stocks were usually kept within a small area because moving sexually active bulls and large boars over long distances was much less practical. It is important to note that true domestication is different from the taming of wild animals. Certain individuals of many species, especially juveniles and females, can be tamed and live in captivity where they are protected from predators and provided with food and shelter. Domesticated livestock are also fed and protected, but many generations breed and spend their entire lives in close association with humans.

For centuries, livestock breeders have nurtured strains of animals that thrive on various diets or in particular climates or that excel in certain roles. Sometimes, domestication was simply due to the whims of the breeder. The variety of such animals seems bewildering but certain changes consistently emerge in a surprisingly wide range of domesticated species and among humans, suggesting that similar mechanisms are operating.

Videos



This 5-minute video explains the current hypothesis for the origins of the modern dog.
Question after watching: Human-initiated selection is a large influence on the evolution of modern dogs. What role did natural selection also play?



This 6-minute video describes how broccoli, cabbage, and kohlrabi are all varieties of the same species.
Question after watching: You go to the garden centre and obtain a few strawberry plants. You want to breed the sweetest berries. How would you go about obtaining such a berry? Link each step to a similar step in the process of natural selection.

Parts adapted from ("Evolution: artificial selection and domestication"; CC BY-NC-SA 2.0 UK)

This page titled 4.1.2: Evidence of Evolution is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **11.1: Discovering How Populations Change** by OpenStax is licensed CC BY 4.0.

Natural Selection and Adaptive Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain how natural selection leads to adaptive evolution
- Contrast stabilizing selection, directional selection, and diversifying selection.
- Describe frequency-dependent selection
- Explain the effects of sexual dimorphism on the reproductive potential of an organism

Introduction to Natural Selection

Natural selection drives adaptive evolution by selecting for and increasing the occurrence of beneficial traits in a population. Natural selection only acts on the population's heritable traits: selecting for beneficial alleles and, thus, increasing their frequency in the population, while selecting against deleterious alleles and, thereby, decreasing their frequency. This process is known as **adaptive evolution** (Figure 4.1.3.1). Natural selection does not act on individual alleles, however, but on entire organisms. An individual may carry a very beneficial genotype with a resulting phenotype that, for example, increases the ability to reproduce. If that same individual also carries an allele that results in a fatal childhood disease, however, the fecundity phenotype will not be passed on to the next generation because the individual will not live to reach reproductive age. Natural selection acts at the level of the individual. It selects for individuals with greater contributions to the gene pool of the next generation, known as an organism's **evolutionary fitness**.

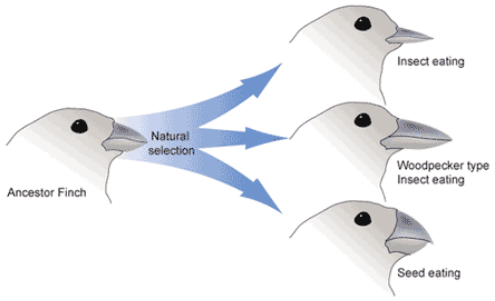


Figure 4.1.3.1: Through natural selection, a population of finches evolved into three separate species by adapting to several different selection pressures. Each of the three modern finches has a beak adapted to its life history and diet.

Evolutionary fitness is often quantifiable as the contribution of genetic information by an individual to subsequent generations. However, it is not the absolute fitness of an individual that counts, but rather how it compares to the other organisms in the population. This concept, called **relative fitness**, allows researchers to determine which individuals are contributing additional offspring to the next generation and, thus, how the population might evolve.

Genetic Variation and Natural Selection

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 for, while deleterious alleles may be selected against. 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, this may be passed to a child.

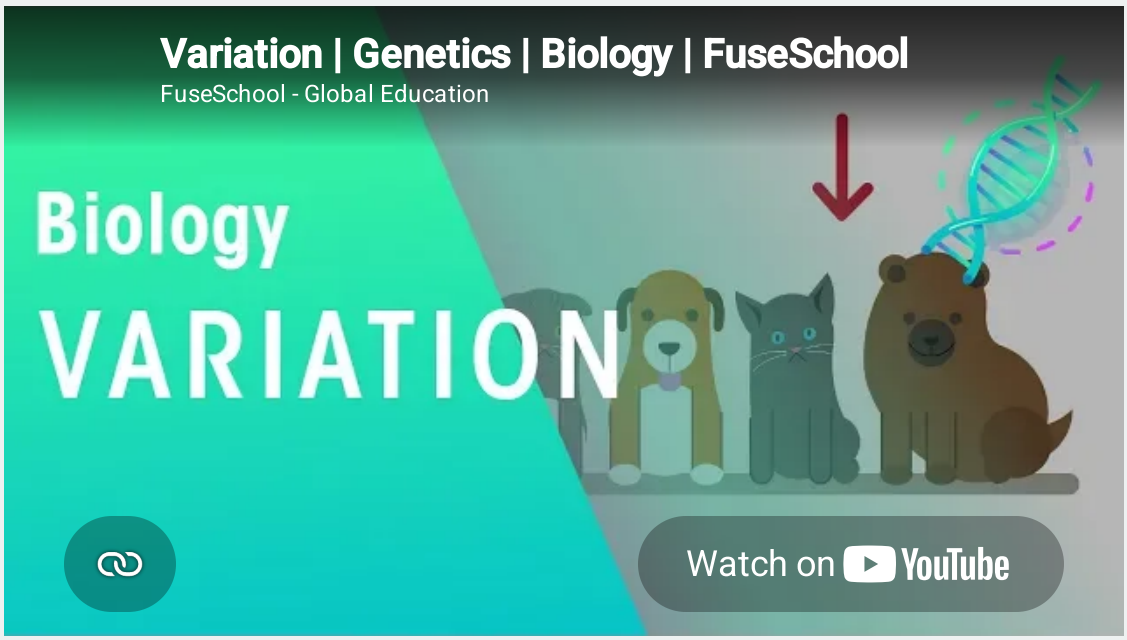
Genetic variation is a measure of the genetic differences (diversity of alleles and genotypes) that exist within a population. The genetic variation of an entire species is often called genetic diversity. Genetic variations are the differences in DNA segments or genes between individuals and each variation of a gene is called an allele. For example, a population with many different alleles at a single chromosome locus has a high amount of genetic variation. Genetic variation is essential for natural selection because natural selection can only increase or decrease the frequency of alleles that already exist in the population.

Genetic variation is caused by:

- mutation (discussed further in Section 2.2.4)
- random mating between organisms (discussed further in Section 2.2.4)
- random fertilization
- genetic recombination during meiosis

Mutations are the only method of creating new alleles; mutations are ultimately the engine that drives evolution. Sexual reproduction (including random mating, random fertilization, and crossing over) are ways to reshuffle and recombine those genes in new ways, giving offspring combinations that differ from their parents and from others.

Video





This 4-minute video provides a brief introduction to variation in humans and a method for identifying traits that are encoded by genetics and those determined by the environment.

Question after watching: In most cases, when a person who has an identical two develops a disease like cancer, their identical twin does not. What does this tell you about the causes of cancer?

Evolution and Adaptation to the Environment

Variation allows some individuals within a population to adapt to the changing environment. Because natural selection acts directly only on phenotypes, more genetic variation within a population usually enables more phenotypic variation. Some new alleles increase an organism's ability to survive and reproduce, which then ensures the survival of the allele in the population. Other new alleles may be immediately detrimental (such as a malformed oxygen-carrying protein) and organisms carrying these new mutations will die out. Neutral alleles are neither selected for nor against and usually remain in the population. Genetic variation is advantageous because it enables some individuals and, therefore, a population, to survive despite a changing environment (Figure 4.1.3.2).

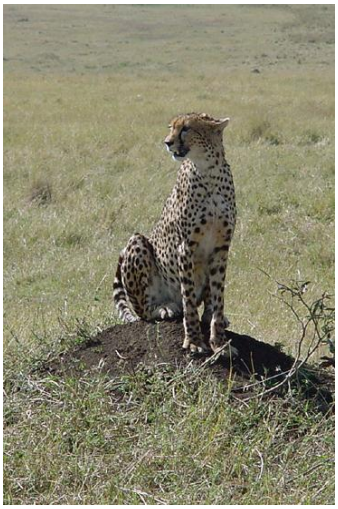


Figure 4.1.3.2: Populations of wild cheetahs have very low genetic variation. Because wild cheetahs are threatened, their species has a very low genetic diversity. This low genetic diversity means they are often susceptible to disease and often pass on lethal recessive mutations; only about 5% of cheetahs survive to adulthood.

Geographic Variation

Some species display geographic variation as well as variation within a population. Geographic variation, or the distinctions in the genetic makeup of different populations, often occurs when populations are geographically separated by environmental barriers or when they are under selection pressures from a different environment. One example of geographic variation are **clines**, gradual changes in a trait across an organism's geographic distribution.

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 considered a *latitudinal cline* (Figure 4.1.3.3). Alternatively, flowering plants tend to bloom at different times depending on where they are along the slope of a mountain, known as an *altitudinal cline*.

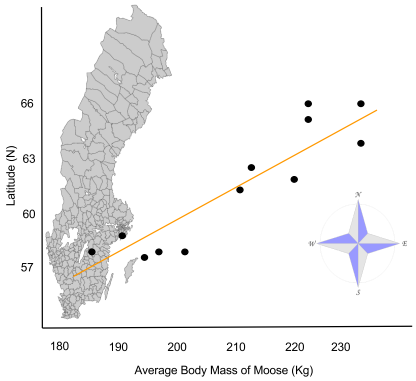


Figure 4.1.3.3: This graph shows geographical variation in moose; body mass increase positively with latitude. Bergmann's Rule is an ecologic principle that states that as latitude increases the body mass of a particular species increases. The data are taken from a Swedish study investigating the size of moose as latitude increases as shows the positive relationship between the two, supporting Bergmann's Rule.

Environmental Variance

Genes are not the only players involved in determining population variation. Phenotypes are also influenced by other factors, such as the environment (Figure 4.1.3.4). Some major characteristics, such as gender, are determined by the environment for some species. 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 4.1.3.4: 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)

Types of Natural Selection

There are several ways selection can affect population variation (each is described in detail below) (Figure 4.1.3.9):

- stabilizing selection
- directional selection
- diversifying selection
- frequency-dependent selection
- sexual selection

As natural selection influences the traits in a population, individuals can either become more or less genetically similar to one another and the phenotypes displayed can become more similar or more disparate. In the end, natural selection cannot produce perfect organisms from scratch, it can only generate populations that are better adapted to survive and successfully reproduce in their environments through the aforementioned selections.

Video





In this 3-minute video, David Attenborough explains how iguana evolved to swim on the Galpagos islands. Question after watching: Propose a series of steps that could have led to this evolution in the iguana population in the Galpagos. Specifically, explain how they evolved to live for short periods underwater from their land ancestor.

Stabilizing, Directional, and Diversifying Selection

Stabilizing Selection

If natural selection favors an average phenotype by selecting against extreme variation, the population will undergo **stabilizing selection** (Figure 4.1.3.5).

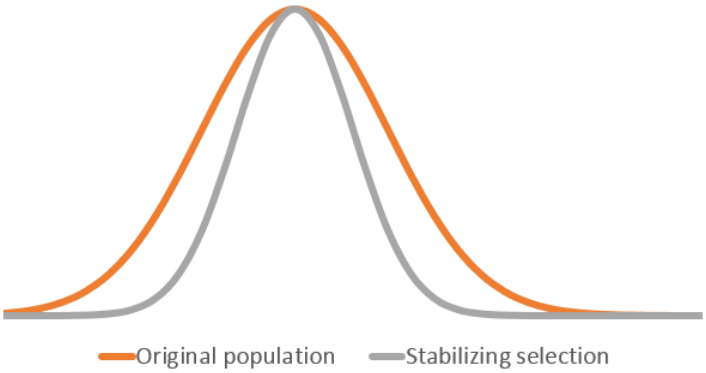


Figure 4.1.3.5: Stabilizing selection occurs when the population stabilizes on a particular trait value and genetic diversity decreases. In the graph above, the x-axis indicates the variation in a trait. The y-axis indicates the percentage of individuals in a population that have a particular trait. In stabilizing selection, the average becomes more common over time, with less variation in the population.

For example, in a population of mice that live in the woods, natural selection will tend to favor individuals that best blend in with the forest floor and are less likely to be spotted by predators. Assuming the ground is a fairly consistent shade of brown, those mice whose fur most closely matches that color will most probably survive and reproduce, passing on their genes for their brown coat. Mice that carry alleles that make them slightly lighter or slightly darker will stand out against the ground and will more probably die from predation. As a result of this stabilizing selection, the population's genetic variance will decrease.

Directional Selection

When the environment changes, populations will often undergo **directional selection**, which selects for phenotypes at one end of the spectrum of existing variation (Figure 4.1.3.6).

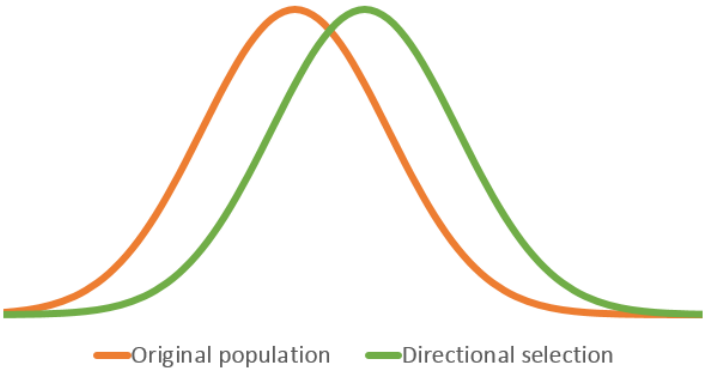


Figure 4.1.3.6: Directional selection occurs when a single phenotype is favored, causing the population to shift towards one end of the trait variation. In the graph above, the x-axis indicates the variation in a trait. The y-axis indicates the percentage of individuals in a population that have a particular trait. In directional selection, the average shifts in one direction or another but the total variation in the population remains.

A classic example of this type of selection is the evolution of the peppered moth (*Biston betularia*) 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. 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 melanic (dark) form of the moth increased because their darker coloration provided camouflage against the sooty tree; they had a higher survival rate in habitats affected by air pollution (Figure 4.1.3.7). Similarly, a hypothetical mouse population may evolve to take on a different coloration if their forest floor habitat changed. The result of this type of selection is a shift in the population's genetic variance toward the new, fit phenotype.



Figure 4.1.3.7: Two morphs of the peppered moth (*Biston betularia*) resting on the same tree. The light-colored typical moroph (below the bark's scar) is nearly invisible on this pollution-free tree, camouflaging it from predators while the carbonaria morph stands out clearly.

Diversifying (or Disruptive) Selection

Sometimes natural selection can select for two or more distinct phenotypes that each have their advantages in **diversifying (disruptive) selection**. In these cases, the intermediate phenotypes are often less fit than their extreme counterparts (Figure 4.1.3.8).

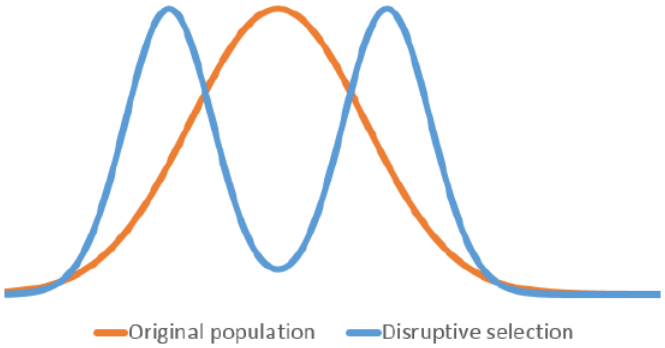


Figure 4.1.3.8: Diversifying selection occurs when extreme values for a trait are favored over intermediate values. This type of selection often drives speciation. In the graph above the x-axis indicates the variation in a trait. The y-axis indicates the percentage of individuals in a population that have a particular trait. In directional selection, the average is selected against, leading to selection for the rarer variations of a trait.

This is seen in many populations of animals that have multiple male mating strategies, such as lobsters. Large, dominant alpha males obtain mates by brute force, 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, which cannot 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 population of mice 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, on the other hand, would not blend in with either the grass or the sand and, thus, would more probably be eaten by predators. The result of this type of selection is increased genetic variance as the population becomes more diverse.

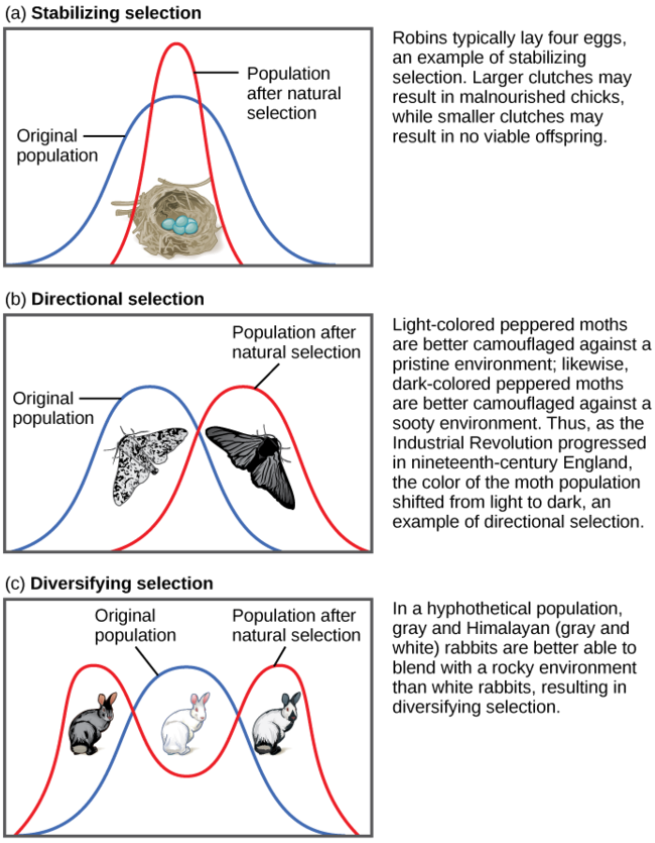
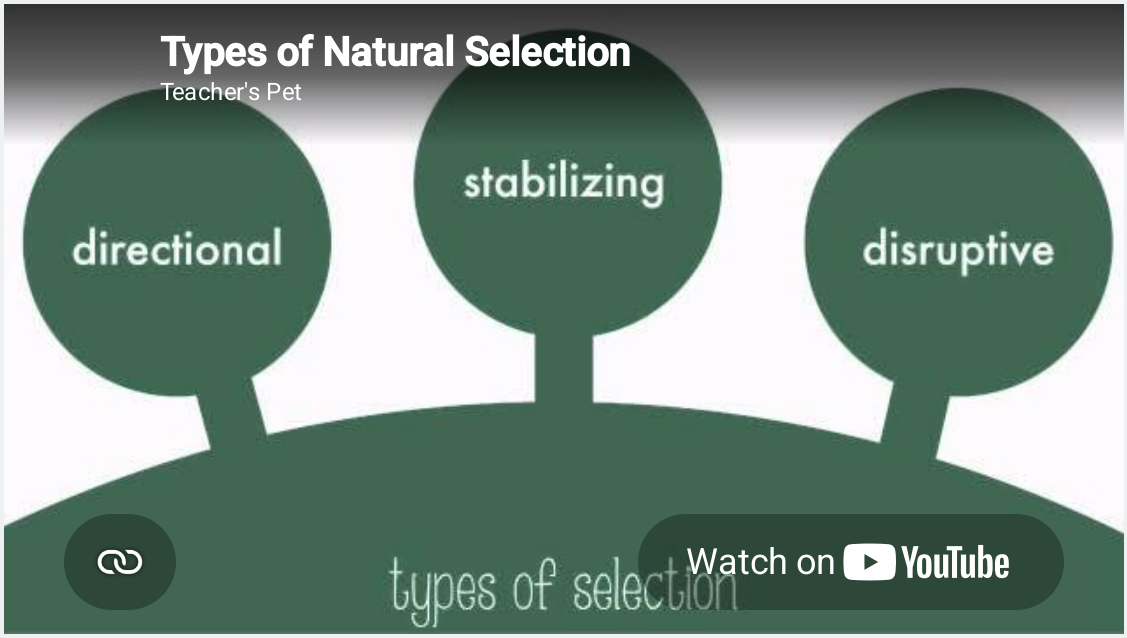
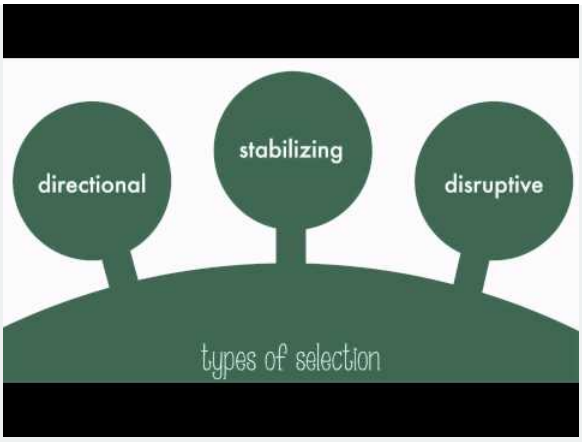


Figure 4.1.3.9: Different types of natural selection can impact the distribution of phenotypes within a population. In (a) stabilizing selection, an average phenotype is favored. In (b) directional selection, a change in the environment shifts the spectrum of phenotypes observed. In (c) diversifying selection, two or more extreme phenotypes are selected for, while the average phenotype is selected against.

Video





This 2.5-minute video highlights directional, stabilizing, and disruptive selection.
Question after watching: In the video, the narrator speaks of disruptive selection (this textbook called it diversifying selection). What is being disrupted?

Frequency-Dependent Selection

Another type of selection, called **frequency-dependent selection**, favors phenotypes that are either common (positive frequency-dependent selection) or rare (negative frequency-dependent selection).

Negative Frequency-Dependent Selection

Negative frequency-dependent selection increases the population's genetic variance by selecting for rare phenotypes. An interesting example of this type of selection is seen in a unique group of lizards in the deserts of the United States. 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; and yellow males are the smallest and look a bit like female, allowing 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. 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 4.1.3.10).

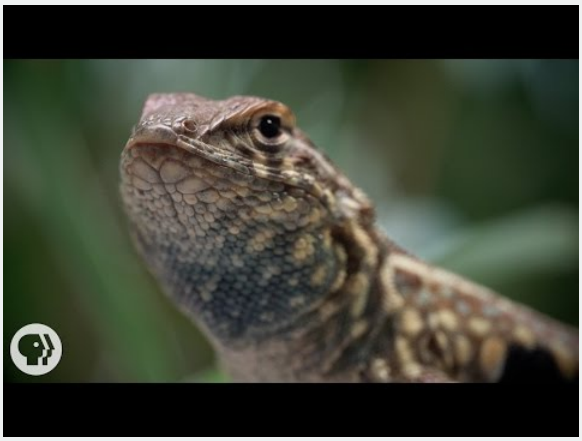
In this scenario, orange males will be favored by natural selection when the population is dominated by blue males, blue males will thrive when the population is mostly yellow males, and yellow males will be selected for when orange males are the most populous. As a result, populations of side-blotched lizards cycle in the distribution of these phenotypes. In one generation, orange might be predominant and then yellow males will begin to rise in frequency. Once yellow males make up a majority of the population, blue males will be selected for. Finally, when blue males become common, orange males will once again be favored. So, orange (strong) > blue (cooperation) > yellow (sneaky) > orange (strong)...etc.



Figure 4.1.3.10: A yellow-throated side-blotched lizard (seen here) 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. Frequency-dependent selection allows for both common and rare phenotypes of the population to appear in a frequency-aided cycle.

Video





This 3.5-minute video illustrates the side-blotched lizard case study of negative frequency-dependent selection. Question after watching: The video mentions that the blues can be altruistic, which is to say exhibit behavior that would benefit not themselves but another animal. Propose a hypothesis about the evolutionary advantage of altruism in this case.

Positive Frequency-dependent Selection

Positive frequency-dependent selection usually decreases genetic variance by selecting for common phenotypes. An example of positive frequency-dependent selection is the mimicry of the warning coloration of dangerous species of animals by other species that are harmless.

The scarlet kingsnake (*Lampropeltis elapsoides*), a harmless species, mimics the coloration of the eastern coral snake *(Micrurus fulvius)*, a venomous species typically found in the same geographical region (Figure 4.1.3.11). Predators learn to avoid both species of snake due to the similar coloration. As a result, the scarlet kingsnake becomes more common and its coloration phenotype becomes more variable due to relaxed selection. This phenotype is, therefore, more "fit" as the population of species that possess it (both dangerous and harmless) becomes more numerous. In geographic areas where the coral snake is less common, the pattern becomes less advantageous to the kingsnake, and much less variable in its expression, presumably because predators in these regions are not "educated" to avoid the pattern.



Figure 4.1.3.11 : The scarlet kingsnake (*Lampropeltis elapsoides*), left, mimics the coloration of the poisonous eastern coral snake (Micrurus fulvius), right. Positive frequency-dependent selection reinforces the common phenotype because predators avoid the distinct coloration. The eastern coral snake (Micrurus fulvius)is venomous and advertises this through its coloring.





In this short 1-minute narrated by David Attenborough, you will see several examples of biomimicry, where animals evolved shapes and colors that make them look like something else. This is a type of positive frequency-dependent selection.

Question after watching: What appears to be the purpose of biomimicry in most organisms? At which step in a process of natural selection would mimicry provide an advantage?

Sexual Selection

Sexual selection, the selection pressure on males and females in mating, can result in traits designed to maximize sexual success. In species with sexual selection, typically one sex is less-limited due to their ability to produce an overabundance of gametes and the other is more-limited due to their higher parental investment (e.g. produce eggs, gestate a fetus, raise young, etc.). The more-limited sex typically reproduces fewer times and has higher parental investment than the less-limited sex; they are typically more discerning about who they mate with in order to optimize those reproductive events.

Sexual selection in animals takes two major forms: **intersexual selection** in which, the less-limited sex (typically males) are chosen by the more-limited sex (typically females) based on certain characteristics and **intrasexual selection** in which members of the less-limited sex compete aggressively among themselves for access to the more-limited sex (Figure 4.1.3.12).



Figure 4.1.3.12: This male elk has large antlers to compete with rival males for available females (intrasexual competition). In addition, the many points on his antlers represent health and longevity, and therefore he may be more desirable to females (intersexual selection).

Video





This 3-minute video highlights extreme behaviors that arise from intense sexual selection pressure.
Question after watching: What can you surmise about which of the sexes are 'choosier' in most mammals, based on morphological and behavioural dimorphism?

Sexual Dimorphism in Animals

Males and females of certain animal species are often quite different from one another in ways beyond the reproductive organs. Male vertebrates are often larger, for example, and display many elaborate colors, adornments, and behaviors such as seen in the figure below, while females of the same species tend to be smaller and less attention-seeking. These differences are called **sexual dimorphisms** and arise from the variation in reproductive success (Figure 4.1.3.13).

Animal females do not have trouble finding mates for reproduction, while reproduction is not guaranteed for males. The bigger, stronger, or more decorated males usually obtain the vast majority of the total reproductive events, while other males receive none. This can occur because the males are better at fighting off other males (intrasexual selection), or because females will choose to mate with the bigger, brasher, or more decorated males (intersexual selection). In either case, this variation in reproductive success generates a strong selection pressure among males to compete for mates, resulting in the evolution of bigger body sizes or elaborate ornaments in order to increase their chances of mating. Females, on the other hand, tend to get a handful of selected matings; therefore, they are more likely to be selective in their mates.



Figure 4.1.3.13: Morphological differences between males and females of the same species is known as sexual dimorphism. These differences can be observed in (a) peacocks and peahens, (b) *Argiope appensa* spiders (the female spider is the large one), and (c) wood ducks.

Sexual dimorphism varies widely among species; some species are even sex-role reversed. In such cases, females tend to have a greater variation in their reproductive success than males and are, correspondingly, selected for the bigger body size and elaborate traits usually characteristic of males.

The Handicap Principle

Sexual selection can be so strong that it selects for traits that are actually detrimental to the individual's survival because they maximize its reproductive success. For example, while the male peacock's tail is beautiful, and the male with the largest, most colorful tail will more probably win a female's attention, it is not practical or advantageous (Figure 4.1.3.14). In addition to making the males more visible to predators, it slows down any needed escapes. There is some evidence that this risk is why females like the big, bright tails. Because large tails carry risk, only the best males can survive that risk, and therefore the bigger the tail the more fit the male must be. This idea is known as the **handicap principle**.



Figure 4.1.3.14: This male ribbon-tailed astrapia, *Astrapia mayeri*, a bird of paradise, carries an extremely long tail as the result of sexual selection. The tail is flamboyant and detrimental to the bird's own survival, but it increases his reproductive success. This may be an example of the handicap principle.

The Good Genes Hypothesis

The **good genes hypothesis** states that males develop these impressive ornaments to show off their efficient metabolism or their ability to fight disease. Females then choose males with the most impressive traits because it signals their genetic superiority, which they will then pass on to their offspring. Though it might be argued that females should not be so selective because it will likely reduce their number of offspring, if better males father more fit offspring, it may be beneficial. Fewer, healthier offspring may increase the chances of survival more than many, weaker offspring.

Video





This 8.5-minute video is an overview of natural and sexual selection.
Questions after watching: How is sexual selection an example or type of natural selection? Explain the following statement: "evolution is just a numbers game"

This page titled 4.1.3: Natural Selection and Adaptive Evolution is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **19.2: Population Genetics** by OpenStax is licensed CC BY 4.0.

4.1.4: Additional Mechanisms of Evolution

Unit 2.2.4 - Additional Mechanisms of Evolution

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to Unit 2.3, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify the four agents of evolutionary change other than natural selection
- Explain genetic drift, including the bottleneck and founder effects
- Describe gene flow and how it maintains genetic variance in a population
- Explain how each evolutionary force can influence the allele frequencies of a population

In addition to natural selection, there are four other agents of evolutionary change: mutation, genetic drift, gene flow, and non-random mating. These serve to either increase or decrease genetic variation in the population. Mutations are changes to an organism’s DNA and are an important driver of diversity in populations. Genetic drift is the impact on a population's genetic variance due to random chance events, such as natural disasters. Gene flow is the exchange of genetic information between populations and serves to keep disparate populations more similar to one another. Nonrandom mating describes the process of "choice" within reproduction based on perceived evolutionary fitness. Each of these additional agents is discussed below in concert with natural selection as none of these forces acts in isolation.

Four Additional Agents of Evolutionary Change

1. Mutation

Species ultimately evolve because of the accumulation of mutations that occur over time. The appearance of new mutations is the most common way to introduce novel genotypic and phenotypic variance (Figure 4.1.4.1). Without new mutations, genetic variance in a population would lessen over time in stable environmental conditions (stabilizing selection) leading populations to be less able to survive future changes. Mutations can only influence evolution if they are heritable (e.g. carried within the gametes).

Some mutations are unfavorable or harmful and are quickly eliminated from the population by natural selection as seen in Figure 4.1.4.2. Others are beneficial and will spread through the population. Whether or not a mutation is beneficial or harmful is determined by whether it helps an organism survive to sexual maturity and reproduce. Some mutations do not do anything and can linger, unaffected by natural selection, in the genome (e.g. in the somatic cells). Some can have a dramatic effect on a gene and the resulting phenotype.



Figure 4.1.4.1: A mutation has caused this garden moss rose to produce flowers of different colors. This mutation has introduced a new allele into the population that increases genetic variation and may be passed on to the next generation.

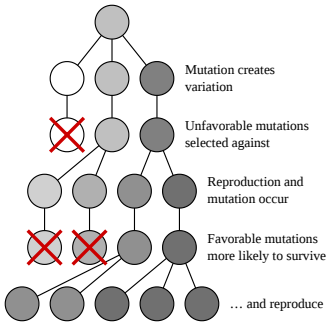
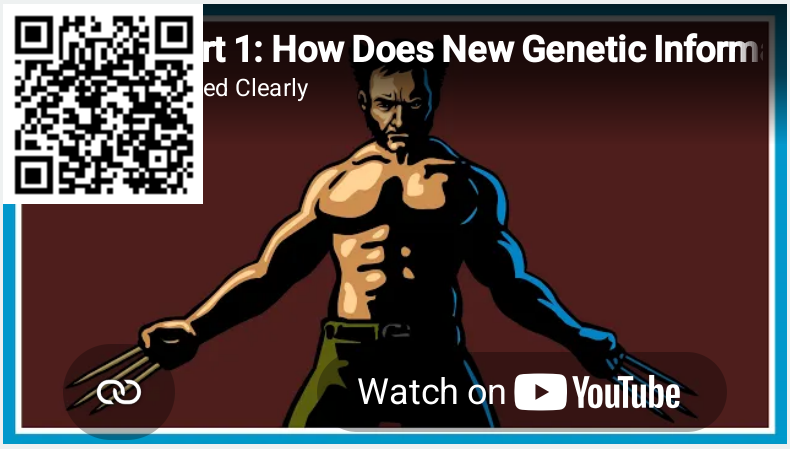


Figure 4.1.4.2: As mutations create variation, natural selection affects the frequency of that trait in a population. Mutations that confer a benefit (such as running faster or digesting food more efficiently) can help that organism survive and reproduce, carrying the mutation to the next generation.

Video



This 7-minute video provides an overview of DNA mutations and their impact on the proteins they encode and the phenotype of an organism.

Question after watching: If a mutation does not impact an organism's phenotype, and this mutation is found over time to increase in a population, does this constitute evolution? If so, what is the likely cause of this evolution?

2. Genetic Drift

Another way a population's allele and genotype frequencies can change is **genetic drift**, which is simply the effect of chance on the population's genetic variation. For example, some individuals will have more offspring than others—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).

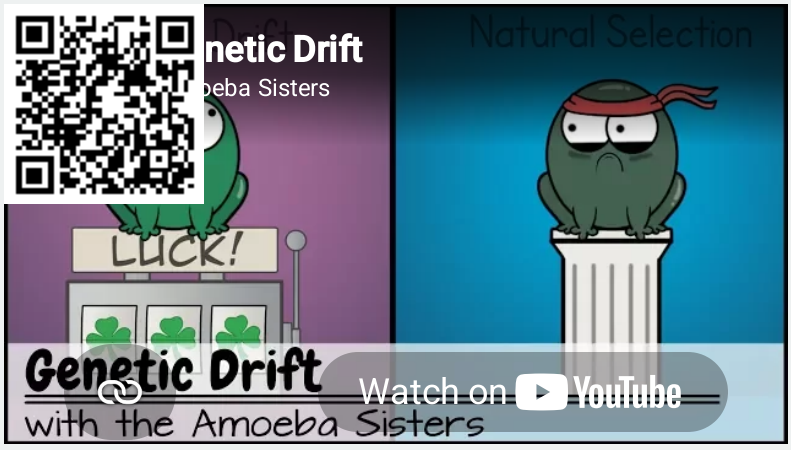
Genetic Drift vs. Natural Selection

Genetic drift is the opposite of natural selection. The theory of natural selection maintains that some individuals in a population have traits that enable them to survive and produce more offspring, while other individuals have traits that are detrimental and may cause them to die before reproducing. Over successive generations, these selection pressures can change the gene pool and the traits within the population. For example, a big, powerful male gorilla will mate with more females than a small, weak male and therefore more of his genes will be passed on to the next generation. His offspring may continue to dominate the troop and pass on their genes as well. Over time, the selection pressure will cause the allele frequencies in the gorilla population to shift toward large, strong males.

Unlike natural selection, genetic drift describes the effect of chance on populations in the absence of positive or negative selection pressure. Through random sampling or the survival or reproduction of a random sample of individuals within a population, allele frequencies within a population may change. Rather than a male gorilla producing more offspring because he is stronger, he may be the only male available when a female is ready to mate. His genes are passed on to future generations because of chance, not because he was the biggest or the strongest. Genetic drift is the shift of alleles within a population due to chance events that cause random samples of the population to reproduce or not.

Small populations are more susceptible to the forces of genetic drift. Large populations, on the other hand, are buffered against the effects of chance. If one individual of a population of 10 individuals happens to die at a young age before leaving 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 individual represents only 1 percent of the overall gene pool; therefore, genetic drift has much less impact on the larger population's genetic structure.

Video



This 4.5-minute video describes how genetic drift occurs by chance.
Question after watching: Describe a situation in which a population would undergo the bottleneck effect and explain what impact that would have on the population's genetic variance.

The Bottleneck Effect

Genetic drift can be magnified by natural events, such as a natural disaster that kills a large portion of the population at random. This **bottleneck effect** occurs when only a few individuals survive and reduce variation in the gene pool of a population (Figure

4.1.4.3). The genetic structure of the survivors becomes the genetic structure of the entire population, which may be very different from the pre-disaster population.

Captive breeding programs can fall victim to the bottleneck effect when species are at endangered or threatened levels. 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.

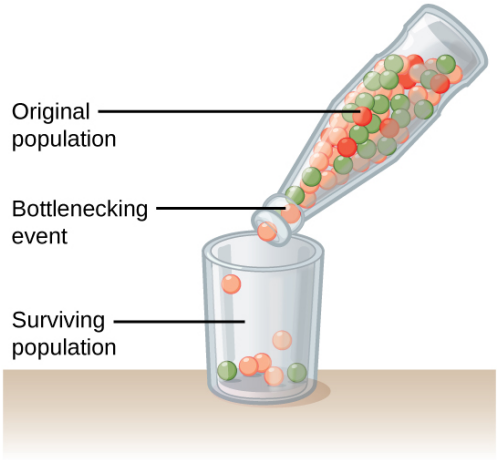


Figure 4.1.4.3: A chance event or catastrophe can reduce the genetic variability within a population.

The 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 population gets divided by a physical barrier of some kind (Figure 4.1.4.4). In this situation, it is improbable that those individuals are representative 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.

The founder effect is believed to have been 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 was 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.

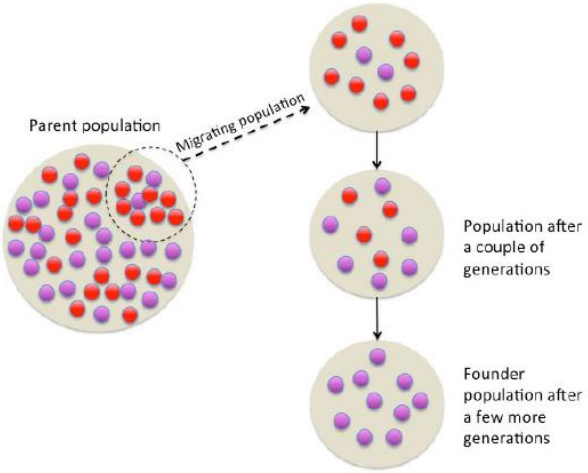
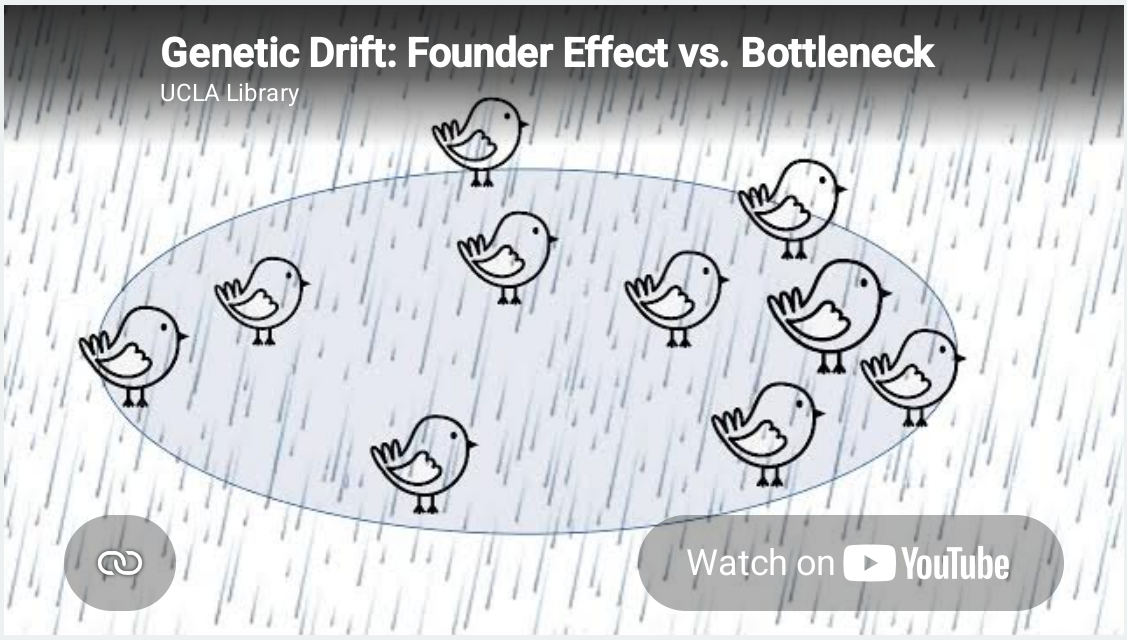
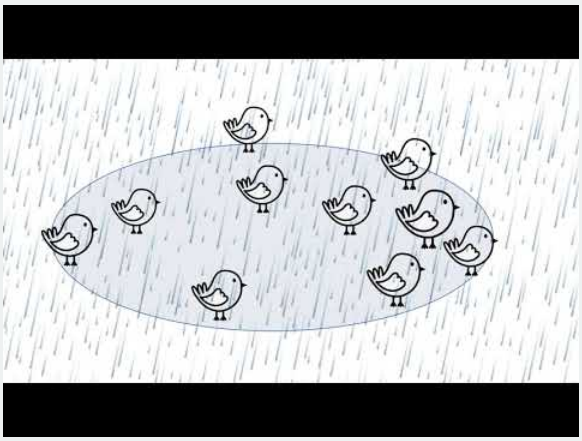


Figure 4.1.4.4: The founder effect occurs when a portion of the population (i.e. “founders”) separates from the old population to start a new population with different allele frequencies. (Tsaneda; CC-BY-SA 4.0)

Video





This 1-minute video differentiates the founder effect from a bottleneck event, which are similar but different. Question after watching: 50,000 years ago, a small group of people migrated out of Africa. Their descendants populated Asia, Europe, and the Americas. Which type of event is this: founder or bottleneck?

[Optional Activity] Scientific Method Connection: Testing the Bottleneck Effect

Question: How do natural disasters affect the genetic structure of a population?

Background: When much of a population is suddenly wiped out by an earthquake or hurricane, the individuals that survive the event are usually a random sampling of the original group. As a result, the genetic makeup of the population can change dramatically. This phenomenon is known as the bottleneck effect.

Hypothesis: Repeated natural disasters will yield different population genetic structures; therefore, each time this experiment is run, the results will vary.

Test the hypothesis: Count out an original parent population of 100 individuals using different colored beads. For example, red, blue, and yellow beads might represent red, blue, and yellow individuals. After recording the number of each individual in the original population, place them all in a bottle with a narrow neck that will only allow a few beads out at a time. Then, pour approximately 33 beads into a bowl. This represents the surviving individuals after a natural disaster kills a majority (67%) of the population. Count the number of the different colored beads in the bowl, and record it. Then, place all of the beads back in the bottle and repeat the experiment four more times.

Analyze the data: Compare the five populations that resulted from the experiment. Do the surviving populations all contain the same number of different colored beads or do they vary? Remember, these populations all came from the same exact parent population.

Form a conclusion: Most likely, the five resulting surviving populations will differ quite dramatically. This is because natural disasters are not selective—they kill and spare individuals at random. Now think about how this might affect a real population. What happens when a hurricane hits the Gulf Coast of the United States? How do the seabirds that live on the beach fare?

[Optional] Activity 4.1.4.1

Do you think genetic drift would happen more quickly on an island or on the mainland? Why?

Answer

Genetic drift is likely to occur more rapidly on an island where smaller populations are expected to occur.

3. 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 4.1.4.5). 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 gene structure of the population but can also introduce new genetic variation to populations in different geological locations and habitats.

Maintained gene flow between two populations can also lead to a combination of the two gene pools, reducing the genetic variation between the two groups. Gene flow strongly acts against speciation, by recombining the gene pools of the groups, thus repairing the developing differences in genetic variation that would have led to full speciation and creation of daughter species.

For example, if a species of grass grows on both sides of a highway, pollen is likely to be transported from one side to the other and vice versa. If this pollen is able to fertilize the plant where it ends up and produce viable offspring, then the alleles in the pollen have effectively linked the population on one side of the highway with the other.

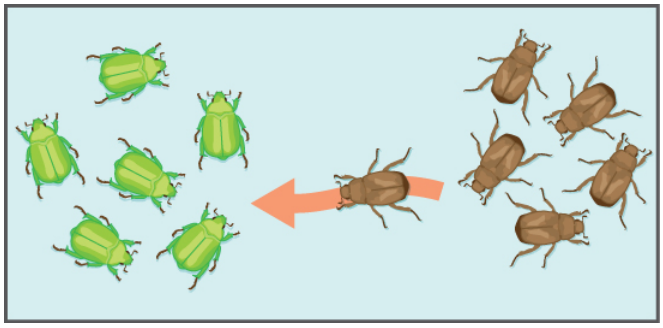


Figure 4.1.4.5: Gene flow can occur when an individual travels from one geographic location to another.

Video





This video takes the examples of the finches in the Galapagos islands and explains how the different sized beaks on each island resulted from the lack of gene flow between the population on each island.
Question after watching: Why does the narrator say that in time the different populations that stop having gene flow can become different species. What step needs to happen for this to occur?

4. Nonrandom Mating

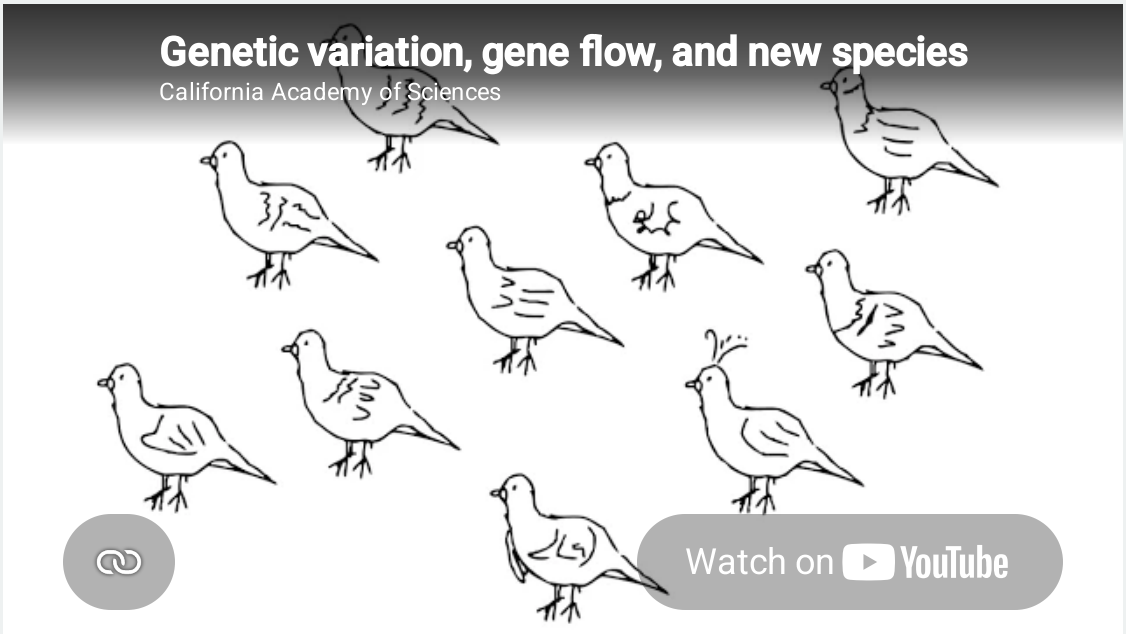
If individuals nonrandomly mate with their peers, the result can be a changing population. There are many reasons nonrandom mating occurs. One reason is simple mate choice; for example, female robins may prefer males with brighter, more orange breast feathers Figure 4.1.4.6. Traits that lead to more matings for an individual become selected for by natural selection.

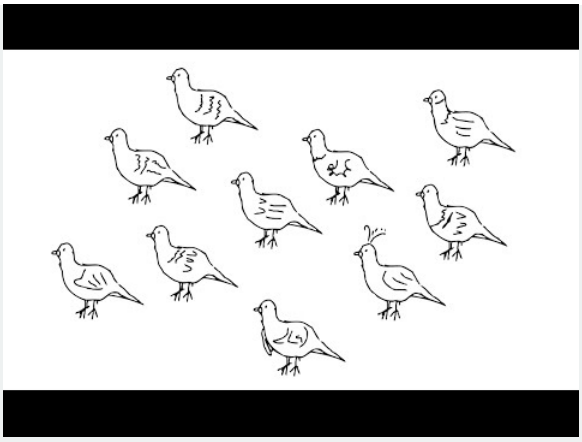
One common form of mate choice, called **assortative mating**, is an individual's preference to mate with partners who are phenotypically similar to themselves. Another cause of nonrandom mating is physical location. This is especially true in large populations spread over large geographic distances where not all individuals will have equal access to one another. Some might be miles apart through woods or over rough terrain, while others might live immediately nearby.



Figure 4.1.4.6: The American robin (*Turdus migratorius*) may practice assortative mating on plumage color, a melanin-based trait, and mate with other robins who have the most similar shade of color. However, there may also be some sexual selection for more vibrant plumage which indicates health and reproductive performance.

Video





This 12-minute video makes the connection between DNA, mutations, genetic reshuffling through sexual reproduction, and phenotypes/variability between individuals.

Question after watching: Imagine that the creation of the Panama canal re-opens a route between the two populations of fish presented in the video that had been separated by the landmass. What sort of evolutionary changes would need to happen in either population to lead to specialization?

This page titled 4.1.4: Additional Mechanisms of Evolution is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **19.2: Population Genetics** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

4.2: The Origin of Species

Learning Objectives

- Define species and describe how scientists identify species as different
- Describe genetic variables that lead to speciation
- Identify prezygotic and postzygotic reproductive barriers
- Explain allopatric and sympatric speciation
- Describe adaptive radiation
- Explain the two major theories on rates of speciation

4.2.1: Species Defined
4.2.2: Speciation
4.2.3: Rates of Speciation and Extinction

This page titled 4.2: The Origin of Species is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

4.2.1: Species Defined

Species Defined

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Confirm whether two organisms belong to the same species using the biological definition of species as a guide
- Explain how reproductive isolation can result in speciation

What is a Species?

A ***biological* species** is defined as a group of individuals that, in nature, are able to mate and produce viable, fertile offspring. There are other definitions of species but, according to the biological definition, one species is distinguished from another when, in nature, it is not possible for matings between individuals from each species to produce fertile, living offspring.

Members of the same species share both external and internal characteristics which develop from their DNA. The closer 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 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 4.2.1.1: Dogs of different breeds still have the ability to reproduce. The (a) poodle and (b) cocker spaniel can reproduce to produce a breed known as (c) the cockapoo.

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. 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)

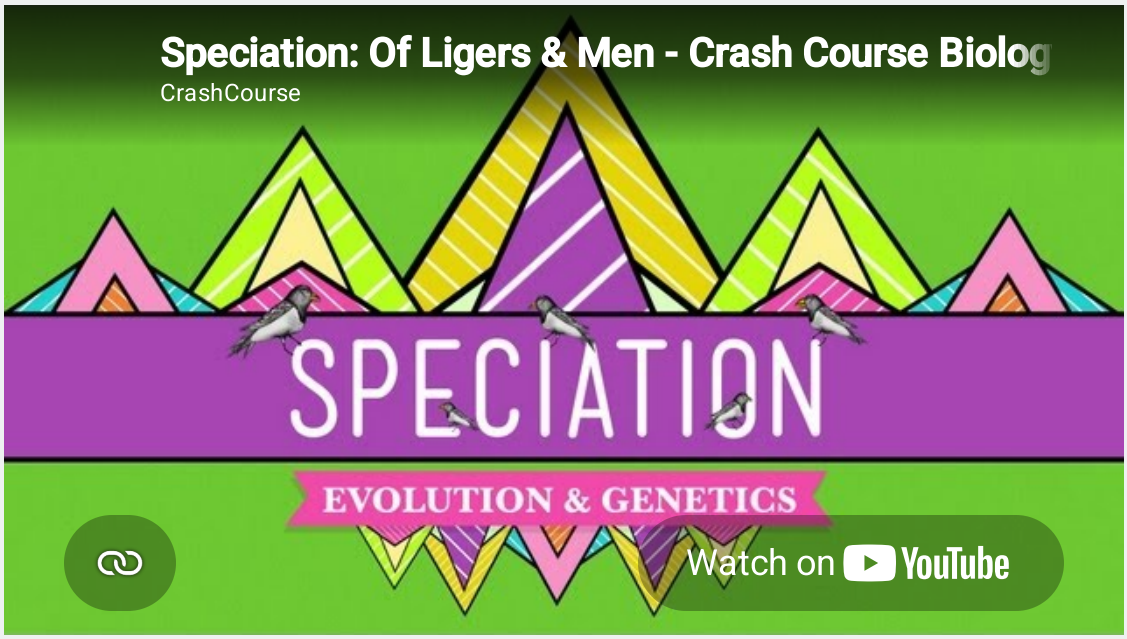
Figure 4.2.1.2: Species that appear similar may not be able to reproduce. The (a) African fish eagle is similar in appearance to the (b) bald eagle, but the two birds are members of different species.

Gene Pools

Populations of species share a **gene pool**: a collection of all the variants of genes in the species. The basis of any change in a group or population of organisms must be genetic; it is the only way to share and pass on traits. Variations within a species can only be passed to the next generation via asexual reproduction or sexual reproduction. Changes will be passed on asexually if the reproducing cell already possesses the changed trait and the offspring will be a genetic copy of the parent.

In sexual reproduction, unlike sexual reproduction, only the changed traits in gametes can be passed down to offspring. In other words, sexually-reproducing organisms can experience genetic changes in their body, or somatic, cells but if these changes do not also occur in a gamete, the changed trait will not appear in the next generation from the parents. Only heritable traits can evolve. Therefore, reproduction plays a large role for genetic changes to take root in a population or species. In summary, organisms must be able to reproduce with each other to pass new traits to offspring.

Video





In this 10.5-minute video explains the concepts of species and speciation.
Questions after watching: There is a colony of green aphids on a tomato plant. On the tomato plant that is next to the first one, there are red aphids. The two colonies started from a third one, that was green, on another nearby plant. The green and the red aphids are distinct species because the green aphids are attracted to green counterparts; and red ones only have interest in other red ones. Which does this example represent: Allopatric or sympatric speciation? Pre-zygotic and post-zygotic speciation?

Reproductive Isolation

Reproductive isolation, through mechanical, behavioral, and physiological barriers, is an important component of speciation. Given enough time, the genetic and phenotypic divergence between populations will affect characters that influence reproduction. In other words, if individuals of the two populations were to be brought together, mating would be improbable, but if mating did occur, offspring would be non-viable or infertile. Many factors may influence this process known as **reproductive isolation**. Reproductive isolation is the inability of two populations to interbreed with one another.

There are two different types of barriers that prevent the members of two different species from mating, to producing offspring, or having fertile offspring: prezygotic barriers and postzygotic barriers. Recall that 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 do not survive the embryonic stage and those that are born sterile.

? Optional Activity 4.2.1.1

Which condition is the basis for a species to be reproductively isolated from others?

a. It does not share its habitat with related species.
b. It does not exist outside of a single habitat.
c. It does not exchange genetic information with other species.
d. It does not undergo evolutionary changes for a significant amount of time.

Answer

c. It does not exchange genetic information with other species.

Prezygotic Barriers

There are several different types of prezygotic barriers, including temporal, habitat, behavioral, gametic, and mechanical. Some of these prezygotic barriers prevent reproduction entirely. Many organisms only reproduce at certain times of the year, often just annually.

Temporal isolation

Differences in breeding schedules, called **temporal isolation**, can act as a form of reproductive isolation. For example, two species of frogs inhabit the same area, but one reproduces from January to March, whereas the other reproduces from March to May.



(a) (b)

Figure 4.2.1.3: These two related frog species exhibit temporal reproductive isolation. (a) Rana aurora breeds earlier in the year than (b) Rana boylii.

Habitat Isolation

In some cases, populations of a species move to a new habitat and take up residence in a place that no longer overlaps with other populations of the same species; this is called **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, the forces of natural selection, mutation, and genetic drift will likely result in the divergence of the two groups.

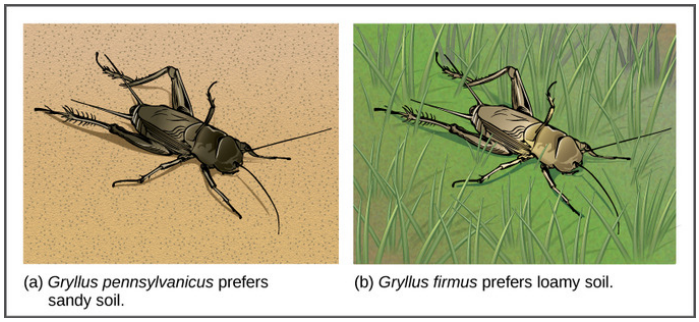


Figure 4.2.1.4: Speciation can occur when two populations occupy different habitats. The habitats need not be far apart. The cricket (a) *Gryllus pennsylvanicus* prefers sandy soil, while the cricket (b) *Gryllus firmus* prefers loamy soil. The two species can live in close proximity, but because of their different soil preferences, they became genetically isolated.

Behavioral Isolation

Behavioral isolation occurs when the presence or absence of a specific behavior prevents reproduction from taking place. For example, male fireflies use specific light patterns to attract females. Various species 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.

Gametic and Mechanical Barriers

Other prezygotic barriers work when differences in their gamete cells 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 (**mechanical barrier**). For example, damselfly males of different species have differently-shaped reproductive organs.

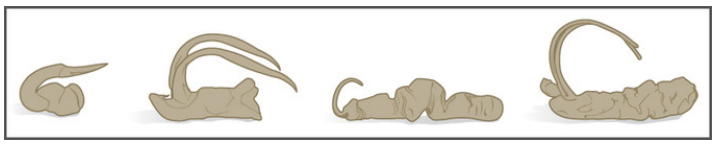


Figure 4.2.1.5: The shape of the male reproductive organ varies among male damselfly species and is only compatible with the female of that species. Reproductive organ incompatibility keeps the species reproductively isolated.

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 in length and diameter, which prevents the plant from

being cross-pollinated with a different species.



(a) Honeybee drinking nectar from a foxglove flower

(b) Ruby-throated hummingbird drinking nectar from a trumpet creeper flower

Figure 4.2.1.6: 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.

Postzygotic Barriers

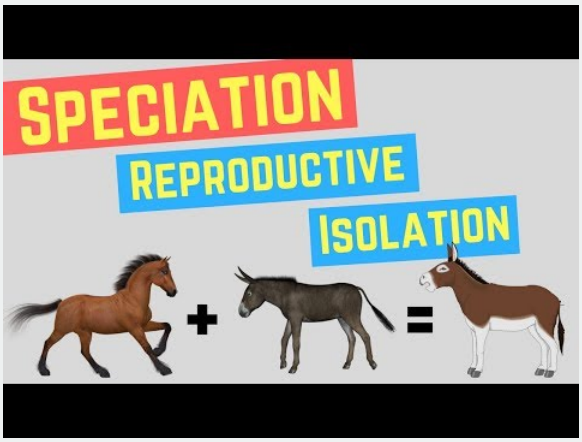
There are different types of postzygotic barriers as well, including hybrid inviability and hybrid sterility. When fertilization takes place and a zygote forms, postzygotic barriers can prevent reproduction.

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**.

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**.

Video





This 3-minute video provides an overview of pre-zygotic and post-zygotic barriers to reproduction, which lead to speciation.

Question after watching: In most cases, which do you hypothesize arises first: pre-zygotic or post-zygotic barriers? Why?

Optional Activity 4.2.1.2

Which situation is not an example of a prezygotic barrier?

a. Two species of turtles breed at different times of year.
b. Two species of flowers attract different pollinators.
c. Two species of birds display different mating dances.
d. Two species of insects produce infertile offspring.

Answer

d. Two species of insects produce infertile offspring.

This page titled 4.2.1: Species Defined is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.2: Formation of New Species** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.

4.2.2: Speciation

Learning Objectives

- Define speciation and discuss the ways in which it may occur
- Give examples of allopatric speciation
- Give examples of sympatric speciation
- Discuss how the fitness of a hybrid will lead to changes in the hybrid zone over time

Speciation Defined

A biological species is a group of potentially interbreeding individuals that produce viable, fertile offspring. For the majority of sexually-reproducing species, this holds true. However, there are exceptions to this rule. Some species are similar enough that hybrid offspring are possible and may occur. The presence of hybrids in nature between similar species suggests that they may have descended from a single interbreeding species and that **speciation**, a process where a single species branches to form two or more new species, may not yet be complete.

There are mechanisms for speciation. Darwin envisioned this process as a branching event. The modern diagram shows that as one species changes over time, it branches repeatedly to form more than one new species as long as the population survives or until the organism becomes extinct.

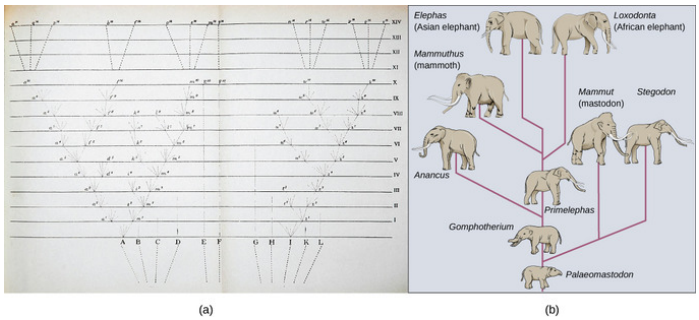


Figure 4.2.2.1: The only illustration in Darwin's On the Origin of Species is (a) a diagram showing speciation events leading to biological diversity. The diagram shows similarities to phylogenetic charts that are drawn today to illustrate the relationships of species. (b) Modern elephants evolved from 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. 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 and sympatric speciation. **Allopatric speciation** (allo- = "other"; -patric = "homeland") involves 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 typically think of speciation events as the splitting of one ancestral species into two descendant species. There is no reason why there might not be more than two species formed at one time except that it is less likely; multiple events can be conceptualized as single splits occurring close in time.

Allopatric Speciation

A geographically-continuous population has a gene pool that is relatively homogeneous. Gene flow, the movement of alleles across the range of the species, is relatively free because individuals can move and then mate with individuals in their new location. Thus, the frequency of an allele at one end of the range will be similar to the frequency of the allele at the other end.

Allopatric speciation occurs when a single species becomes geographically separated from a natural or human barrier, into two or more populations. Each population evolves new and distinctive traits since gene flow is prevented. If the populations are separated for a long enough period of time, the two populations evolve along different trajectories. New alleles arise by mutation and allele

frequencies gradually become different in the two populations. Typically, environmental pressures, such as climate, resources, predators, and competitors for each population will differ causing natural selection to select for different adaptations in each group.

Geographic separation of populations can occur in a variety of ways: a river forming a new branch, erosion forming a new valley, a landslide cutting off a mountain pass, or seeds floating over the ocean to an island. The nature of the geographic separation necessary to isolate populations depends on the biology of the organism 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 two rodent populations became divided by the formation of a new lake, continued gene flow would be improbable and speciation would occur.

Scientists have documented numerous cases of allopatric speciation. For example, along the west coast of the United States, two separate sub-species of spotted owls exist. The northern spotted owl has genetic and phenotypic differences from its close relative, the Mexican spotted owl, which lives in the south. They have been separated by the emergence of mountain ranges and deserts. Additionally, scientists have found that the further the spatial distance between two groups that once were the same species, the more probable it is that speciation will occur. This seems logical because as the distance increases, the various environmental factors would generally have less in common than locations in close proximity. Consider the two owls: in the north, the climate is cooler than in the south causing the types of prey organisms in each ecosystem to differ. Also, the hunting habits and locations of each would vary. These variances can lead to evolved differences in the owls, resulting in speciation.



Figure 4.2.2.2: 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.

Isolated Evolutionary Change

In isolation, changes in the gene pool can occur through some combination of natural selection and genetic drift (the bottleneck or founder effects). These factors may produce distinct subpopulations on the different islands. So long as they remain separate (allopatric) we consider them **subspecies**. In fact, they might not be able to interbreed with other subspecies but so long as we do not have evidence, we assume that they can.

How much genetic change is needed to create a new species? Perhaps not as much as you might think. Changes at one or just a few gene loci might cause speciation. For example, a single mutation altering flower color or petal shape could immediately prevent cross-pollination between the new and the parental types.

Adaptive Radiation

In some cases, a population of one species disperses throughout an area with each finding 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. This is called **adaptive radiation** because many adaptations evolve from a single point of origin, 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, called the founder species, numerous species have evolved. The 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 birds have 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.

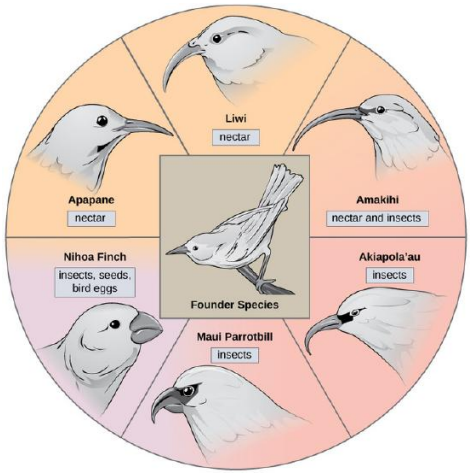


Figure 4.2.2.3: The honeycreeper birds illustrate adaptive radiation. From one original species of bird, multiple others evolved, each with its own distinctive characteristics.

? Optional Activity 4.2.2.1

Which situation would most likely lead to allopatric speciation?

a. A flood causes the formation of a new lake.
b. A storm causes several large trees to fall down.
c. A mutation causes a new trait to develop.
d. An injury causes an organism to seek out a new food source.

Answer

a. A flood causes the formation of a new lake.

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. The process of speciation within the same space is called sympatric speciation. Sympatric speciation occurs when two individual populations diverge from an ancestral species without being separated geographically.

One form of sympatric speciation can begin with a large chromosomal aberration 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 called **aneuploidy**.

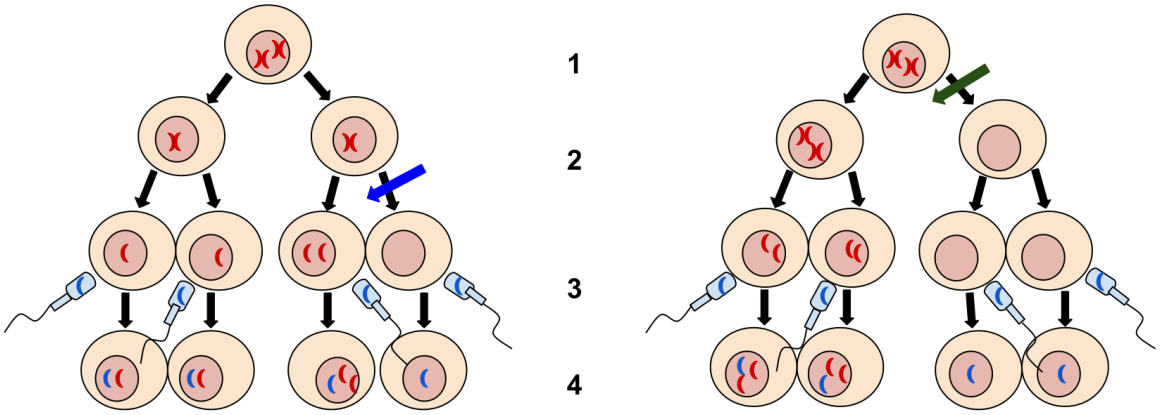


Figure 4.2.2.4: Aneuploidy results when the gametes have too many or too few chromosomes due to nondisjunction during meiosis. In the example shown here, the resulting offspring will have 2n+1 or 2n-1 chromosomes (Tweety207; CC-BY-SA 3.0)

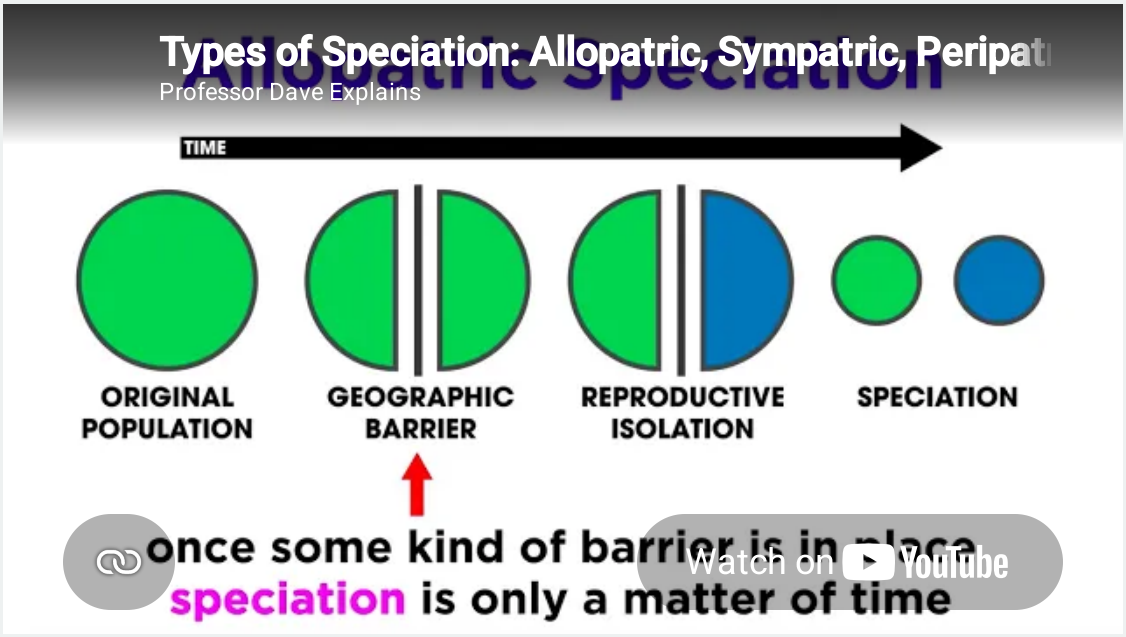
Most organisms without enough chromosomes (2n-1) will not develop. However, **polyploidy** is a condition in which a cell or organism has an extra set, or sets, of chromosomes (2n+1) and some of these organisms can develop and survive. Although polyploidy occurs occasionally in animals, it takes place most commonly in plants. The cultivated forms of wheat, cotton, and tobacco plants are all polyploids. Animals with any of the types of chromosomal aberrations described above are unlikely to survive and produce normal offspring. Scientists have discovered more than half of all plant species studied relate back to an ancestral species 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.

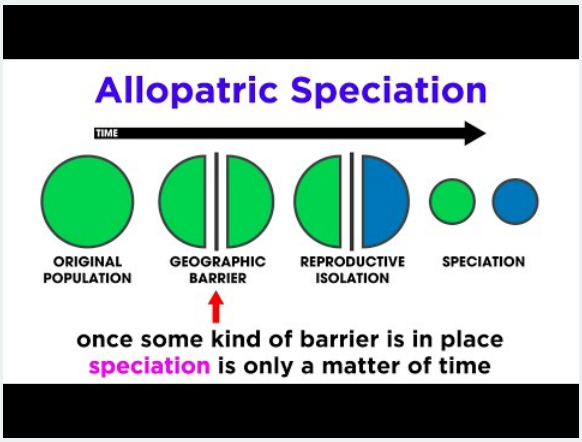
Reunion

The question of two populations' status - subspecies or true new species - is resolved if the two ever come to occupy the same territory again (become sympatric). If successful interbreeding occurs, the differences will gradually disappear, and a single population will be formed again. Speciation will not have occurred. If, on the other hand, two subspecies reunite but fail to resume breeding, speciation has occurred and they have become separate species.

The medium tree finch *Camarhynchus pauper* is found only on Floreana Island in the Galapagos. Its close relative, the large tree finch, *Camarhynchus psittacula*, is found on all the central islands of the Galapagos including Floreana. Were it not for its presence on Floreana, both forms would be considered subspecies of the same species. Because they do coexist and maintain their separate identity on Floreana, we know that speciation has occurred.

Video





Allopatric, sympatric, and parapatric speciation are all summarized in this 7-minute video.

Question after watching:

Why do island chains provide ideal conditions for adaptive radiation to occur?

Continued Isolating Mechanisms

What might keep two subpopulations from interbreeding when reunited geographically? There are several mechanisms.

Prezygotic isolating mechanisms act before fertilization occurs. On Floreana, *Camarhynchus psittacula* has a longer beak than *Camarhynchus pauper*, and the research teams led by Peter and Rosemary Grant have demonstrated that beak size is an important criterion by which Darwin's finches choose their mates. Two subpopulations may occupy different habitats in the same area and thus fail to meet at breeding time. In plants, a shift in the time of flowering can prevent pollination between the two subpopulations. Structural differences in the sex organs may become an isolating mechanism. The sperm may fail to reach or fuse with the egg.

Postzygotic isolating mechanisms act even if fertilization does occur. Even if a zygote is formed, genetic differences may have become so great that the resulting hybrids are less viable or less fertile than the parental types. The sterile mule produced by mating a horse with a donkey is an example. Sterility in the males produced by hybridization is more common than in females. In fact, it is the most common postzygotic isolating mechanism. When *Drosophila melanogaster* attempts to mate with its relative *Drosophila simulans*, no viable males are even produced. Mutations in a single gene are responsible.

Speciation by Hybridization

Speciation occurs over a span of evolutionary time. Over time, two species may further diverge or reconnect, depending on the fitness strength and the reproductive barriers of the hybrids. When a new species arises, there is a transition period during which the closely-related species continue to interact.

After speciation, two species may recombine or even continue interacting indefinitely. Individual organisms will mate with any nearby individual with which they are capable of breeding. An area where two closely-related species continue to interact and reproduce, forming hybrids, is called a **hybrid zone**. Over time, the hybrid zone may change depending on the fitness strength and the reproductive barriers of the hybrids.

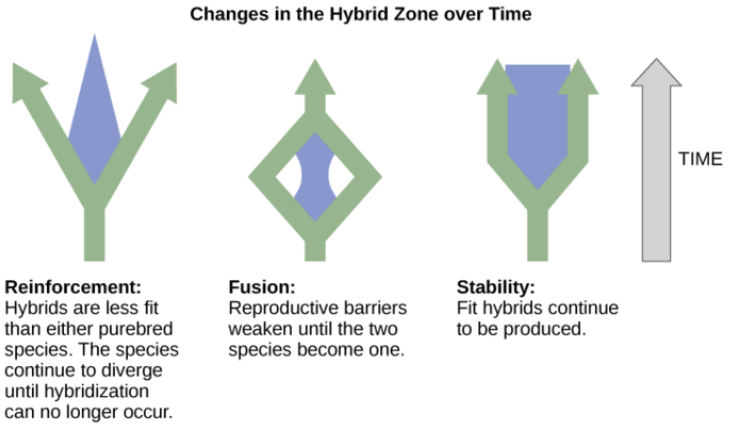


Figure 4.2.2.7: After speciation has occurred, the two separate-but-closely-related species (green lines) may continue to produce offspring in an area called the hybrid zone (blue area). The thicker the blue line, the more hybridization occurs between the two species.

Reinforcement

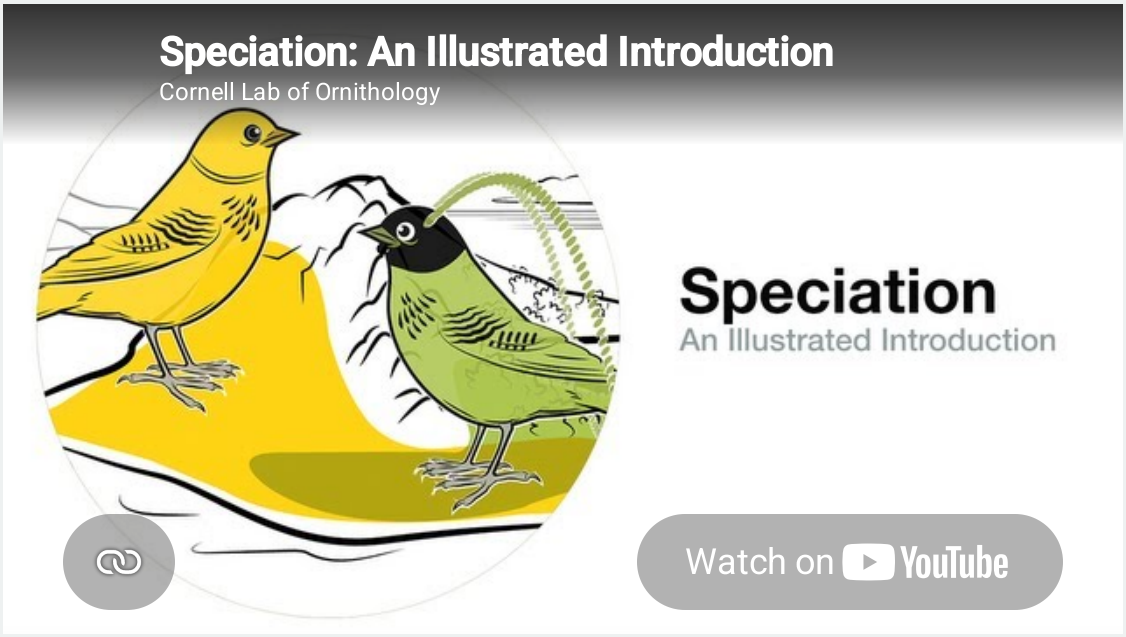
When two species that have separated in allopatry become reunited, their prezygotic and postzygotic isolating mechanisms may become more stringent than those between the same species existing apart from each other. This phenomenon is called **reinforcement**. It arises from natural selection working to favor individuals that avoid interspecific matings, which would produce less-fit hybrids, when the two species are first reunited.

ybrids can have less fitness, more fitness, or about the same fitness level as their purebred parents. Usually, hybrids tend to be less fit; therefore, reproduction to produce hybrids will diminish over time, which nudges the two species to diverge further. This term is used because the low success of the hybrids reinforces the original speciation. If the hybrids are less fit than the parents, reinforcement of speciation occurs, and the species will continue to diverge until they can no longer mate and produce viable offspring.

If the hybrids are as fit or more fit than the parents, or the reproductive barriers weaken, the two species may fuse back into one species. For a hybrid form to persist, it will generally have to be able to exploit the available resources better than either parent species, with which, in most cases, it will have to compete.

Over time, the hybrids themselves can become separate species. Reproductive isolation between hybrids and their parents was once thought to be particularly difficult to achieve; thus, hybrid species were thought to be extremely rare. With DNA analysis becoming more accessible in the 1990s, hybrid speciation has been shown to be a fairly common phenomenon, particularly in plants.

Video





This 8.5-minute animated video explains how species are crated using a fictional bird species that lands on a volcanic island (which mirrors what happened on the Galapagos Islands).

Question after watching:

Given what you have learned about the process of speciation, why do humans not have any sister species? Propose a hypothesis…

This page titled 4.2.2: Speciation is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.2: Speciation** by John W. Kimball is licensed CC BY 3.0. Original source: https://www.biology-pages.info/.

4.2.3: Rates of Speciation and Extinction

Learning Objectives

- Explain how the interaction of an organism's population size in association with environmental changes can lead to different rates of speciation

Varying Rates of Speciation

Scientists around the world study speciation, documenting observations both of living organisms and those found in the fossil record. As their ideas take shape and as research reveals new details about how life evolves, they develop models to help explain rates of speciation. In terms of how quickly speciation occurs, two patterns are currently observed: the gradual speciation model and the punctuated equilibrium model.

In the **gradual speciation** model, species diverge gradually over time in small steps. In the **punctuated equilibrium** model, a new species changes quickly from the parent species and then remains largely unchanged for long periods of time afterward. This early change model is called punctuated equilibrium, because it begins with a punctuated or periodic change and then remains in balance afterward. While punctuated equilibrium suggests a faster tempo, it does not necessarily exclude gradualism.

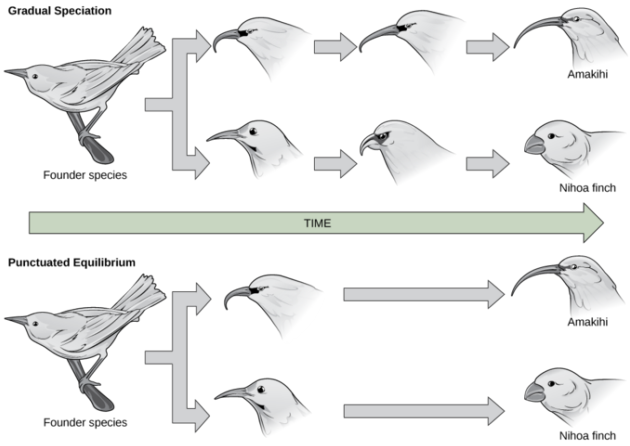


Figure 4.2.3.1: In (a) gradual speciation, species diverge at a slow, steady pace as traits change incrementally. In (b) punctuated equilibrium, species diverge quickly and then remain unchanged for long periods of time.

The primary influencing factor on changes in speciation rate is environmental conditions. Under some conditions, selection occurs quickly or radically. Consider a species of snails that had been living with the same basic form for many thousands of years. Their fossils would appear similar for a long time. When a change in the environment takes place, such as a drop in the water level, a small number of organisms are separated from the rest in a brief period of time, essentially forming one large and one tiny population. The tiny population faces new environmental conditions. Because its gene pool quickly became so small, any variation that aids in surviving the new conditions becomes the predominant form. More on speciation (and extinction) is discussed in Unit 3.3.1.

Optional Activity 4.2.3.1

Which of the following statements is false?

a. Punctuated equilibrium is most likely to occur in a small population that experiences a rapid change in its environment.
b. Punctuated equilibrium is most likely to occur in a large population that lives in a stable climate.
c. Gradual speciation is most likely to occur in species that live in a stable climate.
d. Gradual speciation and punctuated equilibrium both result in the divergence of species.

Answer

B. Punctuated equilibrium is most likely to occur in a large population that lives in a stable climate.

This page titled 4.2.3: Rates of Speciation and Extinction is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

4.3: Genes Within Populations

4.3.1: Evolution of Genomes

4.3.2: Evolution in Populations

This page titled 4.3: Genes Within Populations is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

4.3.1: Evolution of Genomes

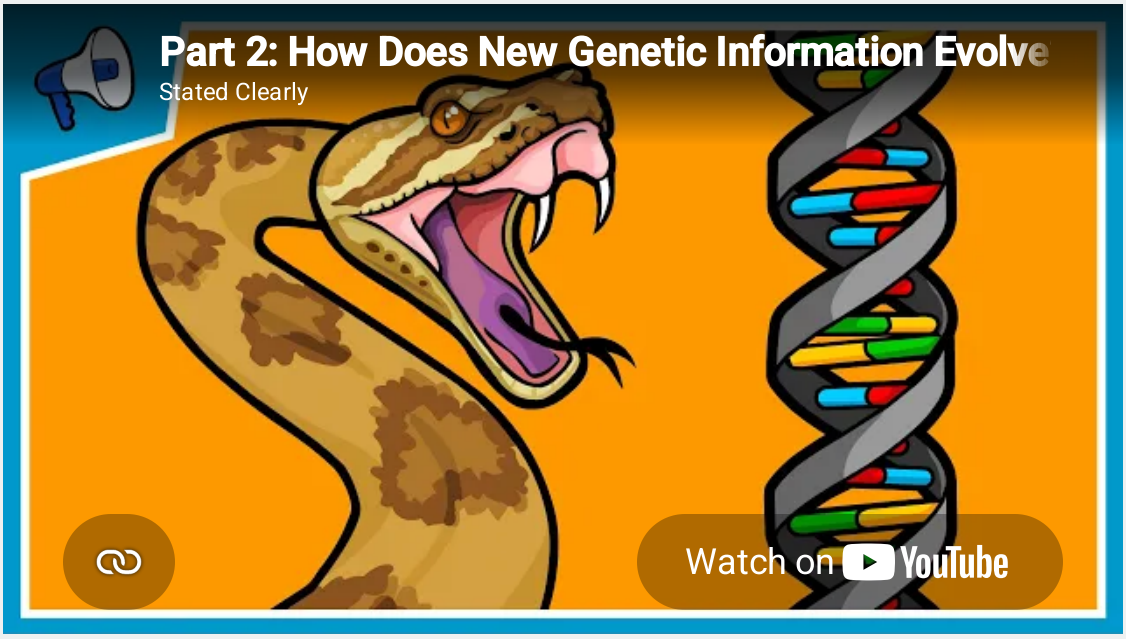
The Evolution of Genomes

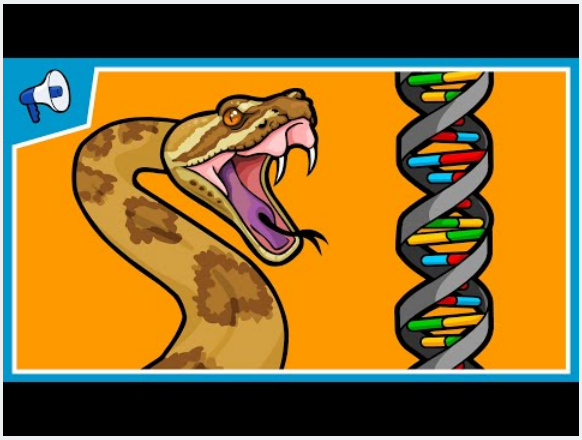
- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify how variations in the size and number of genes in different species can impact evolution;
- Explain the importance of genomic changes in an evolutionary context;
- Recognize the evolutionary implications of observed genome similarities between distant species.

Video





This 9-minute video provides an overview of how the genes and genome of a species can change over time to lead to different species.

Questions after watching: How can a gene duplication event fuel evolution? Can you think of another example where something was duplicated and then repurposed by evolution?

Genetic Diversity

Genetic variation is essential for a species to evolve in response to environmental change, including any variation in nucleotides, genes, chromosomes, or genomes of organisms. Each of these levels of genetic diversity adds to the capacity of a population to evolve.

Variations in Number of Genes

DNA is contained in the chromosomes present within the cell; some chromosomes are contained within specific organelles in the cell (for example, the chromosomes of mitochondria and chloroplast). A gene is a discrete section of a chromosome that codes for one or more proteins. Each gene is a hereditary section of DNA that occupies a specific place on the chromosome and controls a particular characteristic of an organism. Genetic diversity at its most elementary level is represented by differences in the sequence of nucleotides (with one of the following bases: adenine, cytosine, guanine) that form DNA (deoxyribonucleic acid) within the cells of the organism. During sexual reproduction, offspring inherit alleles from both parents. These inherited alleles might be slightly different, especially if there has been migration or hybridization of organisms. Also, when the offspring's chromosomes are copied after fertilization, genes can be exchanged in a process called sexual recombination. Helpful or silent mutations and sexual recombination may allow the evolution of new characteristics.

Sometimes whole genes are duplicated, or deleted. This results in an organism having more or fewer copies of that gene than others. The effect on the phenotype may be to increase or decrease the gene product's function (e.g., if the gene encoded a protein that makes pigment, and now the organism has two genes encoding pigment, the organism may now be twice as pigmented as its parents with only one copy of the gene). Natural selection may then select for or against organisms with this altered number of gene copies.

Sometimes there is no immediate effect of the gene duplication on phenotype. The additional copy of the gene may accumulate mutations without deleterious effects on the organism. These mutations will likely modify the gene product's function if it is transcribed. In doing this, the gene may acquire slightly different abilities, such as the factor X blood clotting example the video above.

Mutation Rates

Mutation rates differ between species and even between different regions of the genome of a single species. Spontaneous mutations often occur which can cause various changes in the genome. Mutations can result in the addition or deletion of one or more nucleotide bases. A change in the code can result in a frameshift mutation which causes the entire code to be read in the wrong order and thus often results in a protein becoming non-functional. A mutation in a promoter region, enhancer region or a region coding for transcription factors can also result in either a loss of function or and upregulation or downregulation in transcription of that gene. Mutations are constantly occurring in an organism's genome and can cause either a negative effect, positive effect or no effect at all.

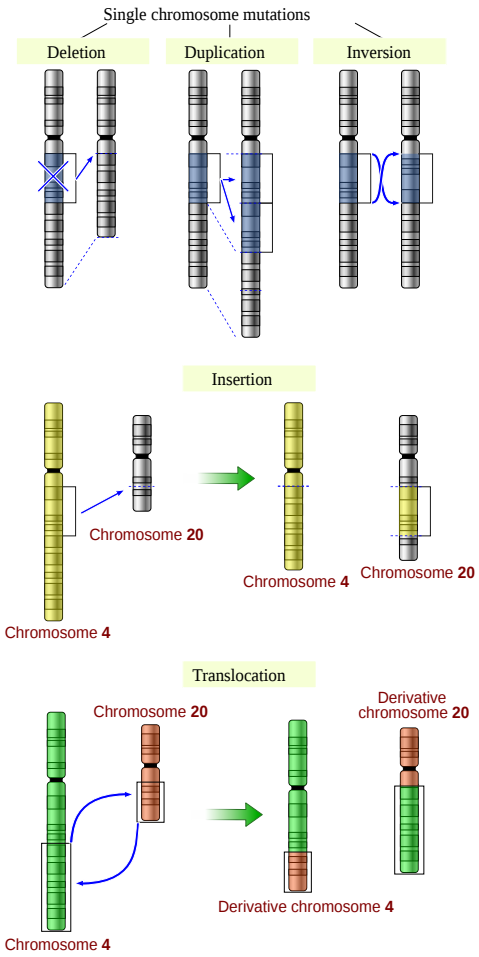


Figure 4.3.1.1: Chromosomal Mutations: Chromosomal mutations over time can accumulate and promote diversity and evolution if a produced trait is favorable.

Transposable Elements

Transposable elements are regions of DNA that can be inserted into the genetic code through one of two mechanisms. These mechanisms work similarly to “cut-and-paste” and “copy-and-paste” functionalities in word processing programs. The “cut-and-paste” mechanism works by excising DNA from one place in the genome and inserting itself into another location in the code. The “copy-and-paste” mechanism works by making a genetic copy or copies of a specific region of DNA and inserting these copies elsewhere in the code. The most common transposable element in the human genome is the Alu sequence, which is present in the genome over one million times.

Pseudogenes

Often a result of spontaneous mutation, pseudogenes are dysfunctional genes derived from previously functional gene relatives. There are many mechanisms by which a functional gene can become a pseudogene including the deletion or insertion of one or multiple nucleotides. This can result in a shift of reading frame, causing the gene to longer code for the expected protein, a premature stop codon or a mutation in the promoter region. Often cited examples of pseudogenes within the human genome include the once functional olfactory gene families. Over time, many olfactory genes in the human genome became pseudogenes and were no longer able to produce functional proteins, explaining the poor sense of smell humans possess in comparison to their mammalian relatives.

Exon Shuffling

Exon shuffling is a mechanism by which new genes are created. This can occur when two or more exons from different genes are combined together or when exons are duplicated. Exon shuffling results in new genes by altering the current intron-exon structure. This can occur by any of the following processes: transposon mediated shuffling, sexual recombination or illegitimate

recombination. Exon shuffling may introduce new genes into the genome that can be either selected against and deleted or selectively favored and conserved.

Genome Reduction and Gene Loss

Many species exhibit genome reduction when subsets of their genes are not needed anymore. This typically happens when organisms adapt to a parasitic life style, e.g. when their nutrients are supplied by a host. As a consequence, they lose the genes need to produce these nutrients. In many cases, there are both free living and parasitic species that can be compared and their lost genes identified. Good examples are the genomes of Mycobacterium tuberculosis and Mycobacterium leprae, the latter of which has a dramatically reduced genome. Another beautiful example are endosymbiont species. For instance, Polynucleobacter necessarius was first described as a cytoplasmic endosymbiont of the ciliate Euplotes aediculatus. The latter species dies soon after being cured of the endosymbiont. In the few cases in which P. necessarius is not present, a different and rarer bacterium apparently supplies the same function. No attempt to grow symbiotic P. necessarius outside their hosts has yet been successful, strongly suggesting that the relationship is obligate for both partners. Yet, closely related free-living relatives of P. necessarius have been identified. The endosymbionts have a significantly reduced genome when compared to their free-living relatives (1.56 Mbp vs. 2.16 Mbp).

Variations in Number of Chromosomes

Many organisms are diploid, having two sets of chromosomes, and therefore two copies (called alleles) of each gene. However, some organisms can be haploid, triploid, or tetraploid (having one, three, or four sets of chromosomes respectively). Within any single organism, there may be variation between the two (or more) alleles for each gene. This variation is introduced either through mutation of one of the alleles or as a result of recombination during sexual reproduction.

During replication events, there can be mutations that involve whole chromosomes or whole chunks of chromosomes. Some mutations duplicate a whole chromosome (a whole stretch of DNA with many genes); some may delete a large portion. Some rearrange chromosomes, keeping all of the DNA information but putting it in different places in the genome. It turns out that in some instances, the location matters because it contains sites that initiate and control transcription. In bacteria, this can matter because one transcription factor can control the transcription of many genes in a row.

Changes in chromosome number or structure can affect many genes at the same time. Like changes in individual genes, this can result in some immediate effects because of the change in the number of genes producing the gene products (proteins). Or there can be little to no immediate effect, but the extra copy gives rise to “spare copies” that are free to mutate and acquire new abilities and functions.

Variation in Genome Size

A **genome** is the total genetic information of a cell or organism. The evolution of the genome is characterized by the accumulation of changes. Analysis of genomes and their changes in sequence or size over time involves various fields.

Genome size is usually measured in base pairs (or bases in single-stranded DNA or RNA). Different species can have different numbers of genes within the entire DNA or genome of the organism. Gene number is the main factor influencing the size of the prokaryotic genome. However, a greater total number of genes might not correspond with greater complexity in the phenotype (behavior, structure, or function) of eukaryotes.

For example, the predicted size of the human genome is not much larger than the genomes of some invertebrates and is far smaller than some species of ferns. However, in humans, more proteins are encoded *per gene* than in other species. In eukaryotic organisms, this is an observed paradox: the number of genes that make up the genome does not correlate with genome size. In other words, the genome size is much larger than would be expected given the total number of protein-coding genes.

Larger amounts of genetic information may allow for more variation in the overall genome, conferring additional adaptability to environmental change. It may also play a role in speciation. On the other hand, longer genomes take more energy and time to duplicate, so there is an evolutionary trade-off.

Genomic Similarities Between Distant Species

Genetic distance refers to the genetic divergence between species or between populations within a species. Smaller genetic distances indicate that the populations have more similar genes, which indicates they are closely related; they have a recent

common ancestor, or recent interbreeding has taken place. Genetic distance is useful in reconstructing the history of populations. For example, evidence from genetic distance suggests that humans arrived in America about 30,000 years ago. By examining the difference between allele frequencies between the populations, genetic distance can estimate how long ago the two populations were together.

Phylogenetic Relationships

Phylogeny describes the relationships of an organism, such as the relationship with its ancestors and the species it is most closely related. Phylogenetic relationships provide information on shared ancestry but not necessarily on how organisms are similar or different. The use of advanced genomic analysis has allowed us to establish phylogenetic trees, which map the relationship between species at a genetic and molecular level. The ability to use these technologies has established previously unknown relationships and has contributed to a more complex evolutionary history. These technologies have established genomic similarities between distant species by establishing genetic distances. In addition, the mechanisms by which genomic similarities between distant species occur can include horizontal gene transfer.

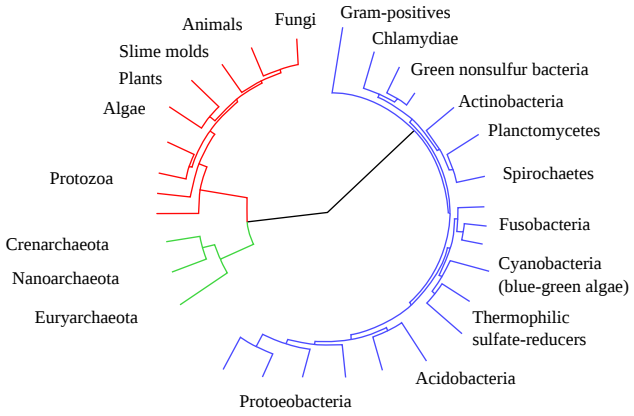


Figure 4.3.1.1: Tree of Life: Diagrammatic representation of the divergence of modern taxonomic groups from their common ancestor. This shows the genomic similarities that can exist between distant species based on their relationship with this ancestor.

Horizontal Gene Transfer

Horizontal gene transfer (HGT), also known as lateral gene transfer, is the transfer of genes between unrelated species. Genes have been shown to be passed between species which are only distantly related using standard phylogeny, thus adding a layer of complexity to the understanding of phylogenetic relationships. The various ways that HGT occurs in prokaryotes is important to understanding phylogenies. Although at present, HGT is not viewed as important to eukaryotic evolution, HGT does occur in this domain as well. Finally, as an example of the ultimate gene transfer, theories of genome fusion between symbiotic or endosymbiotic organisms have been proposed to explain an event of great importance—the evolution of the first eukaryotic cell, without which humans could not have come into existence.

The mechanism of HGT has been shown to be quite common in the prokaryotic domains of Bacteria and Archaea, significantly changing the way their evolution is viewed. The majority of evolutionary models, such as in the endosymbiont theory, propose that eukaryotes descended from multiple prokaryotes, which makes HGT all the more important to understanding the phylogenetic relationships of all extant and extinct species. These gene transfers between species are the major mechanism whereby bacteria acquire resistance to antibiotics. Classically, this type of transfer has been thought to occur by three different mechanisms: transformation, transduction and conjugation.

Although it is easy to see how prokaryotes exchange genetic material by HGT, it was initially thought that this process was absent in eukaryotes, followed by the idea that the gene transfers between multicellular eukaryotes should be more difficult. In spite of this fact, HGT between distantly related organisms has been demonstrated in several eukaryotic species.

In animals, a particularly interesting example of HGT occurs within the aphid species. Aphids are insects that vary in color based on carotenoid content. Carotenoids are pigments made by a variety of plants, fungi, and microbes, and they serve a variety of functions in animals, who obtain these chemicals from their food. Humans require carotenoids to synthesize vitamin A, and we

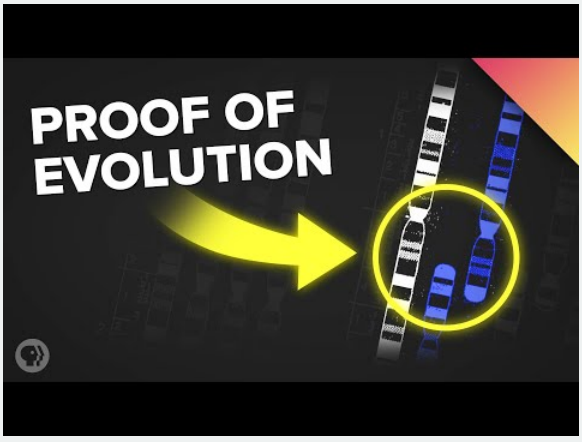
obtain them by eating orange fruits and vegetables: carrots, apricots, mangoes, and sweet potatoes. On the other hand, aphids have acquired the ability to make the carotenoids on their own. According to DNA analysis, this ability is due to the transfer of fungal genes into the insect by HGT, presumably as the insect consumed fungi for food.



Figure 4.3.1.1: Horizontal Gene Transfer in Animals: (a) Red aphids get their color from red carotenoid pigment. Genes necessary to make this pigment are present in certain fungi, and scientists speculate that aphids acquired these genes through HGT after consuming fungi for food. If genes for making carotenoids are inactivated by mutation, the aphids revert back to (b) their green color. Red coloration makes the aphids a lot more conspicuous to predators, but evidence suggests that red aphids are more resistant to insecticides than green ones. Thus, red aphids may be more fit to survive in some environments than green ones.

Video





In this 8-minute video, evidence of human evolution in the human genome is demonstrated.
Question after watching: What are three lines of evidence from the human genome of our evolutionary past?

This page titled 4.3.1: Evolution of Genomes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.

4.3.2: Evolution in Populations

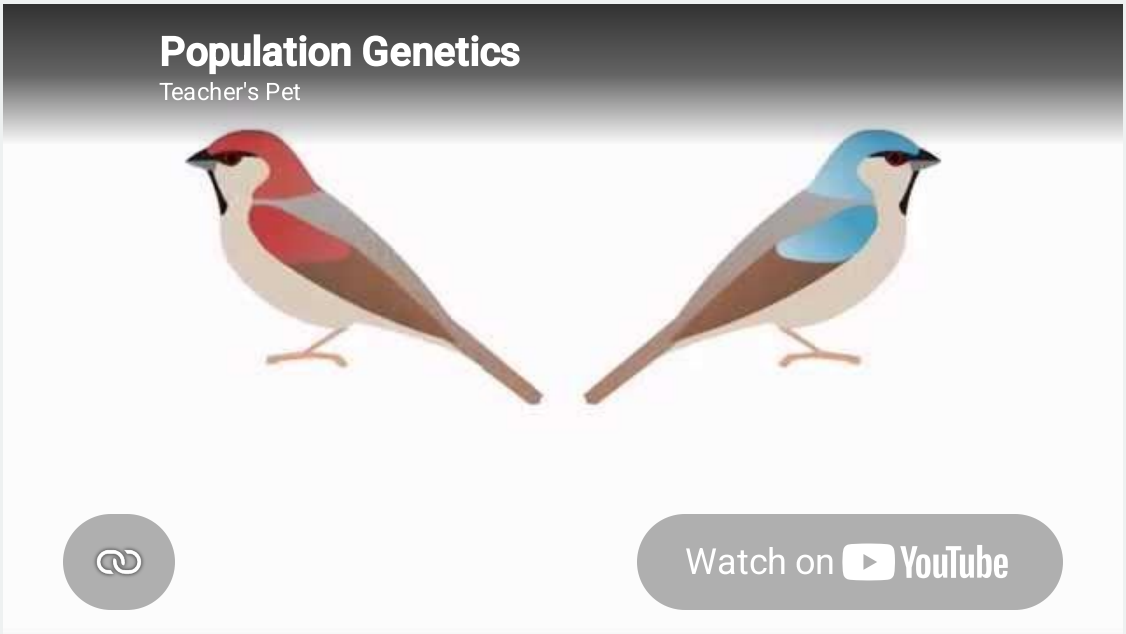
Evolution in Populations

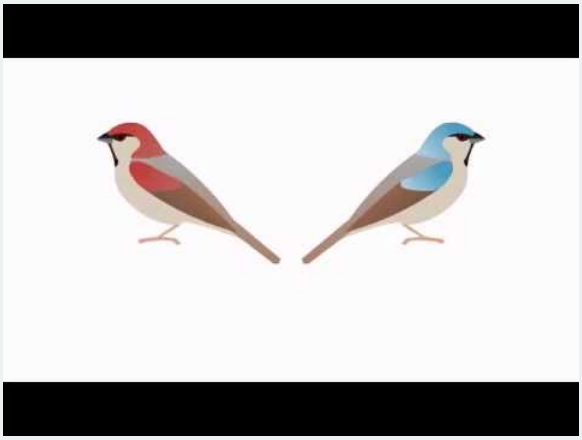
- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe how mutations, natural selection, genetic drift, and gene flow can modify the genes in a population.
- Define a population gene pool.
- Explain how the size of the gene pool can affect the evolutionary success of a population.
- Use the Hardy-Weinberg equation to calculate allelic and genotypic frequencies in a population.
- Use the results of a Hardy-Weinberg analysis to determine whether evolution is taking place in a population.

Video





This short 3-minute video provides a good introduction to population genetics and its relationship to evolution. Question after watching: At 2:13, the slide shows four elements that the narrator says are the elements that make up the gene pool. She is incorrect on one count. Which one? And why? Integrate some of the concepts you have learned previously with the ones introduced in this video. Describe how something like a genetic bottleneck might create changes in a population's gene pool.

The Evolution of Populations

According to evolutionary theory, every organism from humans to beetles to plants to bacteria shares a common ancestor (Figure 4.3.2.1). Millions of years of evolutionary pressure caused some species to go extinct while others survived. Earth is filled with more diversity now than at any other point in its history. All life is still connected, however. For example, all organisms are composed of cells and use DNA. The theory of evolution gives us a unifying theory to explain what caused the diversity of species that now exist.



Figure 4.3.2.1: Evolution has resulted in living things that may be single-celled or complex, multicellular organisms. They may be plants, animals, fungi, bacteria, or Archaea. This diversity results from evolution.

Genetic Variation in Populations

A **population** is a group of individuals that can all interbreed, often distinguished as a species. These individuals can share genes and pass on combinations of genes to the next generation, containing all of the variation in its gene pool. The process of evolution occurs *only* in populations and not in individuals. A single individual cannot evolve alone; evolution is the process of changing the gene frequencies within a gene pool. Five forces can cause genetic variation and evolution in a population: mutations, genetic recombination, natural selection, genetic drift, and gene flow. Refresh your understanding of these concepts in Unit 2.2.

Allele Frequencies

A gene for a particular characteristic may have several variations called **alleles**. These variations code for different traits associated with that characteristic. The **allele frequency** (or gene frequency) is the rate at which a specific allele exists within a population. Allele frequencies can be expressed as a decimal or as a percent and always add up to 1, or 100 percent, of the total population. The **gene pool** is the sum of all the alleles of all genes in a population. When calculating the frequency of an allele in a population, remember that for diploid organisms like humans and animals, there are two alleles of each gene in the population.

For example, in the ABO blood type system in humans, three alleles (I^A, I^B, or i) determine the particular blood-type of red blood cells (Figure 4.3.2.2). Individuals who are phenotypically blood group "A" have the ability to attach certain sugars to the surface of red blood cells. The genotype that confers that ability are I^AI^A or I^Ai. Individuals who are blood group "B" have a different allele of that gene that codes for a protein that adds a different type of sugar on the surface of blood cells. The alleles is labeled I^B, so homozygous I^BI^B or heterozygous I^Bi have that blood type. Individuals who have one allele of each, I^A and I^B can add both sugars on the surface of their blood cells. Finally, people who lack either of these alleles encode an enzyme that cannot add either sugar types and so are blood type "O" and have homozygous alleles ii.

A diploid organism can only carry two alleles for a particular gene. In human blood type, the combinations are composed of two alleles such as I^AI^A or I^AI^B. Although each organism can only carry two alleles, more than those two alleles may be present in the

larger population. In a population of fifty people where all the blood types are represented, there may be more I^A alleles than i alleles.

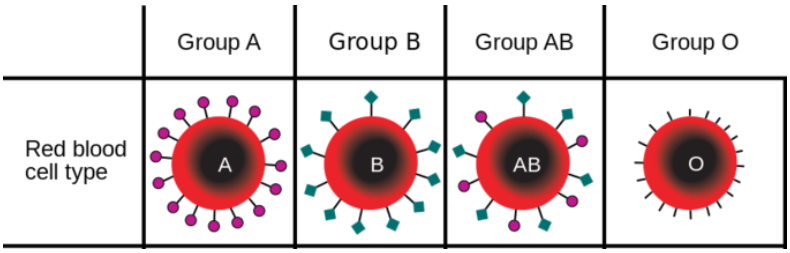
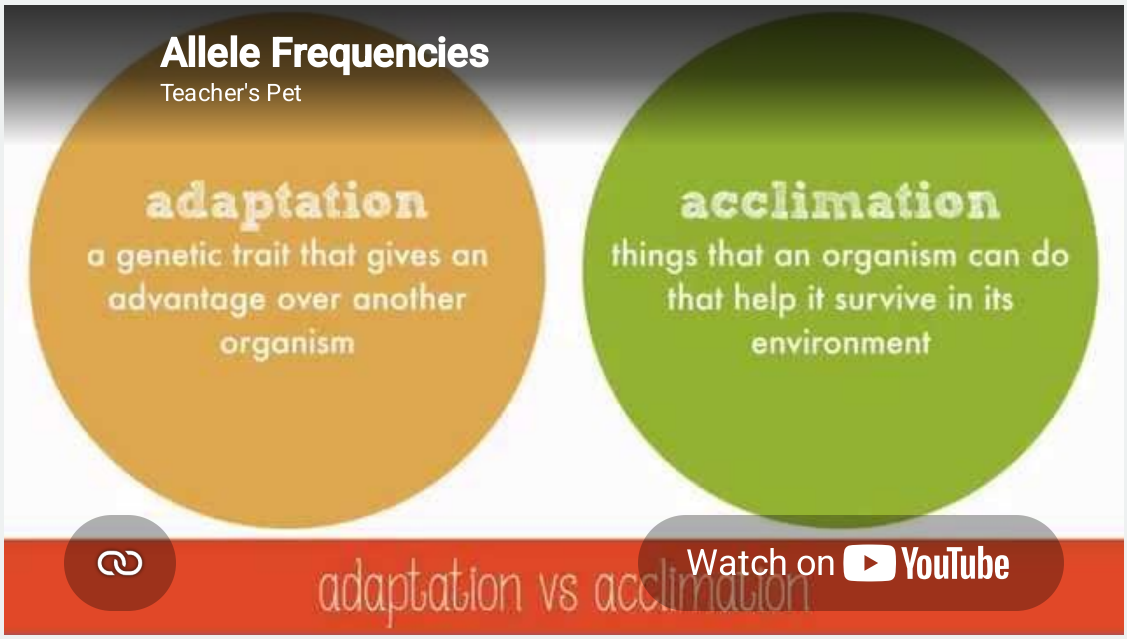


Figure 4.3.2.2: In humans, each blood type corresponds to a combination of two alleles. Human blood types are A, B, AB, and O.

Using the ABO blood type system as an example, the frequency of one of the alleles, for example I^A, is the number of copies of that allele divided by all the copies of the ABO gene in the population, i.e. all the alleles. In a sample population of humans, the frequency of the I^A allele might be 0.26, which would mean that 26% of the chromosomes in that population carry the I^A allele. If we also know that the frequency of the I^B allele in this population is 0.14, then the frequency of the i allele is 0.6, which we obtain by subtracting all the known allele frequencies from 1 (thus: 1 – 0.26 – 0.14 = 0.6). A change in any of these allele frequencies over time would constitute evolution in the population.

Video





This 4.5-minute video explains how to calculate allelic frequencies in a population. It will also introduce the concept of Hardy-Weinberg equilibrium, which we will explore later in this chapter.
Question after watching: How would you explain the concept of allele frequencies to someone not in your course?

Case of the Hamsters (Part I) - Establishing Alleles

Our case begins with hypothetical species of hamster that carries two alleles for coat color in the population: black which is dominant (**B**) and grey, which is recessive (**b**).

Using a Punnett square, if two black hamsters mate that are heterozygous (e.g., **Bb**) (Table 4.3.2.1), we find that

- 25% of their offspring are homozygous for the dominant allele (**BB**)
- 50% are heterozygous like their parents (**Bb**)
- 25% are homozygous for the recessive allele (**bb**) and thus, unlike their parents, express the recessive phenotype.

Note

Find a refresher on Punnett squares here: Punnett Squares

This is what Mendel found when he crossed monohybrids. It occurs because meiosis separates the two alleles of each heterozygous parent so that 50% of the gametes will carry one allele and 50% the other and when the gametes are brought together at random, each **B** (or **b**)-carrying egg will have a 1 in 2 probability of being fertilized by a sperm carrying **B** (or **b**).

Table 4.3.2.1. Results of the random union of the two gametes produced by two individuals, each heterozygous for a given trait. As a result of meiosis, half the gametes produced by each parent will carry allele **B**; the other half allele **b**.

	0.5 **B**	0.5 **b**
0.5 **B**	0.25 **BB**	0.25 **Bb**
0.5 **b**	0.25 **Bb**	0.25 **bb**

However, the frequency of two alleles in an *entire population* of organisms is unlikely to be exactly the same. We will return to this case in a moment.

The Hardy-Weinberg Principle: A Theory of Population Evolution

Theoretical Background

In the early twentieth century, English mathematician Godfrey Hardy and German physician Wilhelm Weinberg stated the principle of equilibrium to describe the population's genetic makeup. The theory, which later became known as the Hardy-Weinberg principle of equilibrium, states that a population's allele and genotype frequencies are inherently stable— unless some kind of evolutionary force is acting upon the population, neither the allele nor the genotypic frequencies would change.

Ultimately, the Hardy-Weinberg principle models a population without evolution under the following conditions:

1. no mutations
2. no immigration/emigration
3. no natural selection
4. only random matings
5. a large population

In theory, if a population is at equilibrium—that is, there are no evolutionary forces such as natural selection, mutation, etc. acting upon it—generation after generation would have the same gene pool and genetic structure, and the allele frequencies would stay the same over time. This is because all of the alleles would have an equal chance of being passed to the next generation and the ratios would remain constant.

Of course, even Hardy and Weinberg recognized that no natural population is immune to evolution. Evolution involves changes in the gene pool. Populations in nature are constantly changing in genetic makeup due to drift, mutation, possibly migration, and selection.

Hardy-Weinberg Principle

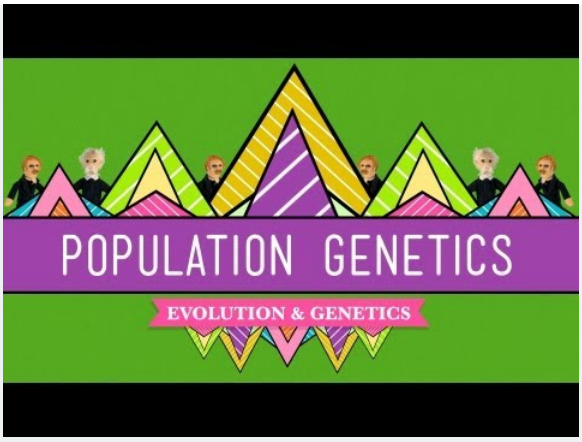
So long as certain conditions are met (discussed below), allele frequencies and genotype ratios in a randomly-breeding population remain constant from generation to generation. This is known as the Hardy-Weinberg Principle.

As a result, the only way to determine the exact distribution of phenotypes in a population is to go out and count them. A population in Hardy-Weinberg equilibrium shows no change. What the law tells us is that populations are able to maintain a reservoir of variability so that if future conditions require it, the gene pool can change. If the frequencies of alleles or genotypes deviate from the value expected from the Hardy-Weinberg equation, then the population is evolving.

When populations are in the Hardy-Weinberg equilibrium, the allelic frequency is stable from generation to generation and the distribution of alleles can be determined. If the allelic frequency measured in the field differs from the predicted value, scientists can make inferences about what evolutionary forces are at play. However, what ultimately interests most biologists is not the frequencies of different alleles, but the frequencies of the resulting genotypes, from which scientists can surmise phenotype distribution.

Video





This 11-minute Crash Course video provides an overview of population genetics in a humorous manner. Questions after watching: In this video, the narrator says there are five ways to alter the gene pool of a population. Explain how this could be. What's another way to say that a population is in Hardy-Weinberg equilibrium?

Applying Hardy-Weinberg

While no population can satisfy those conditions, the principle offers a useful model against which to compare real population changes. The genetic variation of natural populations is constantly changing from genetic drift, gene flow, mutation, migration, and natural selection. **Population genetics** is the study of the distributions and changes of allele frequency in a population. In population genetics, evolution is defined as a change in the frequency of an allele in a population.

The Hardy-Weinberg principle gives scientists a mathematical baseline of a non-evolving population to which they can compare observable populations in the field or laboratory to determine whether they are evolving. If scientists record allele frequencies over time and then calculate the expected frequencies based on Hardy-Weinberg values, then scientists can detect when a population deviates from HW expectations and therefore confirm that the population is evolving. The Hardy-Weinberg principle states that a population's allele and genotype frequencies will remain constant in the absence of evolutionary mechanisms. Note that this conclusion does not inform the researcher as to which mechanism of allelic frequency change is at play, only that allelic frequencies are changing (i.e. that evolution is occurring).

Working under this theory, population geneticists represent different alleles as different variables in their mathematical models (Figure 4.3.2.3). The variable p, for example, represents the frequency of a particular allele, say A for the trait of tall plants in Mendel's peas, while the variable q represents the frequency of alleles that confer the short plant trait, a. If these are the only two possible alleles for a given locus in the population, then $p + q = 1$. In other words, all the p alleles and all the q alleles comprise all of the alleles for that locus in the population.

If we observe the phenotype, we can know only the homozygous recessive allele's genotype. The Hardy-Weinberg calculations provide an estimate of the remaining genotypes. Since each individual carries two alleles per gene, if we know the allele frequencies (p and q), predicting the genotypes' frequencies is a simple mathematical calculation to determine the probability of obtaining these genotypes if we draw two alleles at random from the gene pool, as we will see below.

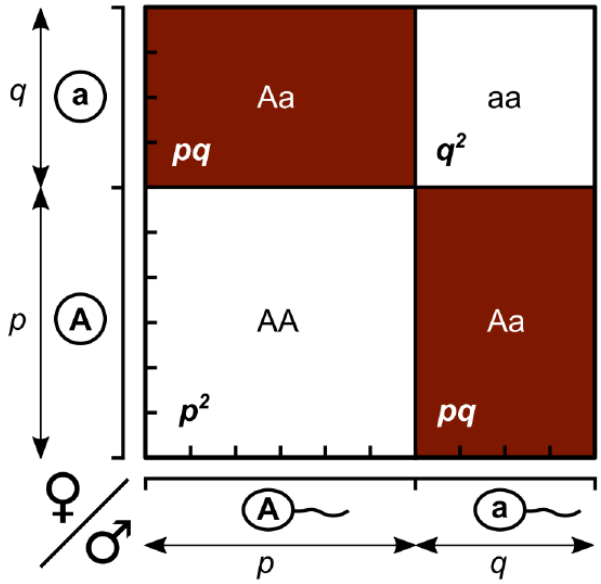


Figure 4.3.2.3: Hardy-Weinberg and the Punnett Square. (CC0 1.0)

Calculating Gene Pools and Genotype Frequencies

Gene pools

The total number of genes in a population is its gene pool.

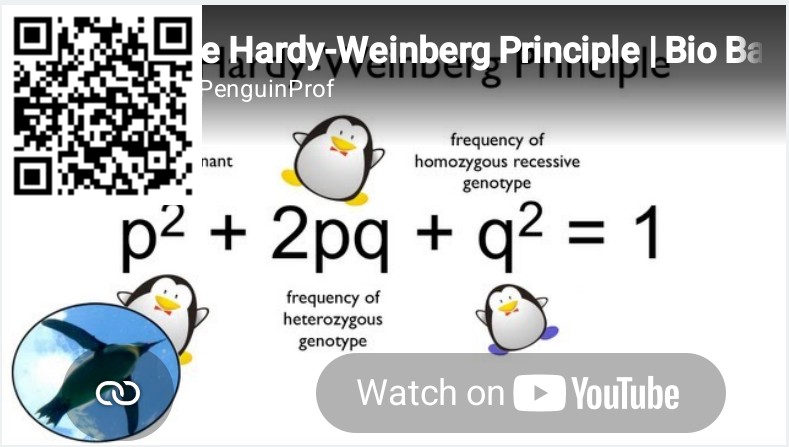
- Let p represent the frequency of the dominant allele in the gene pool and q the frequency of the recessive allele in the gene pool.
- Because p and q together equal all of the alleles in the gene pool, $p + q = 1$

Genotype frequencies

- Homozygous dominant individuals have two p alleles. Their genotype frequency can be determined by p x p or p^2.
- Similarly, homozygous recessive individuals have two q alleles. Their genotype frequency can be determined by q x q or q^2
- Heterozygous individuals are $2pq$. Their genotype frequency can be determined by 2 x p x q or $2pq$. [There are two possible types of heterozygous unions: pq and qp. Therefore, we calculate 2 x p x q]
- Because p^2, q^2, and $2pq$ together equal all of the genotypes in a population, p^2 + $2pq$ + q^2 = **1**

If any one of the variables above is known, the allele frequency or genotype frequencies can be calculated. We will revisit our case study below to see how these equations are put into practice by scientists to understand whether evolution is occurring in a population.

Video



This 11-minute video describes how to calculate allele and gene pool frequencies with the Hardy-Weinberg equations. Examples and practice equations are given below.

Case of the Hamsters (Part II) - Calculating Allele and Genotype Frequency

The frequency of two alleles in an *entire population* of organisms is unlikely to be exactly the same as we saw in the Punnett square of Part 1. However, from a given genotype (or recessive phenotypes since that genotype is known), we can infer the frequencies of the alleles in a population.

Since each diploid individual carries two alleles per gene, we can predict the frequencies of these genotypes using a probability matrix Table 4.3.2.2. If two alleles are drawn at random from the gene pool, we can determine the probability of each genotype. We are now calculating percentages based on overall populations (not individual pairings like a Punnett square). In this type of probability matrix, *all* of the alleles that can mix in a population to produce the next generation are represented.

1. Revisiting our hypothetical case of a population of hamsters, for the purposes of example, we will establish that 80% of all the gametes in the population carry a dominant allele for black coat (B) and 20% carry the recessive allele for gray coat (b). So, p = 0.8 and q = 0.2.
2. We can now use those two values to calculate the genotype frequencies where p^2 = 0.64 and q^2 = 0.04
3. The equation above states $p^2 + 2pq + q^2 = 1$. We have calculated p^2 and q^2 but need to now solve for $2pq$.
4. We can determine from our calculations that 0.64 + $2pq$ + 0.04 = 1
5. From there 0.64 + 0.04 + $2pq$ = 1
6. And 0.68 + $2pq$ = 1
7. So, $2pq$ = 1 - 0.68 = 0.32 or 32%

Therefore, in this case, the random union of these allele frequencies will produce a generation:

- 64% homozygous for BB
- 32% Bb heterozygotes
- 4% homozygous (bb) for gray coat

So 96% of the next generation will have black coats; only 4% gray coats. If you notice, this is the same phenotype ratio as the initial population. No change has occurred, which is explained in more detail below.

Table 4.3.2.2. Results of random union of the gametes produced by an entire population with a gene pool containing 80% **B** and 20% **b**.

	0.8 **B**	0.2 **b**
0.8 **B**	0.64 **BB**	0.16 **Bb**
0.2 **b**	0.16 **Bb**	0.04 **bb**

Hardy-Weinberg and Selection Pressures

Natural selection affects allele and genotype frequency. If an allele confers a phenotype that enables an individual to better survive or have more offspring, the frequency of that allele will increase because the individual carrying these alleles will be effective at transferring them into the next generation. Because many of those offspring will also carry the beneficial allele and, therefore, the phenotype, they will have more offspring of their own that also carry the allele. Over time, the allele will spread throughout the population and may become fixed: every individual in the population carries the allele. If an allele is dominant but detrimental, it may be swiftly eliminated from the gene pool when the individual with the allele does not reproduce. However, a detrimental recessive allele can linger for generations in a population, hidden by the dominant allele in heterozygotes. In such cases, the only individuals to be eliminated from the population are those unlucky enough to inherit two copies of such an allele.

So, will deleterious alleles eventually disappear? No. Let's see why using our case study.

Imagine that the grey coat color carries with it some sore of negative selection pressure. If we calculate the allele frequencies, using our genotype frequencies from Table 4.3.2.2 above, we can recalculate how much of the population carries the dominant allele and what percentage carries the recessive allele.

- All the gametes formed by BB hamsters will contain allele B (0.64) as will one-half the gametes formed by heterozygous (Bb) hamsters (0.32/2).
  - So, 80% (0.64 + (0.32*1/2)) of the pool of gametes formed by this generation will contain B.
- All the gametes of the gray (bb) hamsters (4%) will contain b (0.04) but one-half of the gametes of the heterozygous hamsters will as well (0.32/2).
  - So 20% (0.04 + (0.32*1/2)) of the gametes will contain b.

What we find from this analysis is that in the parental generation, 80% of the alleles were B and 20% of the alleles were b. The organisms of that population mated and produced generation 2. This was a random sampling event of the alleles in the parental gene pool. In the generation 2 alleles, we find that 80% of the alleles are B and 20% are b. This is identical to the parental allelic frequency.

The proportion of allele b in the population has remained the same from the parent generation. The heterozygous hamsters ensure that each generation will contain 4% gray hamsters. Recessive genes do not tend to be lost from a population no matter how small their representation. If recessive alleles were continually tending to disappear, the population would soon become homozygous. Under Hardy-Weinberg conditions, genes that have no present selective value will nonetheless be retained.

If an allele confers a phenotype that enables an individual to better survive or have more offspring, the frequency of that allele will increase because the individual carrying these alleles will be effective at transferring them into the next generation. Because many of those offspring will also carry the beneficial allele and, therefore, the phenotype, they will have more offspring of their own that also carry the allele. Over time, the allele will spread throughout the population and may become fixed: every individual in the population carries the allele. If an allele is dominant but detrimental, it may be swiftly eliminated from the gene pool when the individual with the allele does not reproduce. However, a detrimental recessive allele can linger for generations in a population, hidden by the dominant allele in heterozygotes. In such cases, the only individuals to be eliminated from the population are those unlucky enough to inherit two copies of such an allele.

? Optional Activity 4.3.2.1

In the Punnett square in Figure 4.3.2.4, an individual pea plant could be pp (YY), and thus produce yellow peas; pq (Yy), also yellow; or qq (yy), and thus produce green peas. If 9% of the overall plants in a population produce green peas, what percentage of pea plants are heterozygous for pea color?

Answer (Click here)

According to the Hardy-Weinberg principle, the variable *p* represents the frequency of a particular allele, usually a dominant one. For example, assume that *p* represents the frequency of the dominant allele, Y, for yellow pea pods. The variable *q* represents the frequency of the recessive allele, y, for green pea pods. If p and q are the only two possible alleles for this characteristic, then the sum of the frequencies must add up to 1, or 100 percent. We can also write this as p + q = 1. If the frequency of the Y allele in the population is 0.6, then we know that the frequency of the y allele is 0.4.

In the example, our three genotype possibilities are: pp (YY), producing yellow peas; pq (Yy), also yellow; or qq (yy), producing green peas. The frequency of homozygous dominant individuals is p^2; the frequency of heterozygous individuals is 2pq; and the frequency of homozygous recessive individuals is q^2. If p and q are the only two possible alleles for a given trait in the population, these genotype frequencies will sum to one: $p^2 + 2pq + q^2 = 1$.

In our example, the possible genotypes are homozygous dominant (YY), heterozygous (Yy), and homozygous recessive (yy). If we can only observe the phenotypes in the population, then we know only the recessive phenotype (yy). For example, in a garden of 100 pea plants, 86 might have yellow peas and 16 have green peas. We do not know how many are homozygous dominant (Yy) or heterozygous (Yy), but we do know that 16 of them are homozygous recessive (yy).

Therefore, by knowing the recessive phenotype and, thereby, the frequency of that genotype (16 out of 100 individuals or 0.16), we can calculate the number of other genotypes.

1. If q^2 represents the frequency of homozygous recessive plants, then $q^2 = 0.16$.

2. Therefore, q = 0.4 (the square root of 0.16 is 0.4...we cannot have a negative number when working with allele frequencies).
3. Because p + q = 1 and q = 0.4, then 1 – 0.4 = p.
4. p = 0.6.
5. The frequency of homozygous dominant plants (p^2) is $(0.6)^2 = 0.36$. So, out of 100 individuals, there are 36 homozygous dominant (YY) plants.
6. The frequency of heterozygous plants (2pq) is 2(0.6)(0.4) = 0.48. Therefore, 48 out of 100 plants are heterozygous yellow (Yy).

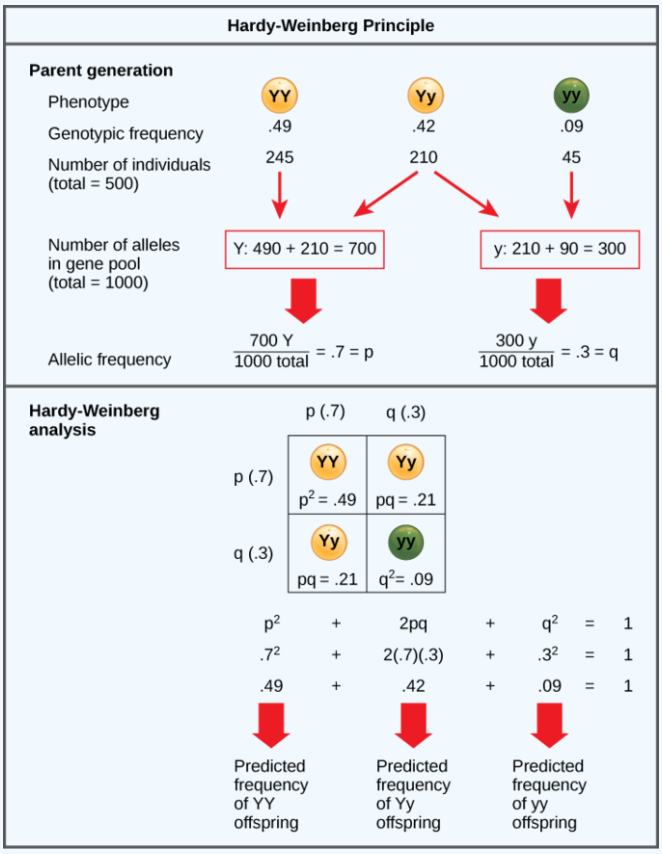


Figure 4.3.2.4: Predicted frequencies of alleles and genotypes of a population with 9% green peas.

Optional Activity 4.3.2.2

In plants, violet flower color (V) is dominant over white (v). If q = 0.2 in a population of 500 plants, how many individuals would you expect to be homozygous dominant (VV), heterozygous (Vv), and homozygous recessive (vv)? How many plants would you expect to have violet flowers, and how many would have white flowers?

Answer

Remember that p indicates the frequency of the dominant allele (V) and q indicates the frequency of the recessive allele (v). It is easier to begin with the recessive allele.

In this population, if q = 0.2, then $q^2 = 0.04$. We know that q^2 is the frequency of homozygous recessive individuals, so 0.04 x 500 total plants (the overall population) = 20. Therefore, 20 plants would be expected to be homozygous recessive (white).

For the dominant allele, p, we need to use the formula p + q = 1. Since q = 0.2, we can calculate p + 0.2 = 1. From there, we get p = 1 - 0.2 so p = 0.8.

If p = 0.8, then p2 = 0.64. We know that p2 is the frequency of homozygous dominant individuals, so 0.64 x 500 total plants (the overall population) = 320. Therefore, 320 plants are expected to be homozygous dominant (violet).

To complete the problem, we calculate 2pq, or the frequency of heterozygous individuals. So, 2 x 0.8 x 0.2 = 0.32. We will then take and calculate 0.32 x 500 to get 160. Therefore, 160 plants are expected to be heterozygous (violet).

Optional Resource

Find an additional Hardy-Weinberg problem to solve, with a solution and walk-through, here.

When the Hardy-Weinberg Law Fails

To see what forces lead to evolutionary change, we must examine the circumstances in which the Hardy-Weinberg law may fail to apply. In any of these cases (which is the reality of the natural world), evolution is occurring. There are five:

1. Mutation

The frequency of gene B and its allele b will not remain in Hardy-Weinberg equilibrium if the rate of mutation of B -> b (or vice versa) changes, or if a new allele B^o comes to be. By itself, this type of mutation probably plays only a minor role in evolution; the rates are simply too low. However, gene (and whole genome) duplication - a form of mutation - probably has played a major role in evolution. In any case, evolution depends on mutations because this is the only way that new alleles are created. After being shuffled in various combinations with the rest of the gene pool, these provide the raw material on which natural selection can act.

2. Gene Flow

Many species are made up of local populations whose members tend to breed within the group. Each local population can develop a gene pool distinct from that of other local populations. However, members of one population may breed with occasional immigrants from an adjacent population of the same species. This can introduce new genes or alter existing gene frequencies in the residents. Whether within a species or between species, gene flow increases the variability of the gene pool.

3. Genetic Drift

Genetic drift is the evolution that happens when there is no selective advantage for the alleles that grow in frequency. That growth is due to chance events. For example, if a rock falls on a population of beetles that have green and red alleles and kills more of those individuals with the red allele, the gene frequency for this gene will change, but it was not adaptive. It just happened due to chance events. The smaller a population, the more susceptible it is to mechanisms such as genetic drift. Random events that alter allele frequencies will have a much larger effect when the gene pool is small.

If the population is small, Hardy-Weinberg may be violated. Chance, including abiotic impacts, alone may eliminate certain members out of proportion to their numbers in the population. In such cases, the frequency of an allele may begin to drift toward higher or lower values. Ultimately, the allele may represent 100% of the gene pool or, just as likely, disappear from it. Drift produces evolutionary change, but there is no guarantee that the new population will be more fit than the original one. Evolution by drift is aimless, not adaptive.

4. Nonrandom Mating

One of the cornerstones of the Hardy-Weinberg equilibrium is that mating in the population must be random. If individuals (usually females) are choosy in their selection of mates, the gene frequencies may become altered.

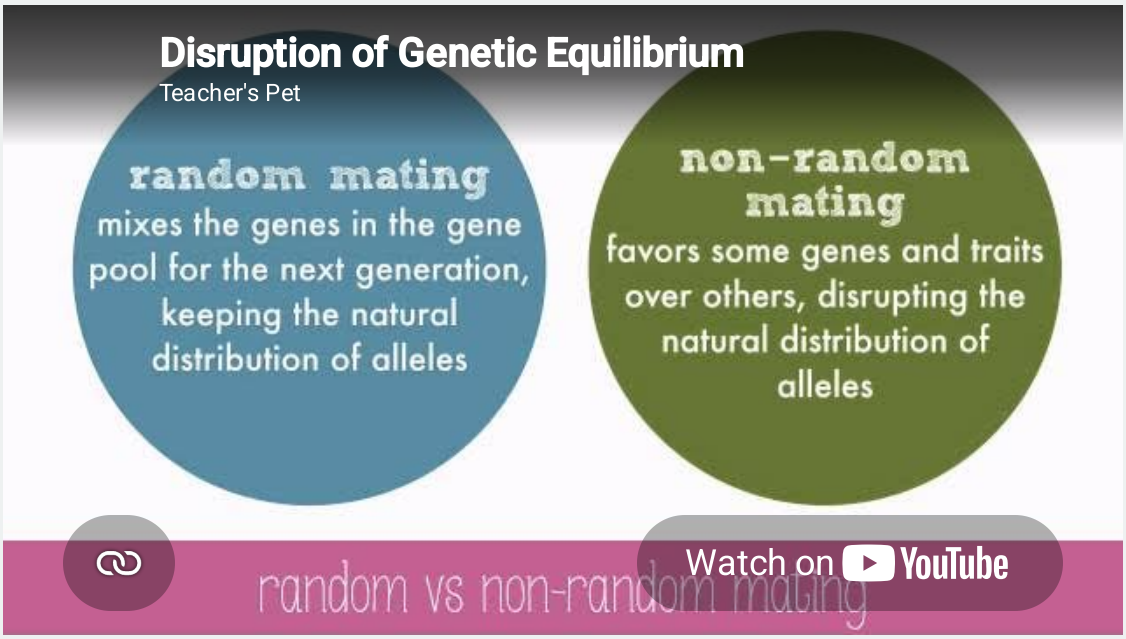
Nonrandom mating seems to be quite common. Breeding territories, courtship displays, "pecking orders" can all lead to it. In each case, certain individuals do not get to make their proportionate contribution to the next generation. If some males reproduce more than others, then more of their genes are represented in the next generation.

5. Natural Selection

If individuals having certain genes are better able to produce mature offspring than those without them, the frequency of those genes will increase in the next generation. This is simply expressing Darwin's natural selection in terms of alterations in the gene pool. Natural selection results from *differential mortality* (some individuals survive longer than others) and/or *differential fecundity (some individuals have more offspring than others)*. Ultimately, this causes the sampling of one generation's gene pool to be

skewed; the next generation's gene pool is different from the first. Not every allele has an equal chance of being passed on to the next generation.

Video





This 4-minute video explains what the Hardy-Weinberg equilibrium is and why finding a population that does not conform to HW expectations tells you that the population is in the process of evolving with regard to one trait. Question after watching: The HW principle is defined using mathematical terms. Based on what you now know about the HW principle, what is being quantified and monitored in the HW principle to assess whether a population is evolving?

This page titled 4.3.2: Evolution in Populations is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg via source content that was edited to the style and standards of the LibreTexts platform.

- **18.1: Understanding Evolution** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **18.6: The Hardy-Weinberg Equilibrium** by John W. Kimball is licensed CC BY 3.0. Original source: https://www.biology-pages.info/.

CHAPTER OVERVIEW

4.4: Systematics, Phylogeny and Comparative Biology

Learning Objectives

- State the theoretical basis for modern classification systems
- Recognize and write scientific names using the binomial classification system
- Explain the purpose of cladistics
- Design a cladogram
- Recognize and interpret a phylogenetic tree
- Explain a phylogenetic tree's components and purpose

4.4.1: Systematics and Classification
4.4.2: Phylogeny and Cladistics

This page titled 4.4: Systematics, Phylogeny and Comparative Biology is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

4.4.1: Systematics and Classification

Systematics and Classification

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 45 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- State the theoretical basis for modern classification systems
- Recognize and write scientific names using the binomial classification system

The Levels of Classification

Taxonomy (which means “arrangement law” in Latin) is the science of classifying organisms to construct internationally-shared classification systems with each organism placed into increasingly more inclusive groupings. Taxonomic classification divides species into a hierarchical system beginning with a **domain** (Bacteria, Archaea, and Eukarya) and ending with a single species. Within each domain is a second level called a **kingdom** (Archaea, Bacteria, Protista, Fungi, Plantae, and Animalia). Each domain contains several kingdoms. Within kingdoms, the subsequent categories of increasing specificity are phylum, class, order, family, genus, and species.

Think about how a grocery store is organized. One large space is divided into departments, such as produce, dairy, and meats. Then each department is further divided 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.

As an example, the classification levels for the domestic dog are shown in Figure 4.4.1.1. The group at each level is called a **taxon** (plural: taxa). In other words, for the dog, Carnivora is 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, such as domestic dog, or wolf.

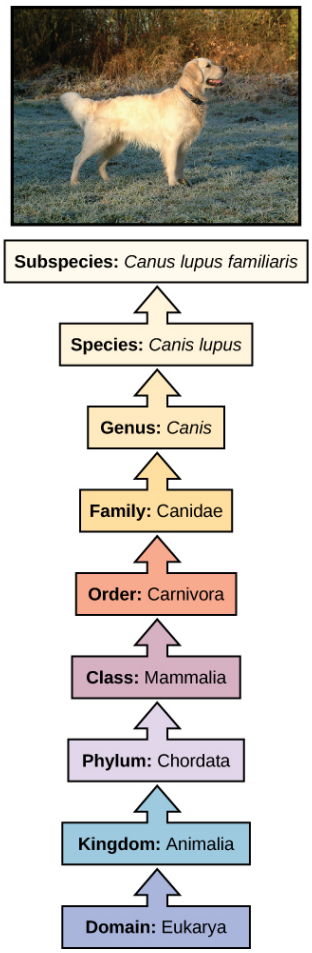
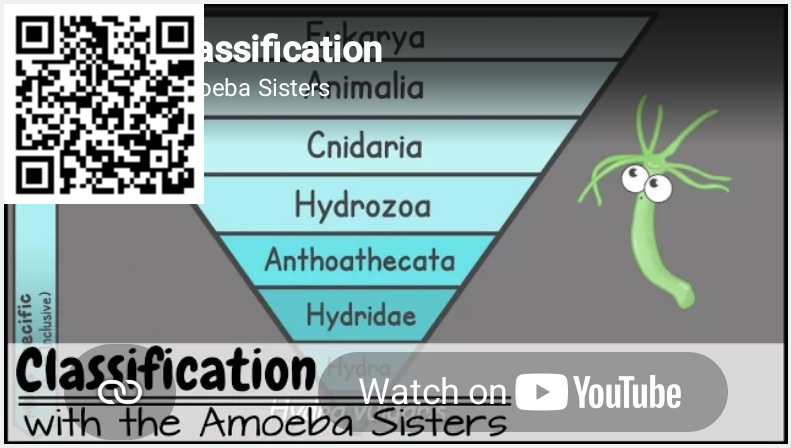


Figure 4.4.1.1: The taxonomic classification system uses a hierarchical model to organize living organisms into increasingly specific categories. The common dog, *Canis lupus familiaris*, is a subspecies of *Canis lupus*, which also includes the wolf and dingo.

Scientists refer to an organism by its genus and species names together, commonly called a **scientific name**, or Latin name. This two-name system is called **binomial nomenclature**. The full name of an organism technically has eight terms. Dogs, for example, are technically: Eukarya, Animalia, Chordata, Mammalia, Carnivora, Canidae, *Canis*, and *lupus*. Notice that each name is capitalized except for species and that genus and species names are italicized. Dogs share a domain (Eukarya) with the widest diversity of organisms, including plants and butterflies.

A recent study of the DNA of domestic dogs and wolves suggests that the domestic dog is a subspecies of the wolf, not its own species, thus it is given an extra name to indicate its subspecies status, *Canis lupus familiaris*. The scientific name of the wolf is therefore *Canis lupus*. Subspecies are members of the same species that are capable of mating and producing viable offspring, but they are considered separate subspecies due to geographic isolation, behavioral isolation, or other factors.

Video



This 7-minute video explores how life is organized using binomial nomenclature and some examples.
Question after watching: Can you come up with a mnemonic device to remember the categories of classification?

Figure 4.4.1.2 also shows how taxonomic levels move toward specificity. Notice how within the domain we find the dog grouped with the widest diversity of organisms. These include plants and other organisms not pictured, such as fungi and protists. The organisms become more similar at each sublevel because they are more closely related. Before Darwin's theory of evolution was developed, naturalists sometimes classified organisms using arbitrary similarities, but since the theory of evolution was proposed in the 19th-century, biologists work to make the classification system reflect evolutionary relationships. This means all members of a taxon should have a common ancestor and be more closely related to each other than to members of other taxa. Historically, scientists classified organisms using physical characteristics, but as DNA technology developed, more precise relationships have been determined.

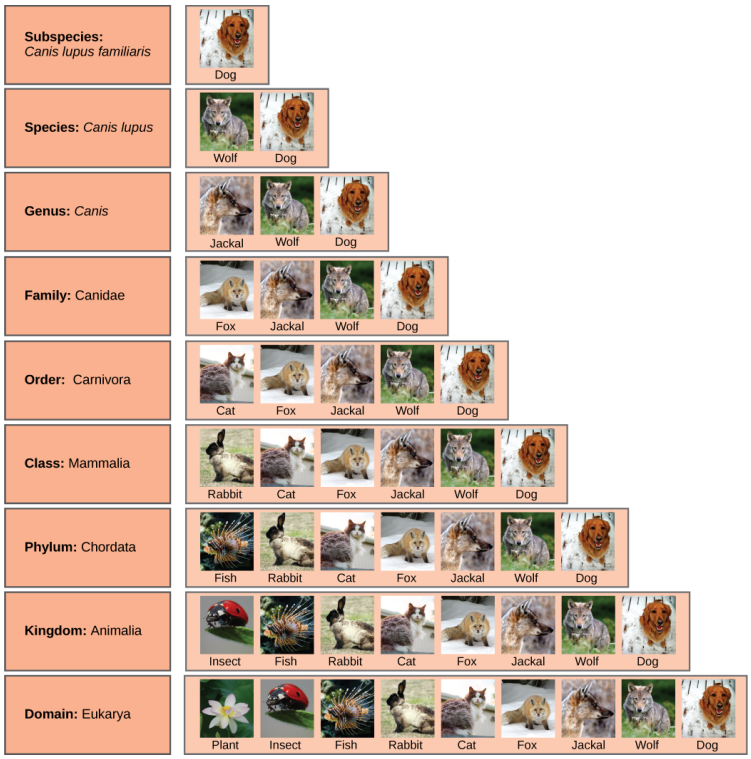


Figure 4.4.1.2: At each sublevel in the taxonomic classification system, organisms become more similar. Dogs and wolves are the same species because they can breed and produce viable offspring, but they are different enough to be classified as different subspecies. (credit “plant”: modification of work 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)

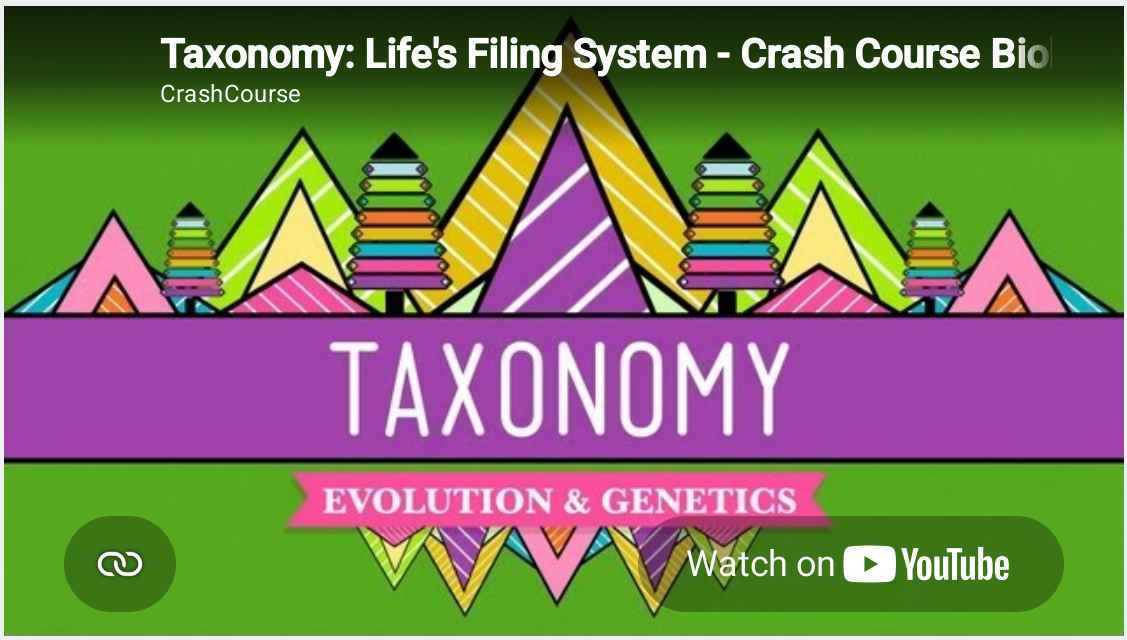
? Optional Activity

Question: Refer to Figure 4.4.1.2. At what levels are cats and dogs considered to be part of the same group?

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.

Video





In this 12-minute video, the science of taxonomy is explained, including an overview of the major kingdoms of life. Question after watching: Using your favorite organism, find its scientific name and try placing it into its appropriate classifications.

Optional Activity

List the different levels of the taxonomic classification system.

Answer

From most inclusive to least inclusive: domain, kingdom, phylum, class, order, family, genus, species.

This page titled 4.4.1: Systematics and Classification is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.1: Organizing Life on Earth** by OpenStax is licensed CC BY 4.0.
- **20.1C: The Levels of Classification** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.

4.4.2: Phylogeny and Cladistics

Phylogeny and Cladistics

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 3 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain the purpose of cladistics
- Design a cladogram
- Recognize and interpret a phylogenetic tree
- Explain a phylogenetic tree's components and purpose

Introduction to Phylogeny

All life on Earth evolved from a common ancestor. Biologists map how organisms are related by constructing **phylogenetic trees**. Phylogenetic trees are diagrams used to reflect evolutionary relationships among organisms or groups of organisms. In other words, a "tree of life" can be constructed to illustrate when different organisms evolved and to show the relationships among different organisms, as shown in Figure 4.4.2.1. Notice that from a single point, the three domains of Archaea, Bacteria, and Eukarya diverge and then branch repeatedly. The small branch that plants and animals (including humans) occupy in this diagram shows how recently these groups had their origin compared with other groups. A **phylogeny** is the evolutionary history and the relationships among a species or group of species. The study of organisms with the purpose of deriving their relationships is called **systematics**.

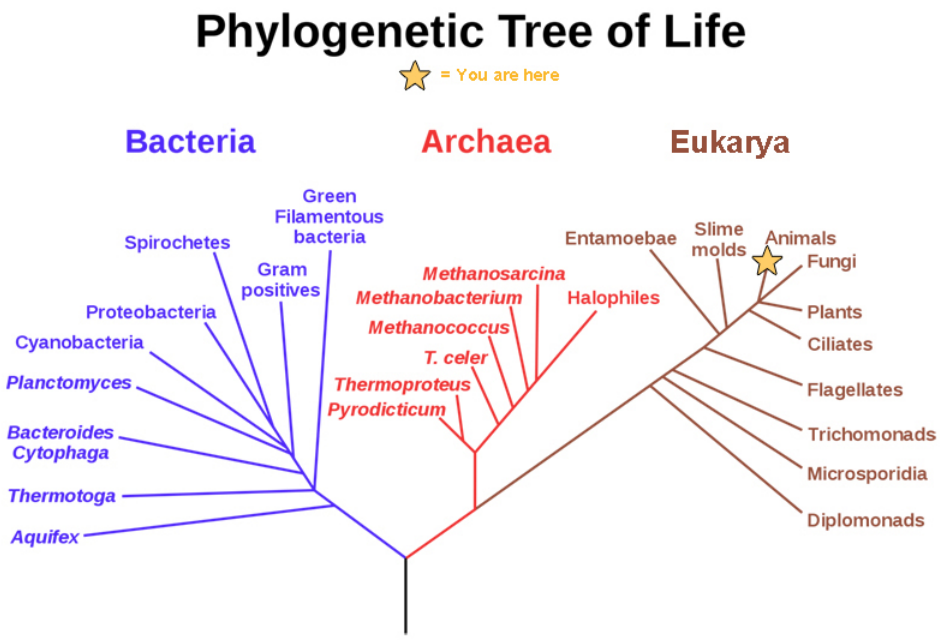


Figure 4.4.2.1: In the evolution of life on Earth, the three domains of life—Archaea, Bacteria, and Eukarya—branch from a single point. (credit: modification of work by Eric Gaba)

Understanding Phylogeny

Two Measures of Similarity

Organisms that share similar physical features *and* genetic sequences tend to be more closely related than those that do not. Features that overlap both morphologically and genetically are referred to as homologous structures; the similarities stem from common evolutionary paths. For example, as shown in Figure 4.4.2.2, the bones in the wings of bats and birds, the arms of humans, and the foreleg of a horse are homologous structures. Notice the structure is not simply a single bone, but rather a grouping of several bones arranged in a similar way in each organism even though the elements of the structure may have changed shape and size.

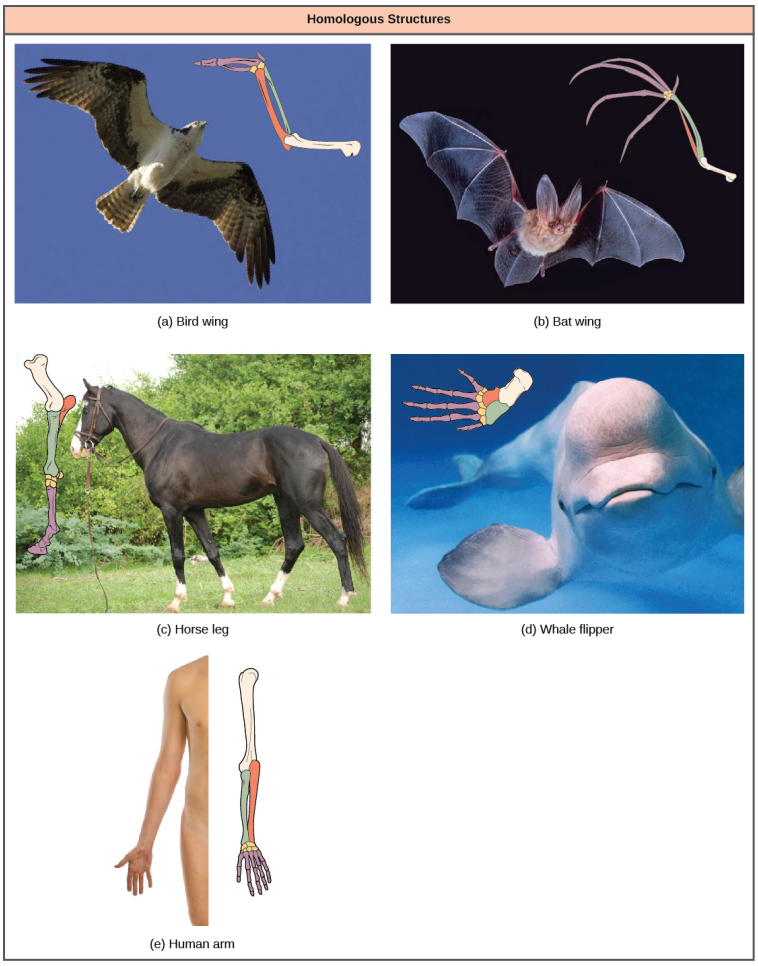


Figure 4.4.2.2: Bat and bird wings, the foreleg of a horse, the flipper of a whale, and the arm of a human are homologous structures, with similar bones indicated by the same color. This indicates that bats, birds, horses, whales, and humans share a common evolutionary past. (credit a photo: modification of work by Steve Hillebrand, USFWS; credit b photo: modification of work by U.S. BLM; credit c photo: modification of work by Virendra Kankariya; credit d photo: modification of work by Russian Gov./Wikimedia Commons)

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. For example, chimpanzees and humans, the skulls of which are shown in Figure 4.4.2.3 are very similar genetically, sharing 99 percent[1] of their genes. However, chimpanzees and humans show considerable anatomical differences, including the degree to which the jaw protrudes in the adult and the relative lengths of our arms and legs.



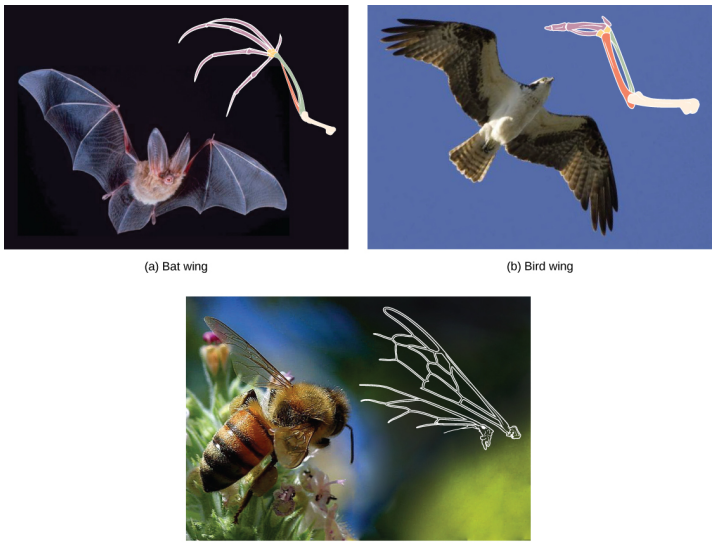
(a) (b)

Figure 4.4.2.3: (a) The chimpanzee jaw protrudes to a much greater degree than (b) the human jaw. (credit a: modification of work by "Pastorius"/Wikimedia Commons)

However, unrelated organisms may be distantly related yet appear very much alike, usually because common adaptations to similar environmental conditions evolved in both independently. An example is the streamlined body shapes, the shapes of fins and appendages, and the shape of the tails in fishes (which are from the fish taxon) and whales (which are from the mammal taxon). These structures bear superficial similarity because they are adaptations to moving and maneuvering in the same environment—water. When a characteristic that is similar occurs by adaptive convergence (convergent evolution), and not because of a close evolutionary relationship, it is called an analogous structure.

In another example, insects use wings to fly like bats and birds. We call them all wings because they perform the same function and have a superficially similar form, but the embryonic origin of the three wings is different. The difference in the development, or embryogenesis, of the wings in each case is a signal that insects versus bats or birds do not share a common ancestor that had a wing. The wing structures, shown in Figure 4.4.2.4 evolved independently in the two lineages (insects versus vertebrates).

Similar traits can be either homologous or analogous. Homologous traits share an evolutionary path that led to the development of that trait. Analogous traits may look similar but they do not share a common evolutionary origin. Scientists must determine which type of similarity a feature exhibits to decipher the phylogeny of the organisms being studied.



(a) Bat wing (b) Bird wing

(c) Insect wing

Figure 4.4.2.4: The wing of a honeybee is similar in shape to a bird wing and a bat wing and it serves the same function (flight). The bird and bat wings are homologous structures. However, the honeybee wing has a different structure (it is made of a chitinous exoskeleton, not a boney endoskeleton) and embryonic origin. The bee versus bird or bat wing types illustrate an analogy—similar structures that do not share an evolutionary history. (credit a photo: modification of work by U.S. BLM; credit b: modification of work by Steve Hillebrand, USFWS; credit c: modification of work by Jon Sullivan)

Optional Activity 4.4.2.1

Which statement about analogies is correct?

a. They occur only as errors.
b. They are synonymous with homologous traits.
c. They are derived due to similar environmental constraints.
d. They are a form of mutation.

Answer

c. They are derived due to similar environmental constraints.

Molecular Comparisons

With the advancement of DNA technology, the area of **molecular systematics**, which describes the use of information on the molecular level including DNA sequencing, has blossomed. New analysis of molecular characters not only confirms many earlier classifications, but also uncovers previously made errors based on morphology alone. **Molecular characters** can include differences in the amino-acid sequence of a protein, shapes of a protein, RNA, location of a gene, differences in the individual nucleotide sequence of a gene, or differences in the arrangements of genes. Phylogenies based on molecular characters assume that the more similar the sequences are in two organisms, the more closely related they are. Different genes change evolutionarily at different rates and this affects the level at which they are useful at identifying relationships. Rapidly evolving sequences are useful for determining the relationships among closely related species. More slowly evolving sequences are useful for determining the relationships between distantly related species. To determine the relationships between very different species such as Eukarya and Archaea, the genes used must be very ancient, slowly evolving genes that are present in both groups, such as the genes for ribosomal RNA. Comparing phylogenetic trees using different sequences and finding them similar helps to build confidence in the inferred relationships.

Sometimes two segments of DNA in distantly related organisms randomly share a high percentage of bases in the same locations, causing these organisms to appear closely related when they are not. For example, the fruit fly shares 60 percent of its DNA with humans.[2] These similar sections are those that make fruit flies and humans both eukaryotes and animals. This 60 percent is important but does not tell us as much about why we are different. In this situation, computer-based statistical algorithms have been developed to help identify how far back our common ancestor was, which is difficult, if not impossible with morphology alone. Ultimately, the coupled use of both morphologic and molecular information is most effective in determining phylogeny.

Optional Resource

This Click and Learn describes the process of aligning DNA sequences from different organisms so that they can be compared to one another: https://media.hhmi.org/biointeractive/click/Phylogenetic_Trees/01.html

To navigate this resource, use the forward and back arrows at the top right of the webpage. There will be short videos on most pages. Click on the Play symbol (arrow in a rectangle) to play the video.

Video





This 12.5-minute video discusses some interesting phylogenetic mysteries.
Question after watching: Of the three cases featured, which one helped you understand phylogeny better?

Classification and Phylogeny

Scientists use phylogenetic trees to show the evolutionary pathways and relationships between organisms. The hierarchical classification of groups nested within more inclusive groups is reflected in diagrams. Scientists consider phylogenetic trees to be a hypothesis of the evolutionary past because one cannot go back through time to confirm the proposed relationships. Unlike taxonomy, a phylogenetic tree can be read like a map of evolutionary history.

Scientists apply the concept of **maximum parsimony**, which states that the likeliest order of events is the simplest shortest path. For evolutionary events, this would be the path with the least number of major divergences that correlate with the evidence.

Recent genetic analysis and other advancements have found that some earlier taxonomic classifications do not reflect actual evolutionary relationships, and therefore, changes and updates must be made as new discoveries take place. Recall that phylogenetic trees are hypotheses and are modified as data becomes available. In addition, classification historically has focused on grouping organisms mainly by shared characteristics and does not necessarily illustrate how the various groups relate to each other from an evolutionary perspective. For example, despite the fact that a hippopotamus resembles a pig more than a whale, the hippopotamus may be the closest living relative to the whale. One dramatic and recent example was the breaking apart of

prokaryotic species which, until the 1970s, were all classified as 'bacteria'. Their division into Archaea and Bacteria came about after the recognition that their large genetic differences warranted their separation into two of three fundamental Domains of life.

Phylogenetic Trees

The phylogenetic tree in Figure 4.4.2.1 illustrates the pathway of evolutionary history. The pathway can be traced 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 backward to any branch point, the organisms related to it by various degrees of relatedness can be identified.

Many phylogenetic trees have a single branch point at the base representing a **common ancestor** of all the branches in the tree. This is known as a **rooted tree.** The branching from that root indicates evolutionary relationships as in Figure 4.4.2.6. The point where a split occurs, called a branch point or "**node**", represents where a single lineage evolved into distinct new ones.

A lineage that evolved early from the root and remains unbranched is called **basal taxon**. When two lineages stem from the same node, they are called **sister taxa**. A node with more than two lineages is called a **polytomy** and serves to illustrate where scientists have not definitively determined all relationships. It is important to note that while sister taxa or polytomy share an ancestor, this does not mean that one taxon evolved from the other. The branch point, or split, represents a common ancestor that existed in the past, but that no longer exists. Organisms in two taxa may have split apart at a specific node, but neither taxon gave rise to the other.

Rooted phylogenetic trees can serve as a pathway to understanding evolutionary history. The pathway can be traced 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 that species’ ancestors, as well as where lineages share a common ancestry. In addition, the tree can be used to study entire groups of organisms.

Another point to mention on phylogenetic tree structure is that *rotation at nodes does not change the information* Figure \(\PageIndex{7}\). For example, if a node was rotated and the taxon order changed, this would not alter the information because the evolution of each taxon from the node was independent of the other.

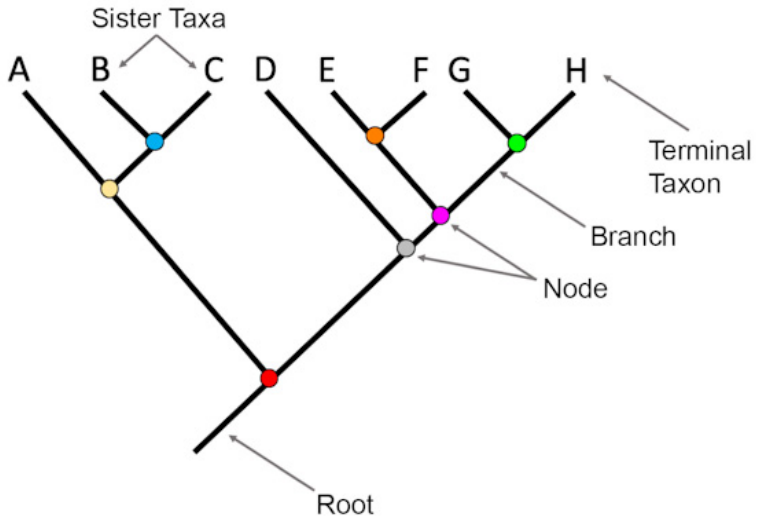


Figure 4.4.2.6: Parts of a phylogenetic tree, including terminal taxa, sister taxa, root, branch, and node. Image by Jonathan R. Hendricks (CC-BY-SA 4.0).

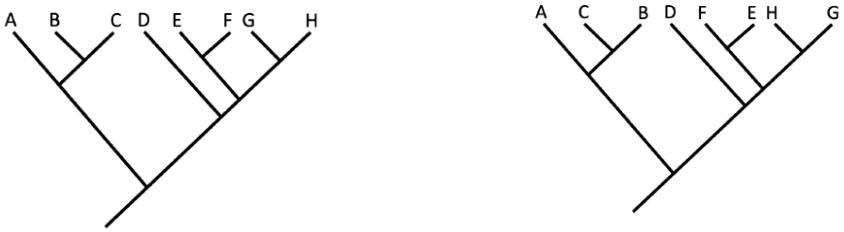
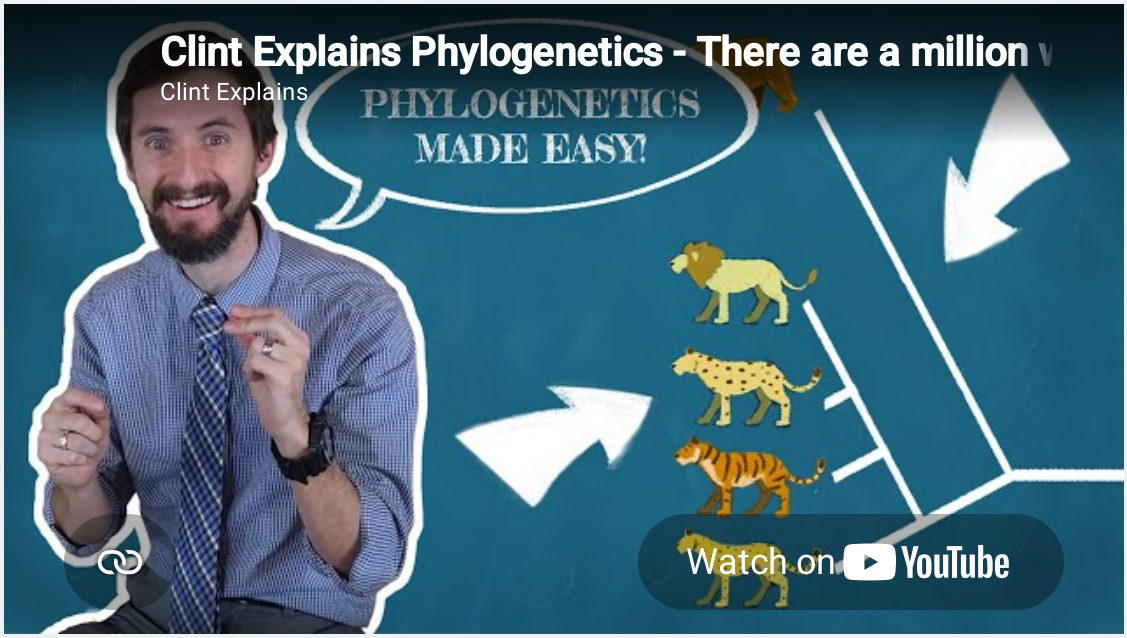
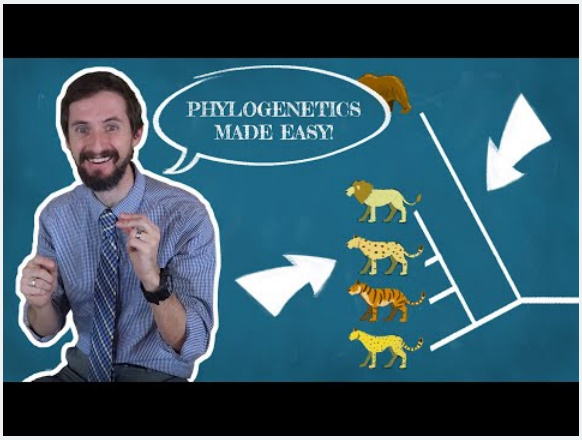


Figure 4.4.2.7: Branches may be rotated about nodes without any change in the hypothesized relationships depicted on a tree diagram. There is no difference in the evolutionary relationships being depicted between these two trees. Images by Jonathan R. Hendricks (CC-BY-SA 4.0).

Video





This 8-minute video explains phylogenetics.
Question after watching: Which big cat is most closely related to the cheetah?

Figure 4.4.2.8 is a rooted tree for the modern great apes. The two species of orangutans are sister taxa. The three branches leading to the gorilla subspecies are a polytomy. The names of the species that are at the tip of the branches are co-existing species at the current time. The common ancestor that gave rise to two currently existing species was neither of these current species, but rather an ancestral species to both that no longer exists. For example, humans did not evolve from bonobos or chimpanzees (nor did chimpanzees evolve from humans) although they are our closest living relatives. Humans, bonobos, and chimpanzees all evolved from a common ancestor that lived, scientists believe, six million years ago and looked different from modern chimpanzees, bonobos, AND humans.

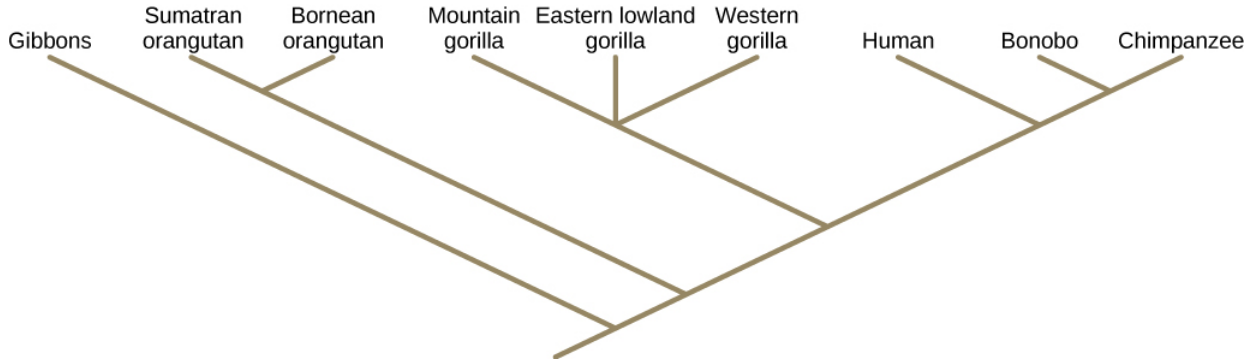


Figure 4.4.2.8: This phylogenetic tree is rooted and shows how different organisms, in this case the species and subspecies of living apes, evolved from a common ancestor.

The nodes and the branches in phylogenetic tree structure imply evolutionary change. Sometimes significant adaptive changes are identified on a branch or node. For example, in Figure 4.4.2.9, the node that gives rise to the mammal and reptile lineage from the frog lineage shows the origin of the amniotic egg character. Also, the node that gives rise to organisms with legs is indicated as the common ancestor of mammals, reptiles, amphibians, and jawed fishes.

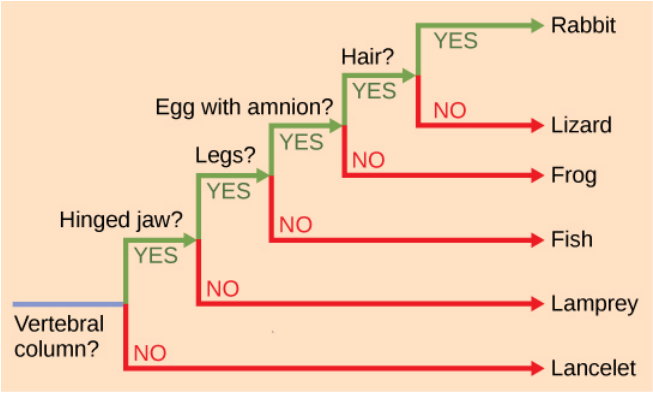


Figure 4.4.2.9: This phylogenetic tree is rooted by an organism that lacked a vertebral column. At each branch point, organisms with different characters are placed in different groups.

Understanding Phylogenetic Trees

One of the most common forms of a phylogenetic tree is a **cladogram**, seen in Figures 4.4.2.10 and 4.4.2.11. To begin this diagram, scientists often organize the homologous and analogous traits of various organisms using a system called **cladistics**. This system sorts organisms into **clades**: groups of organisms that descended from a single ancestor. For example, all organisms in the orange region in Figure 4.4.2.10 evolved from a single ancestor that had amniotic eggs. Consequently, all these organisms also have amniotic eggs and make a single clade, also called a **monophyletic group**. Clades must include all descendants from a branch point.

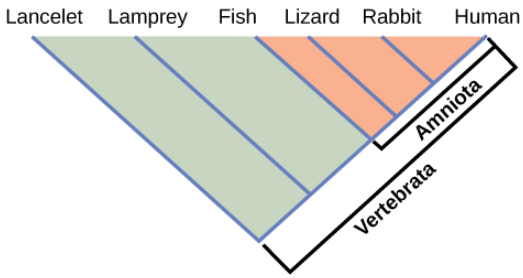


Figure 4.4.2.10: Lizards, rabbits, and humans all descend from a common ancestor that had an amniotic egg. Thus, lizards, rabbits, and humans all belong to the clade Amniota. Vertebrata is a larger clade that also includes fish and lamprey.

Clades can vary in size depending on which branch point is being referenced. The important factor is that all organisms in the clade or monophyletic group stem from a single point on the tree. This can be remembered because monophyletic breaks down into "mono," meaning one, and "phyletic," meaning evolutionary relationship. Notice in the examples of clades how each clade comes from a single point, whereas the non-clade groups show branches that do not share a single point.

? Optional Activity 4.4.2.2

On a phylogenetic tree, which term refers to lineages that diverged from the same place?

a. sister taxa
b. basal taxa
c. rooted taxa
d. dichotomous taxa

Answer

a. sister taxa

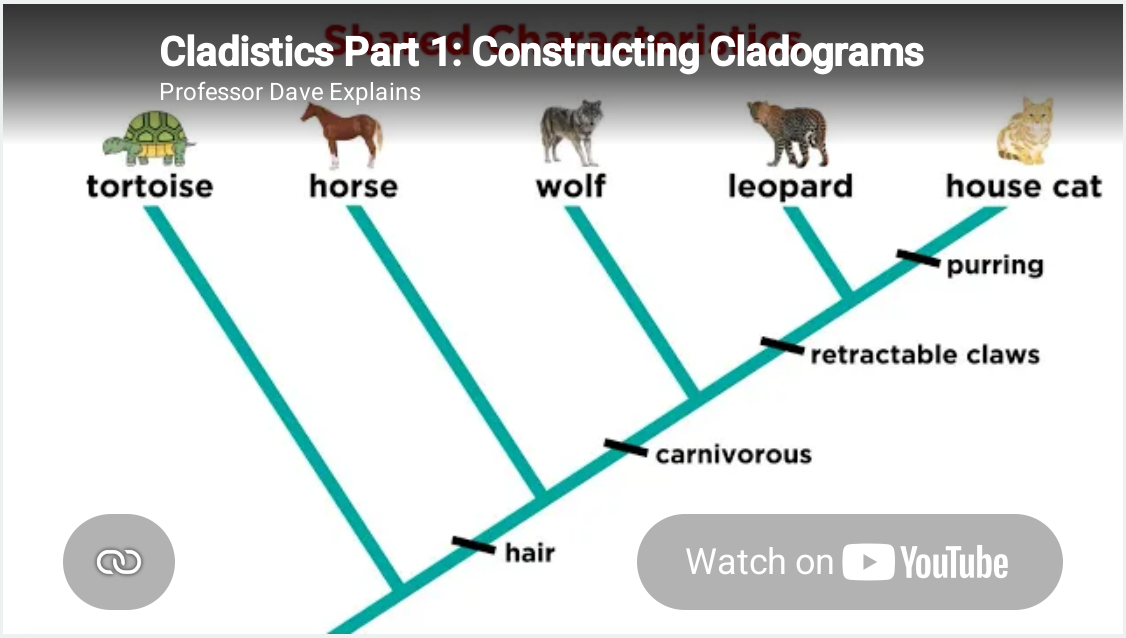
? Optional Activity 4.4.2.3

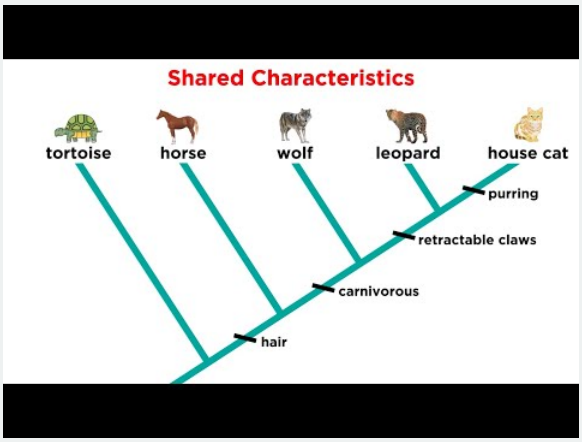
Which animals in the phylogenetic tree in Figure 4.4.2.10 belong to a clade that includes animals with hair? Which evolved first: hair or the amniotic egg?

Answer

Rabbits and humans belong in the clade that includes animals with hair. The amniotic egg evolved before hair, because the Amniota clade branches off earlier than the clade that encompasses animals with hair.

Video





This 10-minute video is the first part of a sequence that describes how cladograms are created.

Question after watching:

How does science represent the relationships between organisms?

Cladistics and 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 the genetic makeup of an organism 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).

Cladistics rests on three assumptions.

1. Living things are related by descent from a common ancestor, which is a general assumption of evolution.

2. Speciation occurs by splits of one species into two, never more than two at a time, and at one point in time. This is a simplification but is accepted by most biologists.
3. Traits change enough over time to be considered to be in a different state.

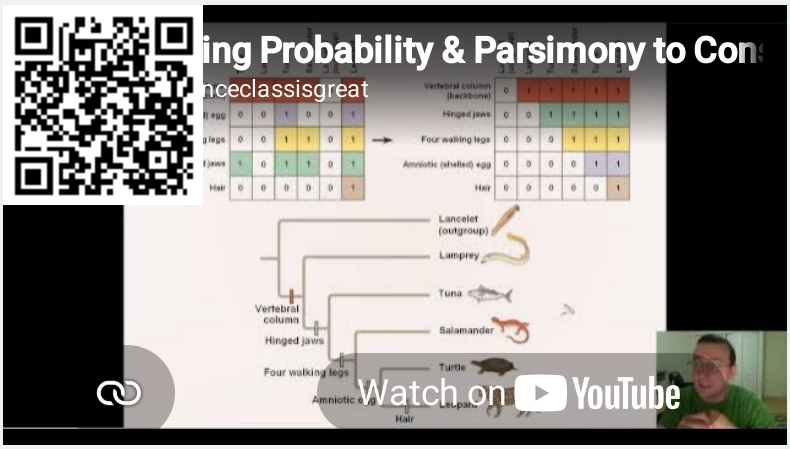
It is also assumed that one can identify the direction of change for an adaptation. In other words, we assume that an amniotic egg is a later character state than non-amniotic eggs. We know this by reference to a group outside the clade: for example, insects have non-amniotic eggs; therefore, this is the older or ancestral character state.

Cladistics compares **ingroups** and **outgroups**. An ingroup (lizard, rabbit and human in our example) is the group of taxa being analyzed in Figure 4.4.2.10. An outgroup (lancelet, lamprey and fish in our example) is a species or group of species that diverged before the lineage containing the group(s) of interest. By comparing ingroup members to each other and to the outgroup members, we can determine which characteristics are evolutionary adaptations determining the branch points of the ingroup's phylogeny.

If a characteristic is found in all members of a group, it is a **shared ancestral character**: there has been no change in the adaptation during the descent of each member of the clade. Although these traits appear interesting because they unify the clade, in cladistics they are considered not helpful when we are trying to determine the relationships of the members of the clade because every member is the same. In contrast, consider the amniotic egg characteristic of Figure 4.4.2.10. Only some of the organisms have this trait; to those that do, it is called a **shared-derived character** because this trait derived at some point but does not include all of the ancestors in the tree. This character tells us about the relationships among the members of the clade; it tells us that lizards, rabbits, and humans group more closely together than any of these organisms do with fish, lampreys, and lancelets.

The tricky aspect to shared-ancestral and shared-derived characters is the fact that these terms are relative. The same trait could be either ancestral or derived depending on the diagram being used and the organisms being compared. Scientists find these terms useful when distinguishing between clades during the building of phylogenetic trees, but it is important to remember that their meaning depends on context.

Video



In this 13-minute video, learn how biologists use genetic data to determine relationships among organisms. Question after watching: Are fungi closest to plants or animals, in evolutionary terms? What is the evidence for this?

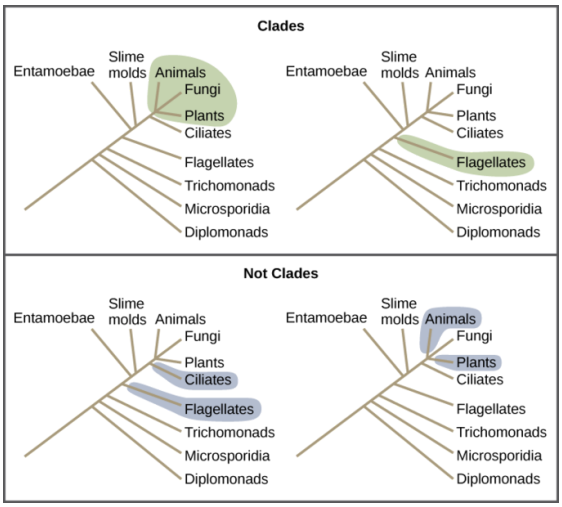


Figure 4.4.2.11: All the organisms within a clade stem from a single point on the tree. A clade may contain multiple groups, as in the case of animals, fungi, and plants, or a single group, as in the case of flagellates. Groups that diverge at a different branch point, or that do not include all groups in a single branch point, are not considered clades.

Optional Activity 4.4.2.4

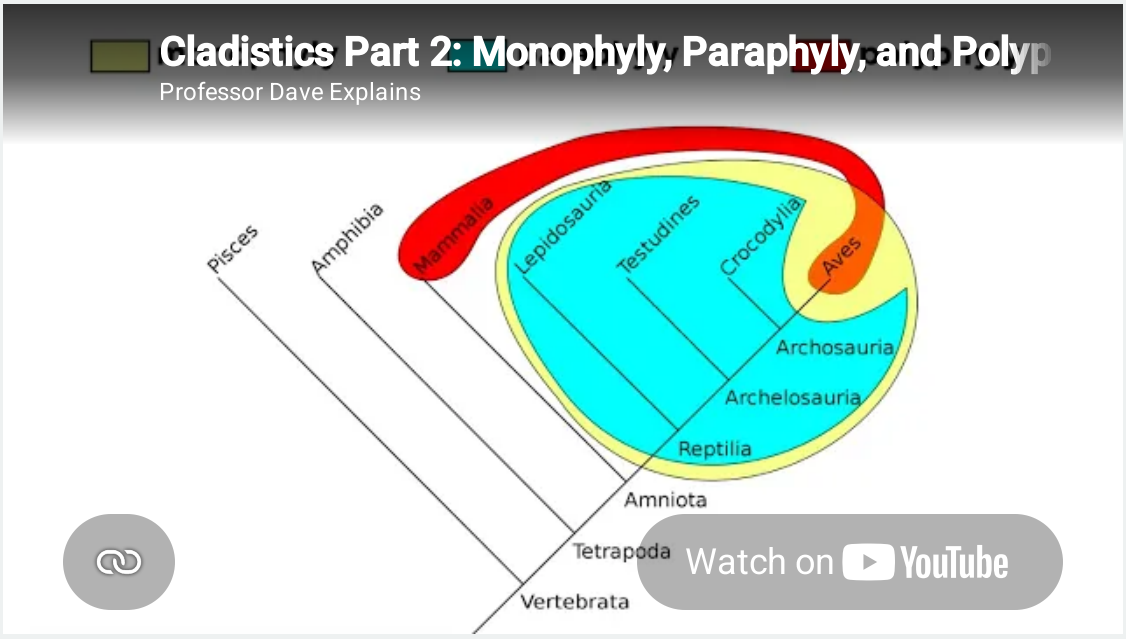
What is true about organisms that are a part of the same clade?

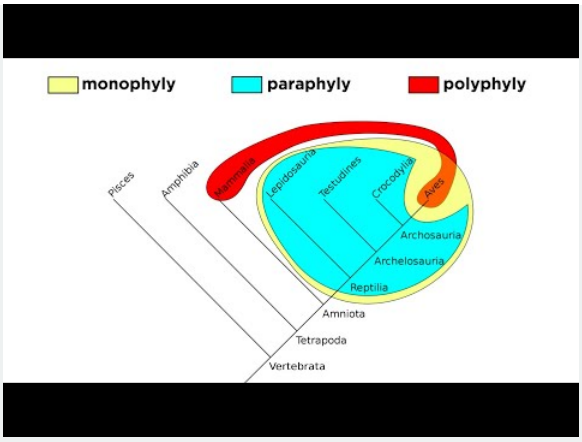
a. They all share the same basic characteristics.
b. They evolved from a shared ancestor.
c. They usually fall into the same classification taxa.
d. They have identical phylogenies.

Answer

b. They evolved from a shared ancestor.

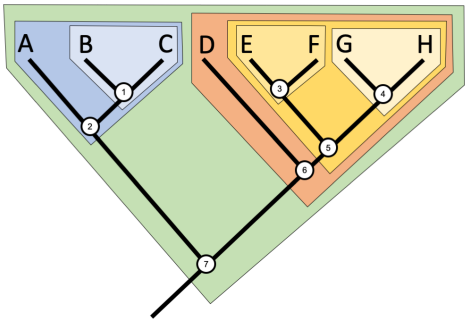
Video





This 6.5-minute video describes clades and their representation on phylogenetic trees.
Question after watching: How can you distinguish between a taxon and a clade?

? Optional Activity 4.4.2.5



Clades are not mutually exclusive, but rather form nested sets on a tree. Thus, any given taxon can belong to many clades. For example, in the tree above, Taxon B belongs to three clades, a clade defined by Node 1, a more inclusive clade defined by Node 2, and an even more inclusive clade defined by Node 7. Taxon E belongs to four clades defined by Nodes 3, 5, 6, and 7, respectively.

Try to figure out how many clades Taxon A and Taxon H belong to, and determine which nodes define each clade. (Jonathan R. Hendricks; CC-BY-SA 4.0)

Answer

Taxon A belongs to two clades and is defined by Node 2 and, more inclusively, Node 7. Taxon H belongs to four clades and is defined by Nodes (from least to most inclusive) 4, 5, 6, and 7.

Limitations of Phylogenetic Trees

It is 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 different surroundings or after the evolution of a major new adaptation, they may look quite different from each other, even more so than other groups that are not as closely related. For example, the phylogenetic tree in Figure 4.4.2.10 shows that lizards and rabbits both have amniotic eggs, whereas salamanders (within the frog lineage) do not. This means that evolutionarily, lizards and rabbits last shared a common ancestor more recently than lizards and salamanders. Superficially, however, lizards and salamanders appear more similar than lizards and rabbits.

Another aspect of phylogenetic trees is that, unless otherwise indicated, *branches do not show length of time*, they show only the order in time of evolutionary events. In other words, a long branch does not necessarily mean more time passed, nor does a short

branch mean less time passed— unless specified on the diagram. For example, in Figure 4.4.2.9, 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 4.4.2.9, 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 similar to a real tree, it does not grow in only one direction after a new branch develops. So, for the organisms in Figure 4.4.2.9, 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 similar to each other than to a close relative.

Why Does Phylogeny Matter?

In addition to enhancing our understanding of the evolutionary history of species, our own included, phylogenetic analysis has numerous practical applications. Two of those applications include understanding the evolution and transmission of disease and making decisions about conservation efforts. A 2010 study[3] of MRSA (methicillin-resistant *Staphylococcus aureus*), an antibiotic-resistant pathogenic bacterium, traced the origin and spread of the strain in 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 contrasts with 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.

A second area of usefulness for phylogenetic analysis is in conservation. Biologists argue that it is important to protect species throughout a phylogenetic tree rather than just those from one branch of the tree. Doing this preserves more of the variation produced by evolution. This is important because genetic variation makes a species more robust to disruption by being more likely to have some individuals with the traits necessary to survive a change in the environment. For example, conservation efforts should focus on a single species without sister species rather than other species that have a cluster of close sister species that recently evolved. If a single evolutionarily distinct species goes extinct, a disproportionate amount of genetic variation from the tree will be lost compared to one species in a cluster of closely related species. Closely related species share more genetic information and, therefore, some of this genetic information will be retained in living organisms versus those who have no sister species.

A study published in 2007[4] 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 several 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.

Choosing the Right Relationships

Constructing a phylogenetic tree, or cladogram, from the character data is a monumental task that is usually left up to a computer. The computer draws a tree such that all clades share the same list of derived characters. However, there are decisions to be made. For example, what if a species present in a clade is supported by all of the shared derived characters for that clade except one? One conclusion is that the trait evolved in the ancestor, but then changed back in that one species. Also, a character state that appears in two clades must be assumed to have evolved independently in those clades. These inconsistencies are common in trees drawn from character data and complicate the decision-making process about which tree most closely represents the real relationships among the taxa.

To aid in the tremendous task of choosing the best tree, scientists use maximum parsimony, which means they assume that events occurred in the simplest, most obvious way. This means that the “best” tree is the one with the fewest number of character reversals, the fewest number of independent character changes, and the fewest number of character changes throughout the tree. Computer programs search through all of the possible trees to find the small number of trees with the simplest evolutionary pathways.

? Optional Activity 4.4.2.6

Why do scientists apply the concept of maximum parsimony?

a. to decipher accurate phylogenies
b. to eliminate analogous traits
c. to identify mutations in DNA codes
d. to locate homoplasies

Answer

a. to decipher accurate phylogenies

Footnotes

1. 1 Gibbons, A. (2012, June 13). *Science Now*. Retrieved from news.sciencemag.org/scienceno...sequenced.html
2. 2 *Background on comparative genomic analysis*. (2002, December). Retrieved from http://www.genome.gov/10005835
3. 3 Harris, S.R. et al. 2010. Evolution of MRSA during hospital transmission and intercontinental spread. *Science* 327:469–474.
4. 4 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

This page titled 4.4.2: Phylogeny and Cladistics is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **12.2: Determining Evolutionary Relationships** by OpenStax is licensed CC BY 4.0.
- **12.1: Organizing Life on Earth** by OpenStax is licensed CC BY 4.0.
- **20.1A: Phylogenetic Trees** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.
- **20.2B: Building Phylogenetic Trees** by Boundless (now LumenLearning) is licensed CC BY-SA 4.0.

SECTION OVERVIEW

5: Unit V- Biological Diversity

Biodiversity is the variety of different types of life found on the Earth and the variations within species and is a measure of the variety of organisms present in different ecosystems. This can refer to genetic variation, ecosystem variation, or species variation (number of species) within an area, biome, or planet. Terrestrial biodiversity tends to be greater near the equator, which seems to be the result of the warm climate and high primary productivity. In Unit 5, the diversity of life is explored with detailed study of various organisms and discussion of emerging phylogenetic relationships. This unit moves from viruses to living organisms like bacteria, discusses the organisms formerly grouped as protists, and devotes multiple chapters to plant and animal life.

5.3: Prokaryotes - Bacteria and Archaea

- 5.3.E: Prokaryotes - Bacteria and Archaea (Exercises)

5.4: Protists

- 5.4.E: Protists (Exercises)

5.5: Fungi

- 5.5.E: Fungi (Exercises)

5.6: Introduction to Animal Diversity

- 5.6.1: Introduction
- 5.6.2: The Evolutionary History of the Animal Kingdom
- 5.6.3: Features of the Animal Kingdom
- 5.6.4: Features Used to Classify Animals
- 5.6.5: Animal Phylogeny
- 5.6.E: Introduction to Animal Diversity (Exercises)

5.7: Invertebrates

- 5.7.1: Prelude to Invertebrates
- 5.7.2: Phylum Porifera
- 5.7.3: Phylum Cnidaria
- 5.7.4: Superphylum Lophotrochozoa
- 5.7.5: Superphylum Ecdysozoa
- 5.7.6: Superphylum Deuterostomia
- 5.7.E: Invertebrates (Exercises)

5.8: Vertebrates

- 5.8.1: Prelude to Vertebrates
- 5.8.2: Chordates
- 5.8.3: Fishes
- 5.8.4: Amphibians
- 5.8.5: Reptiles
- 5.8.6: Birds
- 5.8.7: Mammals

5.8.8: The Evolution of Primates
5.8.E: Vertebrates (Exercises)

5.9: Plantae

5.9.1: Kingdom Plantae - Evolution and Phylogeny
5.9.2: Kingdom Plantae - Adaptations
5.9.E1: Seedless Plants (Exercises)
5.9.E2: Seed Plants (Exercises)

5.1: The Origin and Diversity of Life

5.1.1: Deep Time
5.1.2: Origins of Life
5.1.3: Evidence for Early Life
5.1.4: Eukaryotic Origins

5.2: Acellular Entities - Viruses, Prions, and Viroids

5.2.E: Viruses (Exercises)

Contributors

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 5: Unit V- Biological Diversity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

5.3: Prokaryotes - Bacteria and Archaea

Kingdoms Bacteria and Archaea

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
    - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe the basic structure of a typical prokaryote
- Describe important differences in structure between Archaea and Bacteria
- Identify the macronutrients needed by prokaryotes, and explain their importance
- Describe the ways in which prokaryotes get energy and carbon for life processes
- Describe the roles of prokaryotes in the carbon and nitrogen cycles

Introduction

The domain Bacteria comprises all organisms in the kingdom Bacteria, the domain Archaea comprises the rest of the prokaryotes, and the domain Eukarya comprises all eukaryotes—including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista (Figure 5.3.1).

Unit 5.1 explored the diversity of prokaryotes, their formation, and the role they played in the early Earth. Two of the three domains—Bacteria and Archaea—are prokaryotic. Prokaryotes were the first inhabitants on Earth, appearing 3.5 to 3.8 billion years ago. These organisms are abundant and ubiquitous; that is, they are found everywhere on the planet. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling springs to permanently frozen environments in Antarctica; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively contaminated regions (Figure 5.3.2). In addition, the evolution from prokaryotic to eukaryotic life was explored.

In this section, the focus will be on prokaryotes beginning with the definition of what they are. There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: the plasma membrane, which functions as a barrier for the cell and separates the cell from its environment; the cytoplasm, a jelly-like substance inside the cell; nucleic acids, the genetic material of the cell; and ribosomes, where protein synthesis takes place. Prokaryotes come in many shapes, but most fall into three categories: **cocci** (spherical), **bacilli** (rod-shaped), and **spirilli** (spiral-shaped) (Figure 5.3.3).

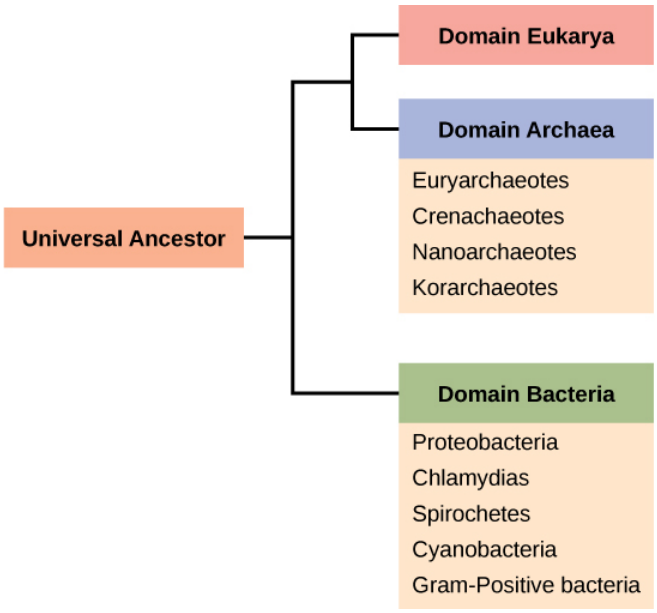


Figure 5.3.1: Bacteria and Archaea are both prokaryotes but differ enough to be placed in separate domains. An ancestor of modern Archaea is believed to have given rise to Eukarya, the third domain of life. Archaeal and bacterial phyla are shown; the evolutionary relationship between these phyla is still open to debate.



Figure 5.3.2: Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park, Wyoming, USA. The spring's vivid blue color is from the prokaryotes that thrive in its very hot waters. (credit: modification of work by Jon Sullivan)

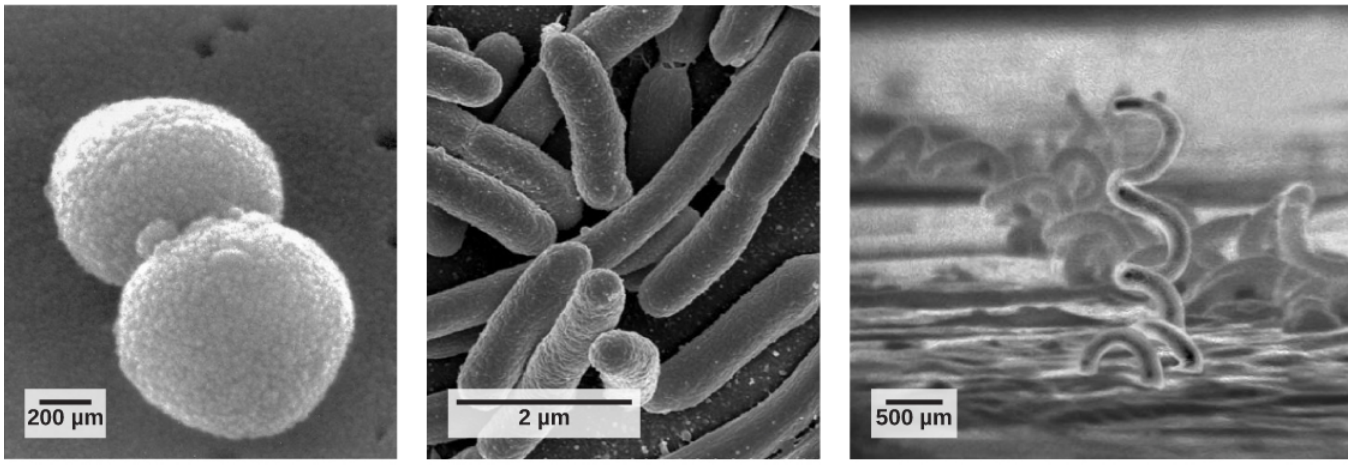
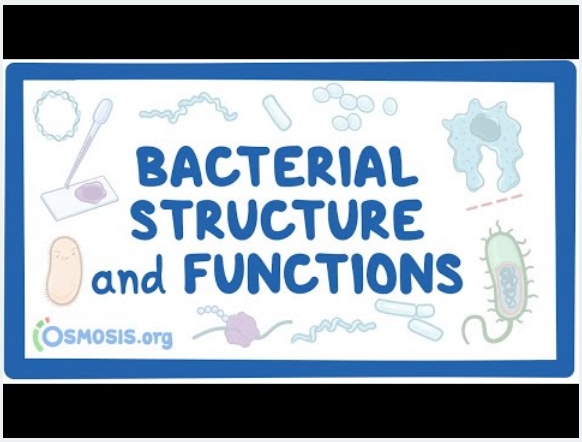


Figure 5.3.3: Prokaryotes fall into three basic categories based on their shape, visualized here using scanning electron microscopy: (a) cocci or spherical (a pair is shown); (b) bacilli or rod-shaped; and (c) spirilli or spiral-shaped. (credit a: modification of work by Janice Haney Carr, Dr. Richard Facklam, CDC; credit c: modification of work by Dr. David Cox; scale-bar data from Matt Russell)

Video





This 7-minute video describes the prokaryotic cells that play an important role in human disease and health. They can cause disease but are also part of the human microbiota and live on our skin, body and on everyday objects in our environment.

Question after watching: In Section 3.3.3, you were asked, in the section called "Current Model", to draw a Venn Diagram showing the similarities and differences between prokaryotes and eukaryotes. While watching this video, add to this Venn Diagram with new information.

Evolution Connection: The Evolution of Prokaryotes

How do scientists answer questions about the evolution of prokaryotes? Unlike animals, prokaryotes have few fossils to offer clues. Fossils of ancient prokaryotes look like tiny bubbles in rock. Scientists turn to genetics and to the principle of the molecular clock to piece together the evolution of prokaryotes. The principle of the molecular clock holds that the more recently two species have diverged, the more similar their genes (and thus proteins) will be. Conversely, species that diverged long ago will have independently accumulated more mutations and will have more dissimilar genes.

Scientists at the NASA Astrobiology Institute and at the European Molecular Biology Laboratory collaborated to analyze the molecular evolution of 32 specific proteins common to 72 species of prokaryotes.[1] The model they derived from their data indicates that three important groups of bacteria—Actinobacteria, *Deinococcus*, and Cyanobacteria (which the authors call

Terrabacteria)—were the first to colonize land. (*Deinococcus* is a genus of prokaryote that is highly resistant to ionizing radiation.) Cyanobacteria are photosynthesizers, while Actinobacteria are a group of common bacteria that include species important in the decomposition of organic wastes.

The timelines of divergence suggest that Bacteria diverged from common ancestral species between 2.5 and 3.2 billion years ago, whereas Archaea diverged earlier: between 3.1 and 4.1 billion years ago. Eukarya later diverged off the Archaean line. The work further suggests that stromatolites that formed prior to the advent of cyanobacteria (about 2.6 billion years ago) photosynthesized in an anoxic environment and that because of the modifications of the Terrabacteria for land (which includes resistance to drying and the possession of compounds that protect the organism from excess light), photosynthesis producing oxygen may be closely linked to adaptations to survive on land.

? Optional Activity 5.3.1

Which of the following consist of prokaryotic cells?

A. Bacteria and Fungi
B. Archaea and Fungi
C. Protista and Animalia
D. Bacteria and Archaea

Answer

D. Bacteria and Archaea.

The Prokaryotic Cell

Recall that prokaryotes (Figure 5.3.4) are unicellular organisms that lack organelles or internal membrane-bound structures. Therefore, they do not have a nucleus. They generally have a single chromosome—a piece of circular, double-stranded DNA located in an area of the cell called the nucleoid. Most prokaryotes have a cell wall outside the plasma membrane.

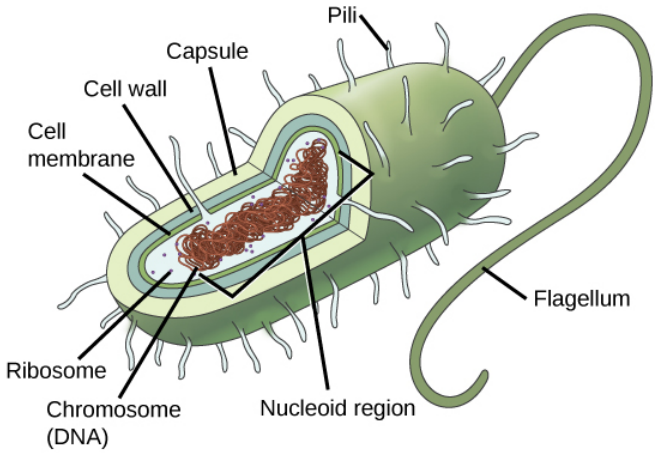
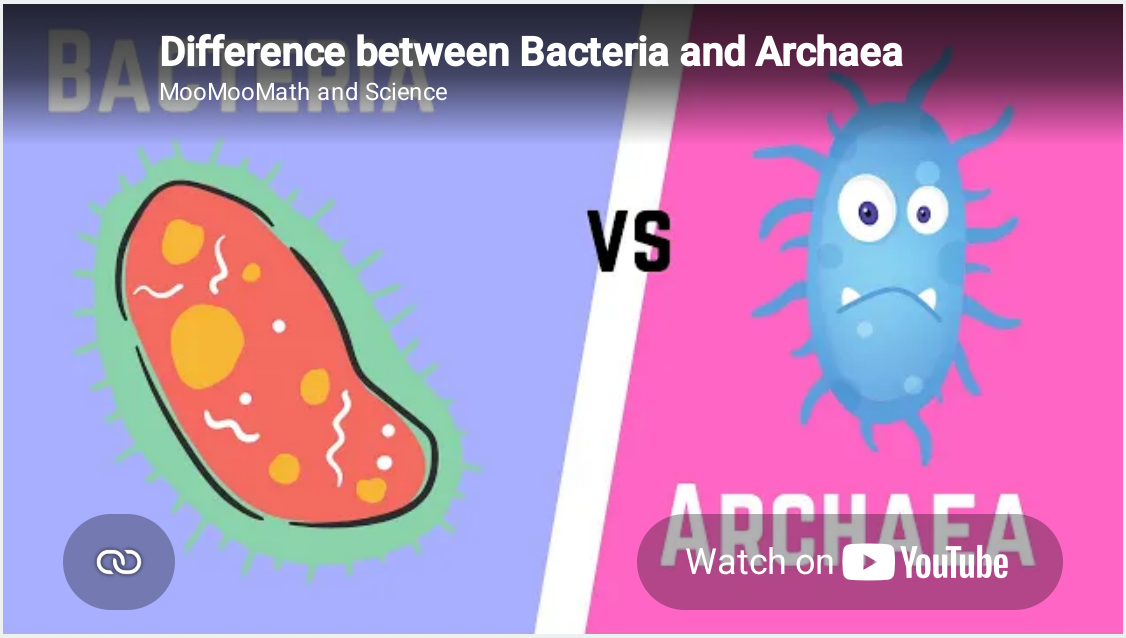
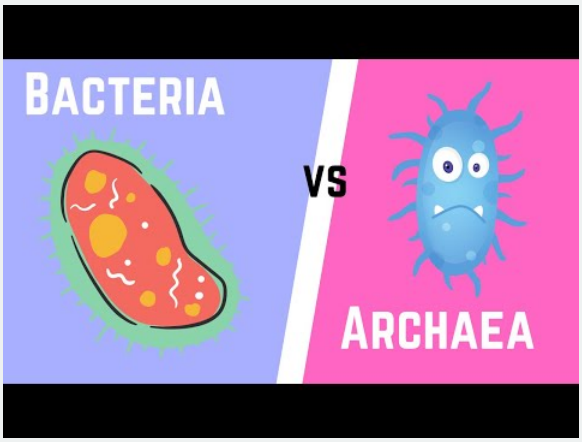


Figure 5.3.4: The features of a typical prokaryotic cell are shown. Note the absence of compartmentalization inside of the cell (which is a feature of eukaryotes)

Video





This quick 2-minute video describes the similarities and differences between the two types of prokaryotes: Bacteria and Archaea.

Question after watching: What are three similarities and three differences between Bacteria and Archaea?

The Cell Wall

The cytoplasm of prokaryotic cells has a high concentration of dissolved solutes that the cell needs to function. Therefore, the osmotic pressure within the cell is relatively high. The prokaryotic **cell wall** is a protective layer that surrounds some cells and gives them shape and rigidity. It is located outside the cell membrane and prevents osmotic lysis (bursting due to increasing volume). The chemical composition of the cell walls varies between Archaea and Bacteria and between bacterial species. The composition of their cell walls is also different from the eukaryotic cell walls found in plants (cellulose) or fungi and insects (chitin).

Bacterial cell walls contain **peptidoglycan**, composed of polysaccharide chains that are cross-linked by unusual peptides. Many of our antibiotics work by mimicking portions of these chains and therefore have specific effects on bacterial cell wall synthesis. There are more than 100 different forms of peptidoglycan. Surface layer proteins are also present on the outside of cell walls of both Archaea and Bacteria.

Some bacteria have a **capsule** outside the cell wall. Other structures are present in some prokaryotic species, but not in others (Table 5.3.1). Up to 90 percent of the cell wall in bacteria without a capsule is composed of peptidoglycan. Most of the rest is composed of acidic substances called **teichoic acids**. Teichoic acids may be covalently linked to lipids in the plasma membrane to form lipoteichoic acids. Lipoteichoic acids anchor the cell wall to the cell membrane.

Bacterial cells with a capsule have a relatively thin cell wall composed of a few layers of peptidoglycan (only 10 percent of the total cell wall), surrounded by an outer envelope containing lipopolysaccharides (LPS) and lipoproteins. This outer envelope is sometimes referred to as a second lipid bilayer. The chemistry of this outer envelope is very different, however, from that of the typical lipid bilayer that forms plasma membranes.

Researchers and clinicians like to categorize bacteria as belonging to either **Gram-positive** or **Gram-negative**. This grouping is based on the result of a quick and easy-to-administer laboratory test that can help researchers and clinicians identify a bacterial species known as Gram staining. Under the Domain Bacteria and the Kingdom Eubacteria, Gram-positive bacteria belong to one phylum; bacteria that are Gram-negative are spread over several phyla.

The different bacterial responses to the staining procedure are ultimately due to cell wall structure. The different bacterial responses to the staining procedure are ultimately due to cell wall structure. Gram-positive organisms typically lack a capsule. Gram-negative organisms have a capsule outside of their cell wall (Figure 5.3.8).

The Plasma Membrane

As with all living organisms, Bacteria and Archaea have a thin lipid bilayer, the plasma membrane, that surrounds the cell and separates the inside from the outside. Its selectively permeable nature keeps ions, proteins, and other molecules within the cell and prevents them from diffusing into the extracellular environment, while other molecules (usually small, non-polar ones) may move through the membrane. Recall that the general structure of a cell membrane is a phospholipid bilayer composed of two layers of lipid molecules. In archaeal cell membranes, glycerol is linked to isoprene (phytanyl) chains instead of fatty acids chains as in cell membranes of Bacteria and Eukarya. Some archaeal membranes are lipid monolayers instead of bilayers (Figure 5.3.5 and Table 5.3.1).

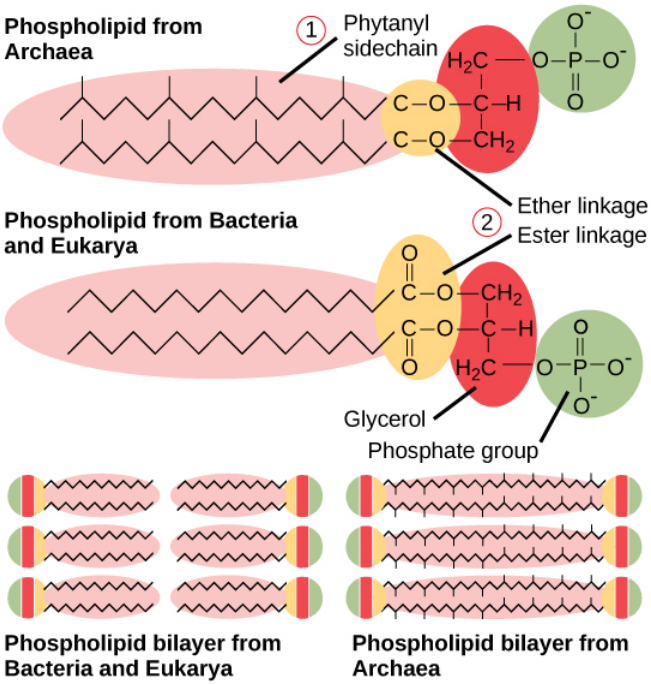
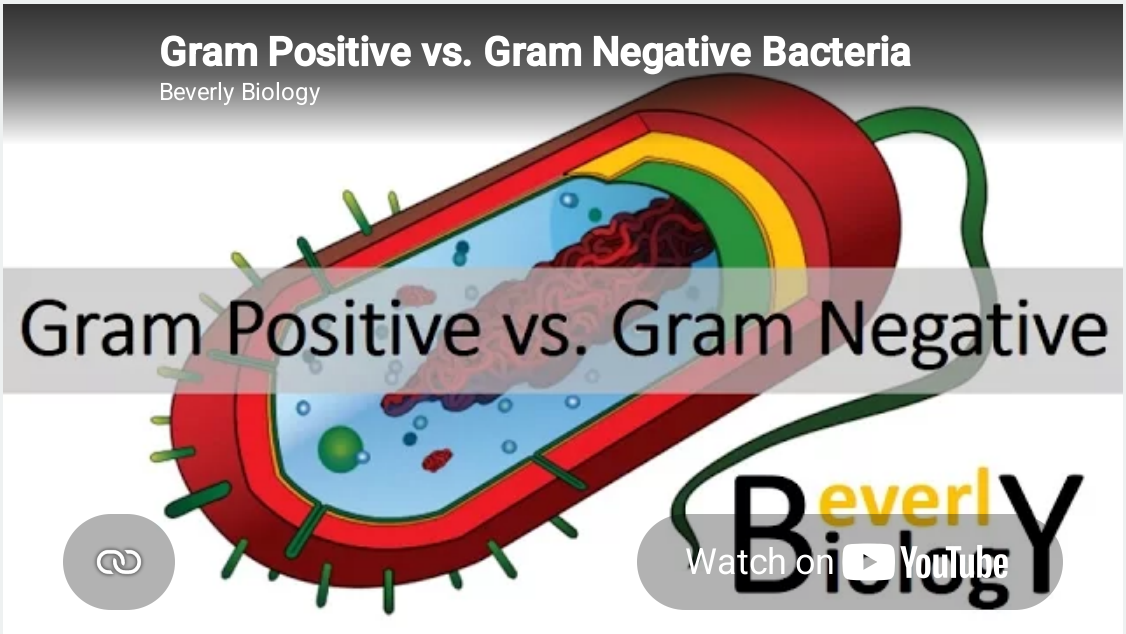
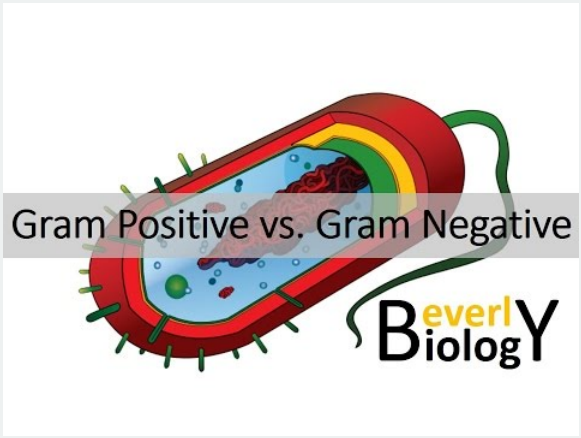


Figure 5.3.5: Archaeal phospholipids differ from those found in Bacteria and Eukarya in two ways. First, they have branched phytanyl sidechains instead of linear ones. Second, an ether bond instead of an ester bond connects the lipid to the glycerol.

Video





This 9-minute video highlights the similarities and differences between Gram-positive and Gram-negative bacteria. Question after watching: How does the process of Gram staining differentiate between the two types of bacteria?

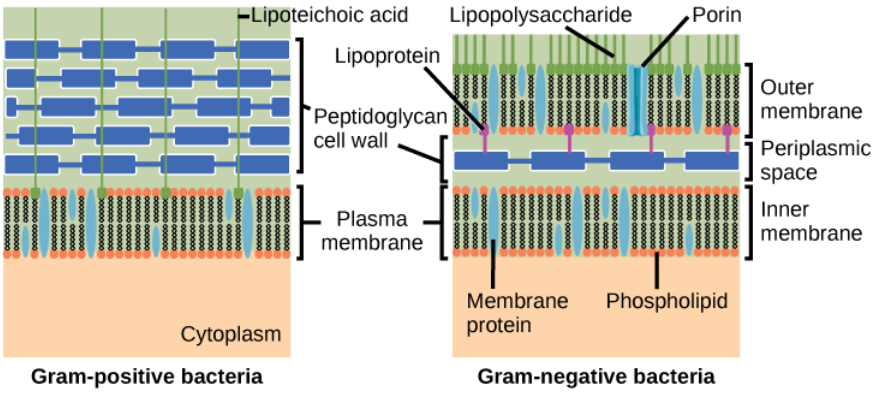


Figure 5.3.6: Bacteria are divided into two major groups: Gram-positive and Gram-negative. Both groups have a cell wall composed of peptidoglycan: in Gram-positive bacteria, the wall is thick, whereas in Gram-negative bacteria, the wall is thin. In Gram-negative bacteria, the cell wall is surrounded by an outer membrane that contains lipopolysaccharides and lipoproteins. Porins are proteins in this cell membrane that allow substances to pass through the outer membrane of Gram-negative bacteria. In Gram-positive bacteria, lipoteichoic acid anchors the cell wall to the cell membrane. (credit: modification of work by "Franciscosp2"/Wikimedia Commons)

Archaean cell walls do not have peptidoglycan (Table 5.3.1). There are four different types of Archaean cell walls. One type is composed of pseudopeptidoglycan, which is similar to peptidoglycan in morphology but contains different sugars in the polysaccharide chain. The other three types of cell walls are composed of polysaccharides, glycoproteins, or pure protein.

Table 5.3.1: Structural Differences and Similarities between Bacteria and Archaea

Structural Characteristic	Bacteria	Archaea
Cell type	Prokaryotic	Prokaryotic
Cell morphology	Variable	Variable
Cell wall	Contains peptidoglycan	Does not contain peptidoglycan
Cell membrane type	Lipid bilayer	Lipid bilayer or lipid monolayer
Plasma membrane lipids	Fatty acids	Phytanyl groups (contains the lipid isoprene)

Optional Activity 5.3.2

Prokaryotes stain as Gram-positive or Gram-negative because of differences in the cell _____.

A. wall
B. cytoplasm
C. nucleus
D. chromosome

Answer

A. wall

Optional Activity 5.3.3

Identify three differences between Bacteria and Archaea.

Answer

Responses will vary. A possible answer is: Bacteria contain peptidoglycans in the cell wall; Archaea do not. The cell membrane in Bacteria is a lipid bilayer; in Archaea, it can be a lipid bilayer or a monolayer. Bacteria contain fatty acids on the cell membrane, whereas Archaea contain phytanyl (the lipid isoprene).

Prokaryotic Reproduction

Reproduction in prokaryotes is asexual and usually takes place by **binary fission**. Recall that the DNA of a prokaryote exists as a single, circular chromosome. Prokaryotes do not undergo mitosis. Rather the chromosome is replicated and the two resulting copies separate from one another, due to the growth of the cell. The prokaryote, now enlarged, is pinched inward at its equator, and the two resulting cells, which are clones, separate. Binary fission does not provide an opportunity for genetic recombination or the generation of genetic diversity, but prokaryotes can share genes by three other mechanisms: transformation, transduction, and conjugation. All three depend on the presence of plasmids. Plasmids, which are extra-chromosomal DNA, are also present in many species of Bacteria and Archaea.

In **transformation**, the prokaryote takes in DNA found in its environment that is shed by other prokaryotes. If a nonpathogenic bacterium takes up DNA for a toxin gene from a pathogen and incorporates the new DNA into its own chromosome, it also may become pathogenic.

In **transduction**, bacteriophages, the viruses that infect bacteria, move short pieces of chromosomal DNA from one bacterium to another. Transduction results in a recombinant organism. Archaea are not affected by bacteriophages but instead have their own viruses that translocate genetic material from one individual to another.

In **conjugation**, DNA is transferred from one prokaryote to another by means of a **pilus**, which brings the organisms into contact with one another. The DNA transferred can be in the form of a plasmid or as a hybrid, containing both plasmid and chromosomal DNA. These three processes of DNA exchange are shown in Figure 5.3.7.

Reproduction can be very rapid: a few minutes for some species. This short generation time coupled with mechanisms of genetic recombination and high rates of mutation results in the rapid evolution of prokaryotes, allowing them to respond to environmental changes (such as the introduction of an antibiotic) very quickly.

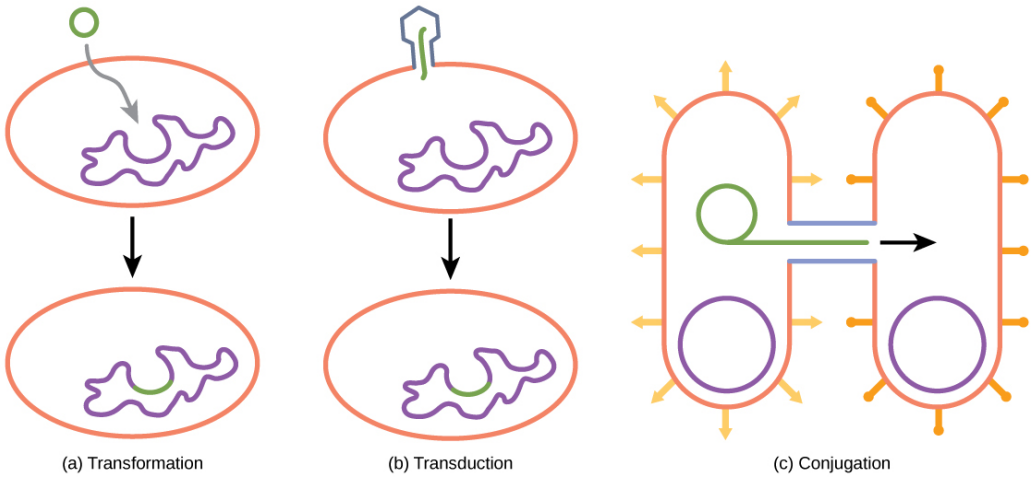
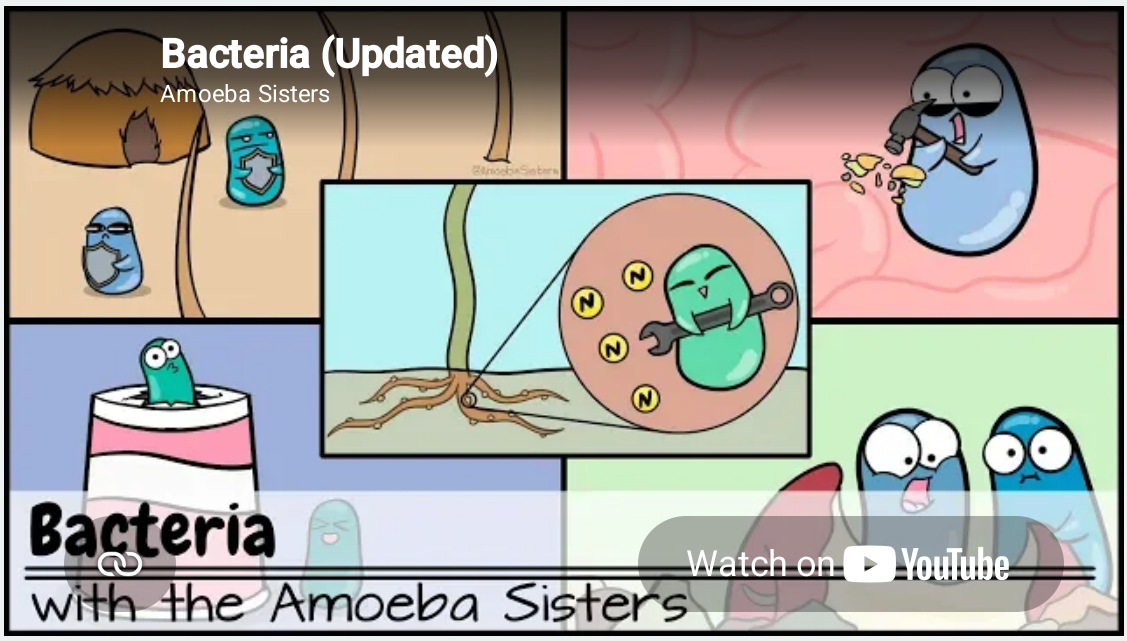
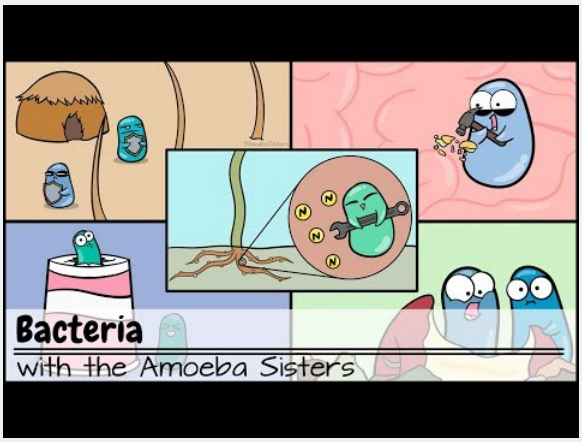


Figure 5.3.7: Besides binary fission, there are three other mechanisms by which prokaryotes can exchange DNA. In (a) transformation, the cell takes up prokaryotic DNA directly from the environment. The DNA may remain separate as plasmid DNA or be incorporated into the host genome. In (b) transduction, a bacteriophage injects DNA into the cell that contains a small fragment of DNA from a different prokaryote. In (c) conjugation, DNA is transferred from one cell to another via a mating bridge that connects the two cells after the sex pilus draws the two bacteria close enough to form the bridge.

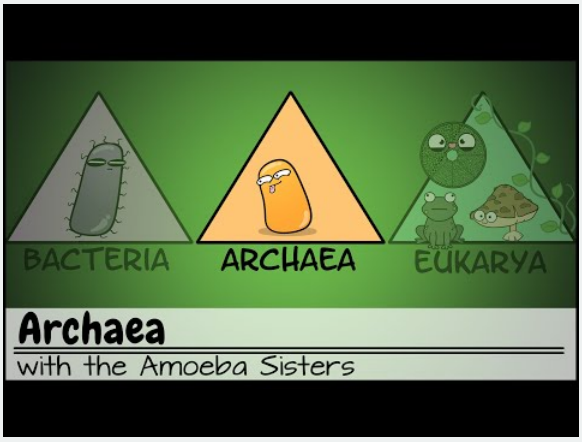
https://bio.libretexts.org/@go/page/82988

Video


Bacteria (Updated)
Amoeba Sisters
Bacteria
with the Amoeba Sisters
Watch on YouTube


Bacteria
with the Amoeba Sisters





These two videos (7.5-minutes and 6-minutes, respectively) summarize the two Domains and Kingdoms of prokaryotes: Bacteria and Archaea

Question after watching: In what ways are prokaryotes problematic and helpful for humans?

Prokaryotic Metabolism

The diverse environments and ecosystems on Earth have a wide range of conditions in terms of temperature, available nutrients, acidity, salinity, and energy sources. Prokaryotes are very well equipped to make their living out of a vast array of nutrients and conditions. To live, prokaryotes need a source of energy, a source of carbon, and some additional nutrients.

Energy and Carbon Sources

Prokaryotes can use different sources of energy to assemble macromolecules from smaller molecules. **Photoautotrophs** (or phototrophic organisms) obtain their energy from sunlight. **Chemoautotrophs** (or chemosynthetic organisms) obtain their energy from chemical compounds. Chemoautotrophs that can use organic compounds as energy sources are called **chemoorganotrophs**. Those that can also use inorganic compounds as energy sources are called **chemolitotrophs**.

Prokaryotes not only can use different sources of energy but also different sources of carbon compounds. Organisms that can fix inorganic carbon into organic molecules are called **autotrophs**. Autotrophic prokaryotes synthesize organic molecules from carbon dioxide. In contrast, **heterotrophic** prokaryotes obtain carbon from organic compounds.

To make the picture more complex, the terms that describe how prokaryotes obtain energy and carbon can be combined. Thus, photoautotrophs use energy from sunlight, and carbon from carbon dioxide and water, whereas chemoheterotrophs obtain energy and carbon from an organic chemical source. Chemolitoautotrophs obtain their energy from inorganic compounds, and they build their complex molecules from carbon dioxide. Table 5.3.2 summarizes carbon and energy sources in prokaryotes.

Table 5.3.2: Carbon and Energy Sources in Prokaryotes

	Energy Source	
Carbon Source	*Sunlight*	*Chemicals (such as sulfur dioxide, iron, etc.)*
Carbon Dioxide (from the atmosphere or water)	Photoautotrophs	Chemoautotrophs
Organic Compounds (from other organic matter)	Photoheterotrophs	Chemoheterotrophs

? Optional Activity 5.3.4

Prokaryotes that obtain their energy from chemical compounds are called _____.

A. phototrophs
B. auxotrophs
C. chemotrophs
D. lithotrophs

Answer

C. chemotrophs

Prokaryote Niches and Habitats

Prokaryotes are ubiquitous: There is no niche or ecosystem in which they are not present. Prokaryotes play many roles in the environments they occupy. The roles they play in the carbon and nitrogen cycles are vital to life on Earth.

Beneficial Prokaryotes

Not all prokaryotes are pathogenic. On the contrary, pathogens represent only a very small percentage of the diversity of the microbial world. In fact, our life would not be possible without prokaryotes. Just think about the role of prokaryotes in biogeochemical cycles.

Prokaryotes and the Carbon Cycle

Carbon is one of the most important macronutrients, and prokaryotes play an important role in the carbon cycle (Figure 5.3.8). Carbon is cycled through Earth's major reservoirs: land, the atmosphere, aquatic environments, sediments and rocks, and biomass. The movement of carbon is via carbon dioxide, which is removed from the atmosphere by land plants and marine prokaryotes in photosynthesis and is returned to the atmosphere via the respiration of chemoorganotrophic organisms, including prokaryotes, fungi, and animals. Although the largest carbon reservoir in terrestrial ecosystems is in rocks and sediments, that carbon is not readily available.

A large amount of available carbon is found in land plants. Plants, which are producers, use carbon dioxide from the air to synthesize carbon compounds (i.e. organic molecules). Related to this, one very significant source of carbon compounds is humus, which is a mixture of prokaryotes and organic materials from dead plants that have resisted decomposition. Consumers such as animals use organic compounds generated by producers and release carbon dioxide into the atmosphere when they respire. Then, bacteria and fungi, collectively called decomposers, carry out the breakdown (decomposition) of plants and animals and their organic compounds. The most important contributor of carbon dioxide to the atmosphere is microbial decomposition of dead material (dead animals, plants, and humus) through respiration.

In aqueous environments and their anoxic sediments, there is another carbon cycle taking place. In this case, the cycle is based on one-carbon compounds. In anoxic sediments, prokaryotes, mostly archaea, produce methane (CH_4). This methane moves into the zone above the sediment, which is richer in oxygen and supports bacteria called methane oxidizers that oxidize methane to carbon dioxide as a way to fuel their energy needs. The carbon dioxide produced then returns to the atmosphere.

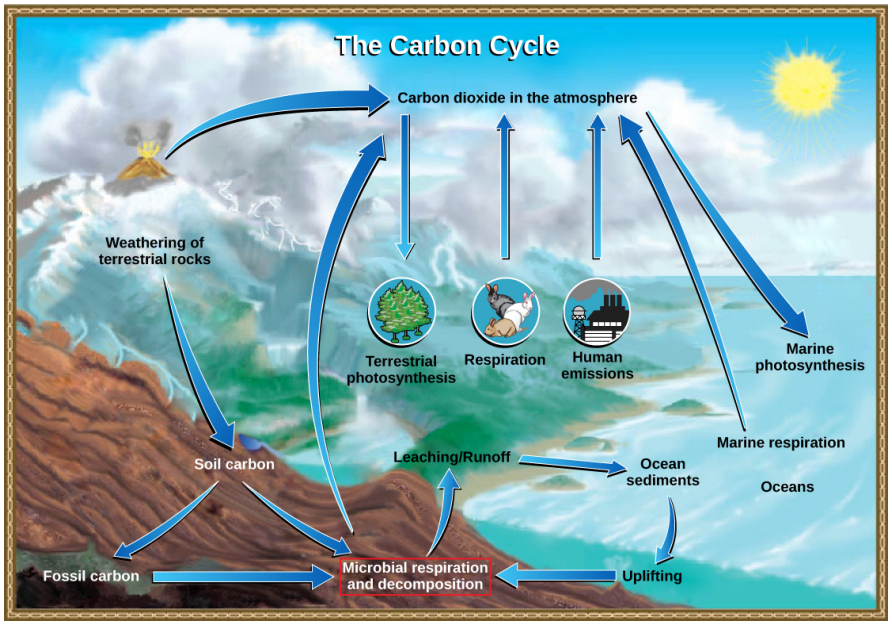


Figure 5.3.8: Prokaryotes play a significant role in continuously moving carbon through the biosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Prokaryotes and the Nitrogen Cycle

Nitrogen is a very important element for life because it is part of proteins and nucleic acids. It is a macronutrient, and in nature, it is recycled from organic compounds to ammonia (NH_3), ammonium ions (NH_4^+), nitrate (NO^{-3}), nitrite (NO^{-2}), and nitrogen gas (N_2) by myriad processes, many of which are carried out only by prokaryotes. As illustrated in Figure 5.3.9, prokaryotes are key to the nitrogen cycle. The largest pool of nitrogen available in the terrestrial ecosystem is gaseous nitrogen from the air, but this nitrogen is not usable by plants, which are primary producers.

Gaseous nitrogen is transformed, or "**fixed**" into more readily available forms such as ammonia through the process of nitrogen fixation. Bacteria in the soil or living on or in plant roots perform this function, making nitrogen available to plants. Ammonia can be used by plants or converted to other forms.

Another source of ammonia is **ammonification**, the process by which ammonia is released during the decomposition of nitrogen-containing organic compounds. The majority of the nitrogen produced during ammonification is N_2. The rest is as NH_4^+ and nitrous oxides (N_xO). Ammonia is catabolized anaerobically, meaning no oxygen needs to be present. This process can therefore take place deep in the soil by some prokaryotes.

Nitrification is the conversion of ammonium to nitrite and nitrate. Nitrification in soils is carried out by bacteria belonging to the genera *Nitrosomas*, *Nitrobacter*, and *Nitrospira*. The bacteria performs the reverse process, the reduction of nitrate from the soils to gaseous compounds such as N_2O, NO, and N_2, a process called **denitrification**. In this way, nitrogen is returned from the soil to the atmosphere.

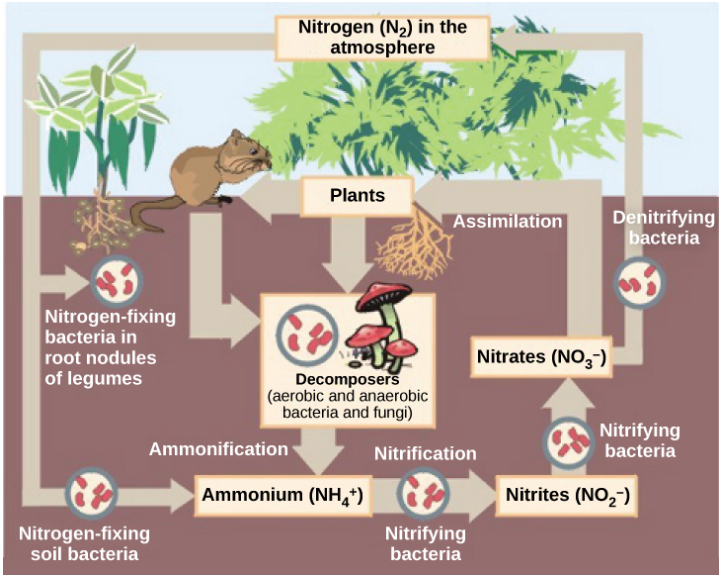


Figure 5.3.9: Prokaryotes play a key role in the nitrogen cycle. (credit: Environmental Protection Agency)

? Optional Activity 5.3.5

Ammonification is the process by which _____.

A. ammonia is released during the decomposition of nitrogen-containing organic compounds
B. ammonium is converted to nitrite and nitrate in soils
C. nitrate from soil is transformed to gaseous nitrogen compounds such as NO, N_2O, and N_2
D. gaseous nitrogen is fixed to yield ammonia

Answer

A. ammonia is released during the decomposition of nitrogen-containing organic compounds

Early Biotechnology: Cheese, Bread, Wine, Beer, and Yogurt

According to the United Nations Convention on Biological Diversity, biotechnology is “any technological application that uses biological systems, living organisms, or derivatives thereof, to make or modify products or processes for specific use."[1] The concept of “specific use” involves some sort of commercial application. Genetic engineering, artificial selection, antibiotic production, and cell culture are current topics of study in biotechnology. However, humans have used prokaryotes before the term biotechnology was even coined. In addition, some of the goods and services are as simple as cheese, bread, wine, beer, and yogurt, which employ both bacteria and other microbes, such as yeast, a fungus (Figure 5.3.2).

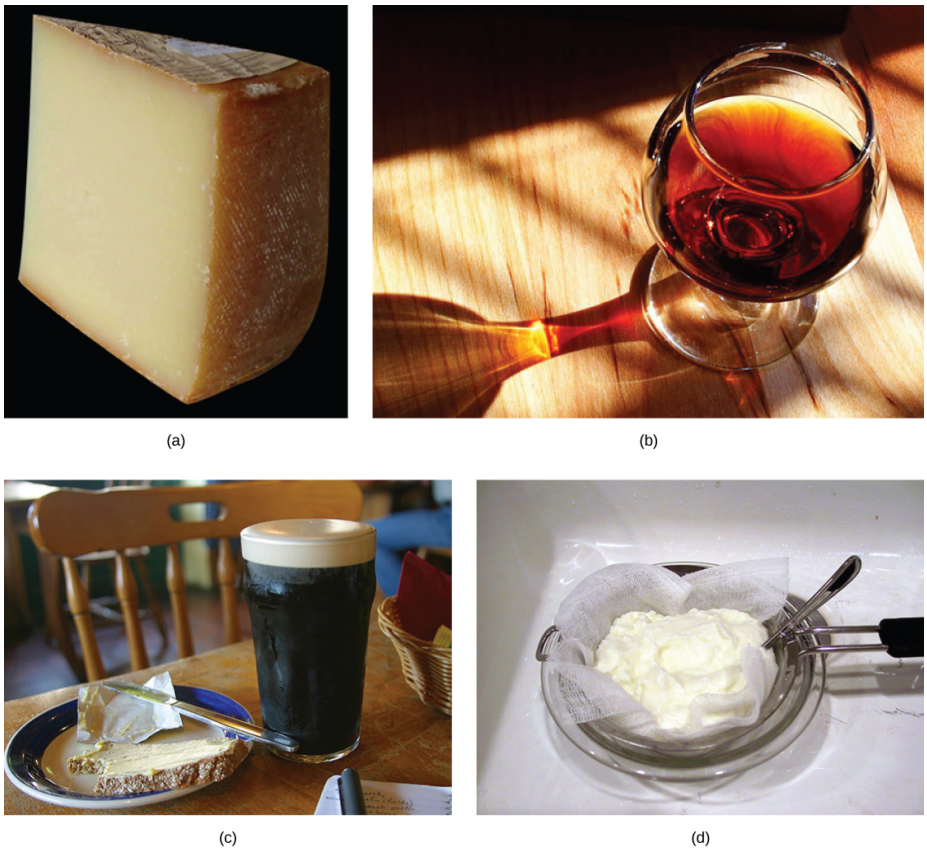
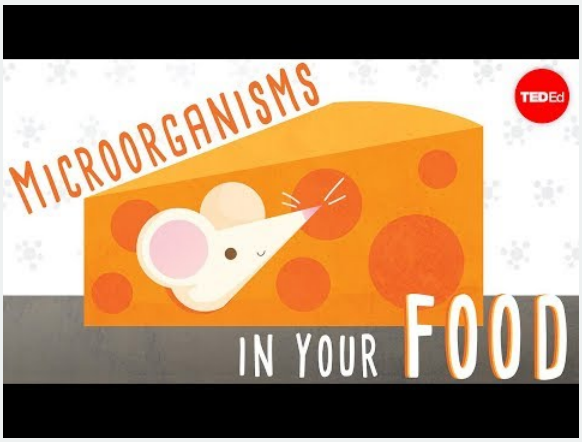


Figure 5.3.10 : Some of the products derived from the use of prokaryotes in early biotechnology include (a) cheese, (b) wine, (c) beer and bread, and (d) yogurt. (credit bread: modification of work by F. Rodrigo/Wikimedia Commons; credit wine: modification of work by Jon Sullivan; credit beer and bread: modification of work by Kris Miller; credit yogurt: modification of work by Jon Sullivan)

Cheese production began around 4,000–7,000 years ago when humans began to breed animals and process their milk. Fermentation in this case preserves nutrients: Milk will spoil relatively quickly, but when processed as cheese, it is more stable. As for beer, the oldest records of brewing are about 6,000 years old and refer to the Sumerians. Evidence indicates that the Sumerians discovered fermentation by chance. Wine has been produced for about 4,500 years, and evidence suggests that cultured milk products, like yogurt, have existed for at least 4,000 years.

Video





Where does bread get its fluffiness? Swiss cheese its holes? And what makes vinegar so sour?
Question after watching: Can you think of everyday products outside the kitchen being made using biological processes?

Microbes on the Human Body

The commensal 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.

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 5.3.11). 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.

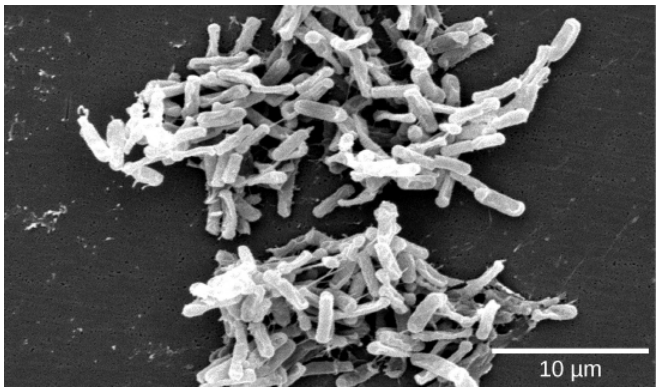
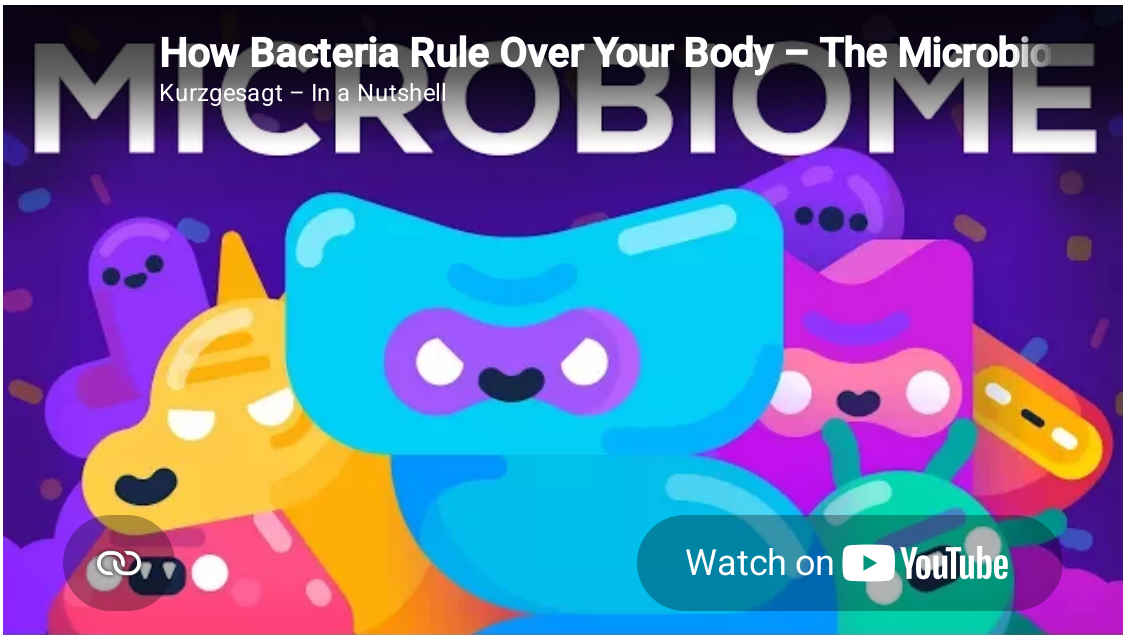
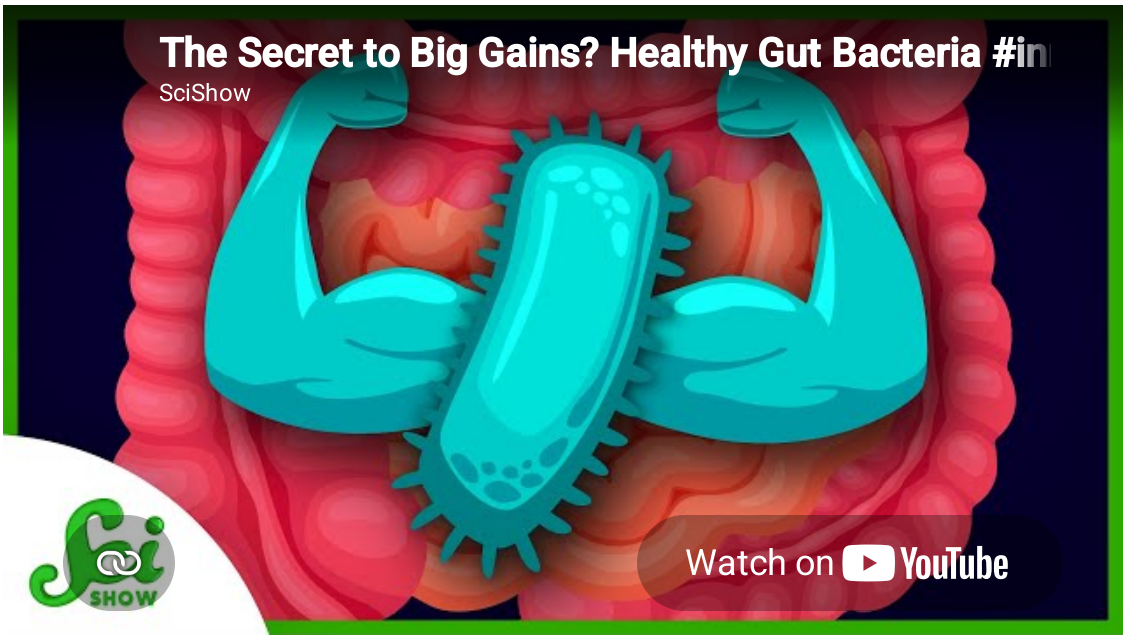


Figure 5.3.11: This scanning electron micrograph shows *Clostridium difficile*, a Gram-positive, rod-shaped bacterium that causes severe diarrhea. Infection commonly occurs after the normal gut fauna is eradicated by antibiotics. (credit: modification of work by CDC, HHS; scale-bar data from Matt Russell)

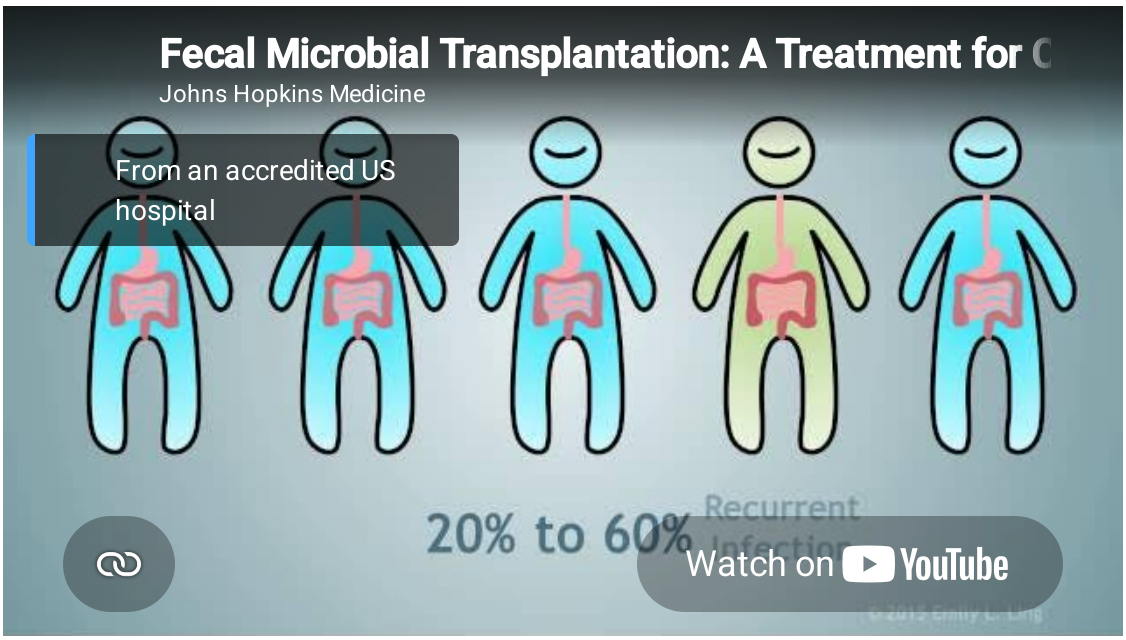
Scientists are also discovering that the absence of certain key microbes from our intestinal tract may set us up for a variety of problems. This seems to be particularly true regarding the appropriate functioning of the immune system. There are intriguing findings that suggest that the absence of these 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.

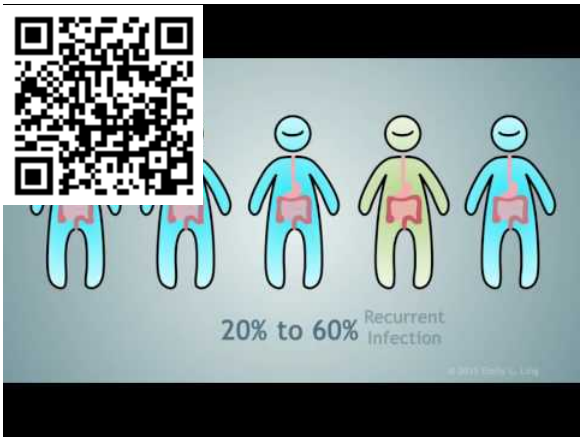





The Secret to Big Gains? Healthy Gut Bacteria #in
SciShow
Watch on YouTube




Fecal Microbial Transplantation: A Treatment for C
Johns Hopkins Medicine
From an accredited US hospital
20% to 60%
Recurrent
Watch on YouTube



Using Prokaryotes to Clean up Our Planet: Bioremediation

Microbial bioremediation is the use of prokaryotes (or microbial metabolism) to remove pollutants. Bioremediation has been used to remove agricultural chemicals (pesticides, fertilizers) that leach from soil into groundwater and the subsurface. Certain toxic metals and oxides, such as selenium and arsenic compounds, can also be removed from water by bioremediation. The reduction of SeO_4^{-2} to SeO_3^{-2} and to Se^0 (metallic selenium) is a method used to remove selenium ions from water. Mercury is an example of a toxic metal that can be removed from an environment by bioremediation. As an active ingredient of some pesticides, mercury is used in industry and is also a by-product of certain processes, such as battery production. Methyl mercury (Hg^{+2}) is usually present in very low concentrations in natural environments, but it is highly toxic because it accumulates in living tissues. Several species of bacteria can carry out the biotransformation of toxic mercury into nontoxic forms. These bacteria, such as *Pseudomonas aeruginosa*, can convert Hg^{+2} into Hg^0, which is nontoxic to humans.

One of the most useful and interesting examples of the use of prokaryotes for bioremediation purposes is the cleanup of oil spills. The importance of prokaryotes to petroleum bioremediation has been demonstrated in several oil spills in recent years, such as the Exxon Valdez spill in Alaska (1989) (Figure 5.3.12), the Prestige oil spill in Spain (2002), the spill into the Mediterranean from a Lebanon power plant (2006), and more recently, the BP oil spill in the Gulf of Mexico (2010). To clean up these spills, bioremediation is promoted by the addition of inorganic nutrients that help bacteria to grow. Hydrocarbon-degrading bacteria feed on hydrocarbons in the oil droplet, breaking down the hydrocarbons. Some species, such as *Alcanivorax borkumensis*, produce surfactants that solubilize the oil, whereas other bacteria degrade the oil into carbon dioxide. In the case of oil spills in the ocean, ongoing, natural bioremediation tends to occur, inasmuch as there are oil-consuming bacteria in the ocean prior to the spill. In addition to naturally occurring oil-degrading bacteria, humans select and engineer bacteria that possess the same capability with increased efficacy and spectrum of hydrocarbon compounds that can be processed. Under ideal conditions, it has been reported that up to 80 percent of the nonvolatile components in oil can be degraded within one year of the spill. Other oil fractions containing aromatic and highly branched hydrocarbon chains are more difficult to remove and remain in the environment for longer periods of time.



(a) (b)

Figure 5.3.12: (a) Cleaning up oil after the Valdez spill in Alaska, workers hosed oil from beaches and then used a floating boom to corral the oil, which was finally skimmed from the water surface. Some species of bacteria are able to solubilize and degrade the oil. (b) One of the most catastrophic consequences of oil spills is the damage to fauna. (credit a: modification of work by NOAA; credit b: modification of work by GOLUBENKOV, NGO: Saving Taman)





Bacteria as Pathogens

Devastating pathogen-borne diseases and plagues, both viral and bacterial in nature, have affected humans since the beginning of human history. The true cause of these diseases was not understood at the time, and some people thought that diseases were a

spiritual punishment. Over time, people came to realize that staying apart from afflicted persons, and disposing of the corpses and personal belongings of victims of illness, reduced their own chances of getting sick.

Epidemiologists study how diseases affect a population. An epidemic is a disease that occurs in an unusually high number of individuals in a population at the same time. A pandemic is a widespread, usually worldwide, epidemic. An endemic disease is a disease that is constantly present, usually at low incidence, in a population.

There are records about infectious diseases as far back as 3000 B.C. A number of significant pandemics caused by bacteria have been documented over several hundred years. Some of the most memorable pandemics led to the decline of cities and nations.

In the 21st century, infectious diseases remain among the leading causes of death worldwide, despite advances made in medical research and treatments in recent decades. A disease spreads when the pathogen that causes it is passed from one person to another. For a pathogen to cause disease, it must be able to reproduce in the host's body and damage the host in some way.

The Plague of Athens

In 430 B.C., the Plague of Athens killed one-quarter of the Athenian troops that were fighting in the great Peloponnesian War and weakened Athens' dominance and power. The plague impacted people living in overcrowded Athens as well as troops aboard ships that had to return to Athens. The source of the plague may have been identified recently when researchers from the University of Athens were able to use DNA from teeth recovered from a mass grave. The scientists identified nucleotide sequences from a pathogenic bacterium, *Salmonella enterica* serovar Typhi (Figure 5.3.13), which causes typhoid fever. This disease is commonly seen in overcrowded areas and has caused epidemics throughout recorded history.

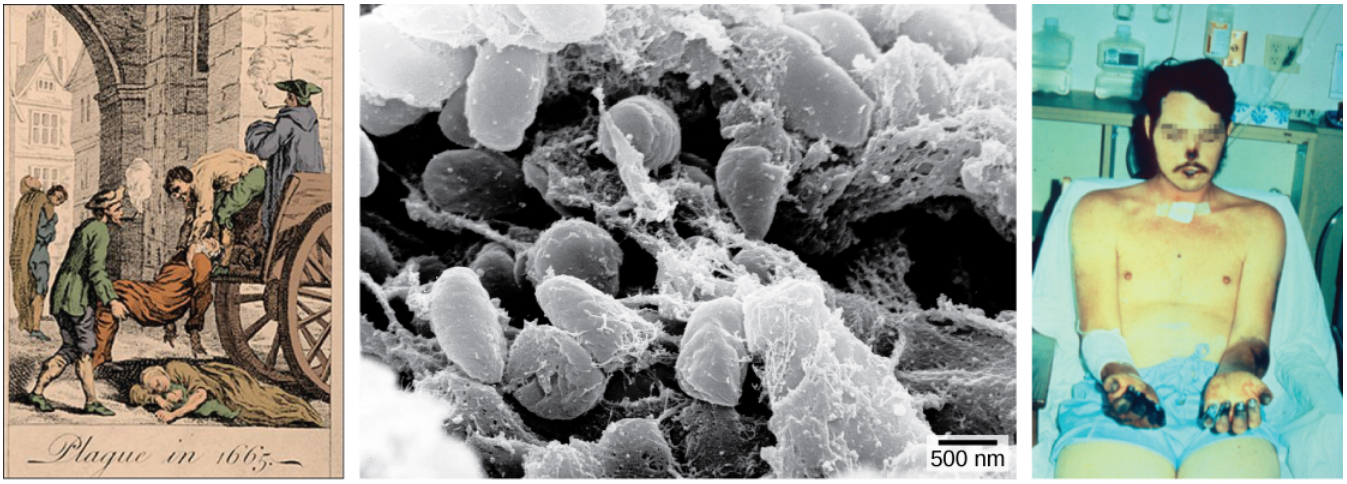


Figure 5.3.13: Salmonella enterica serovar Typhi, the causative agent of Typhoid fever, is a Gram-negative, rod-shaped gamma protobacterium. Typhoid fever, which is spread through feces, causes intestinal hemorrhage, high fever, delirium and dehydration. Today, between 16 and 33 million cases of this re-emerging disease occur annually, resulting in over 200,000 deaths. Carriers of the disease can be asymptomatic. In a famous case in the early 1900s, a cook named Mary Mallon unknowingly spread the disease to over fifty people, three of whom died. Other *Salmonella* serotypes cause food poisoning. (credit: modification of work by NCI, CDC)

Bubonic Plagues

From 541 to 750, an outbreak of what was likely a bubonic plague (the Plague of Justinian), eliminated one-quarter to one-half of the human population in the eastern Mediterranean region. The population in Europe dropped by 50 percent during this outbreak. Bubonic plague would strike Europe more than once.

One of the most devastating pandemics was the Black Death (1346 to 1361) that is believed to have been another outbreak of bubonic plague caused by the bacterium *Yersinia pestis*. It is thought to have originated initially in China and spread along the Silk Road, a network of land and sea trade routes, to the Mediterranean region and Europe, carried by rat fleas living on black rats that were always present on ships. The Black Death reduced the world's population from an estimated 450 million to about 350 to 375 million. Bubonic plague struck London hard again in the mid-1600s (Figure 5.3.14). In modern times, approximately 1,000 to 3,000 cases of plague arise globally each year. Although contracting bubonic plague before antibiotics meant almost certain death, the bacterium responds to several types of modern antibiotics, and mortality rates from plague are now very low.



(a) (b) (c)

Figure 5.3.14: The (a) Great Plague of London killed an estimated 200,000 people, or about twenty percent of the city's population. The causative agent, the (b) bacterium *Yersinia pestis*, is a Gram-negative, rod-shaped bacterium from the class Gamma Proteobacteria. The disease is transmitted through the bite of an infected flea, which is infected by a rodent. Symptoms include swollen lymph nodes, fever, seizure, vomiting of blood, and (c) gangrene. (credit b: Rocky Mountain Laboratories, NIAID, NIH; scale-bar data from Matt Russell; credit c: Textbook of Military Medicine, Washington, D.C., U.S. Dept. of the Army, Office of the Surgeon General, Borden Institute)

Migration of Diseases to New Populations

Over the centuries, Europeans tended to develop genetic immunity to endemic infectious diseases, but when European conquerors reached the western hemisphere, they brought with them disease-causing bacteria and viruses, which triggered epidemics that completely devastated populations of Native Americans, who had no natural resistance to many European diseases. It has been estimated that up to 90 percent of Native Americans died from infectious diseases after the arrival of Europeans, making conquest of the New World a foregone conclusion.

Emerging and Re-emerging Diseases

The distribution of a particular disease is dynamic. Therefore, changes in the environment, the pathogen, or the host population can dramatically impact the spread of a disease. According to the World Health Organization (WHO) an **emerging disease** is one that has appeared in a population for the first time, or that may have existed previously but is rapidly increasing in incidence or geographic range. This definition also includes re-emerging diseases that were previously under control. Approximately 75 percent of recently emerging infectious diseases affecting humans are zoonotic diseases, zoonoses, diseases that primarily infect animals and are transmitted to humans; some are of viral origin and some are of bacterial origin. Brucellosis is an example of a prokaryotic zoonosis that is re-emerging in some regions, and necrotizing fasciitis (commonly known as flesh-eating bacteria) has been increasing in virulence for the last 80 years for unknown reasons.

Some of the present emerging diseases are not actually new, but are diseases that were catastrophic in the past (Figure 5.3.15). They devastated populations and became dormant for a while, just to come back, sometimes more virulent than before, as was the case with bubonic plague. Other diseases, like tuberculosis, were never eradicated but were under control in some regions of the world until coming back, mostly in urban centers with high concentrations of immunocompromised people. The WHO has identified certain diseases whose worldwide re-emergence should be monitored. Among these are two viral diseases (dengue fever and yellow fever), and three bacterial diseases (diphtheria, cholera, and bubonic plague). The war against infectious diseases has no foreseeable end.

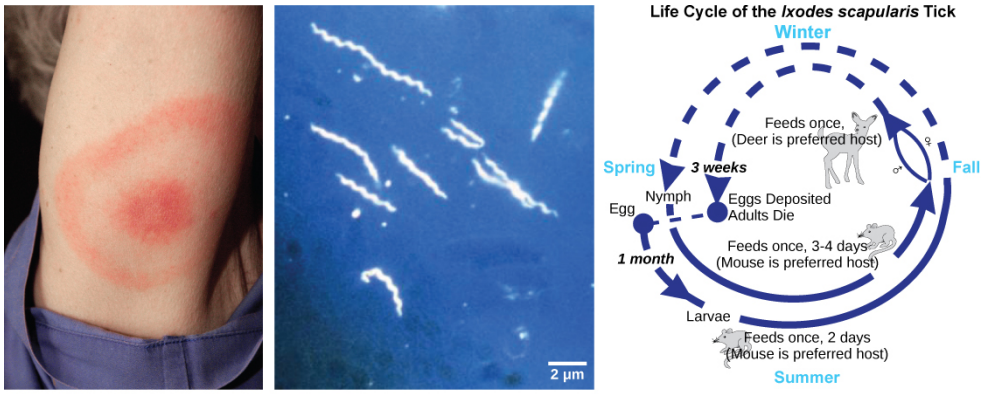


Figure 5.3.15: Lyme disease often, but not always, results in (a) a characteristic bullseye rash. The disease is caused by a (b) Gram-negative spirochete bacterium of the genus *Borrelia*. The bacteria (c) infect ticks, which in turns infect mice. Deer are the preferred secondary host, but the ticks also may feed on humans. Untreated, the disease causes chronic disorders in the nervous system, eyes, joints, and heart. The disease is named after Lyme, Connecticut, where an outbreak occurred in 1995 and has subsequently spread. The disease is not new, however. Genetic evidence suggests that Ötzi the Iceman, a 5,300-year-old mummy found in the Alps, was infected with *Borrelia*. (credit a: James Gathany, CDC; credit b: CDC; scale-bar data from Matt Russell)

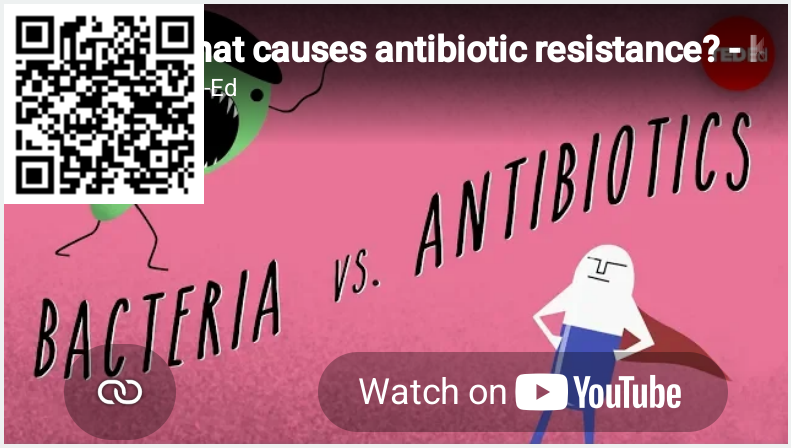
Biofilms and Disease

Recall that biofilms are microbial communities that are very difficult to destroy. They are responsible for diseases such as infections in patients with cystic fibrosis, Legionnaires' disease, and otitis media. They produce dental plaque and colonize catheters, prostheses, transcutaneous and orthopedic devices, contact lenses, and internal devices such as pacemakers. They also form in open wounds and burned tissue. In healthcare environments, biofilms grow on hemodialysis machines, mechanical ventilators, shunts, and other medical equipment. In fact, 65 percent of all infections acquired in the hospital (nosocomial infections) are attributed to biofilms. Biofilms are also related to diseases contracted from food because they colonize the surfaces of vegetable leaves and meat, as well as food-processing equipment that isn't adequately cleaned.

Biofilm infections develop gradually; sometimes, they do not cause symptoms immediately. They are rarely resolved by host defense mechanisms. Once an infection by a biofilm is established, it is very difficult to eradicate, because biofilms tend to be resistant to most of the methods used to control microbial growth, including antibiotics. Biofilms respond poorly or only temporarily to antibiotics; it has been said that they can resist up to 1,000 times the antibiotic concentrations used to kill the same bacteria when they are free-living or planktonic. An antibiotic dose that large would harm the patient; therefore, scientists are working on new ways to get rid of biofilms.

Antibiotics: Are We Facing a Crisis?

Video



Explore how bacteria become resistant to antibiotics and turn into superbugs, and what scientists are doing to stop it.

> *Question after watching: Not all bacteria are antibiotic-resistant. How might some of those non-resistant bacteria become antibiotic-resistant?*

The word *antibiotic* comes from the Greek *anti* meaning “against” and *bios* meaning “life.” An antibiotic is a chemical, produced either by microbes or synthetically, that is hostile to the growth of other organisms. Today’s news and media often address concerns about an antibiotic crisis. Are the antibiotics that easily treated bacterial infections in the past becoming obsolete? Are there new “superbugs”—bacteria that have evolved to become more resistant to our arsenal of antibiotics? Is this the beginning of the end of antibiotics? All these questions challenge the healthcare community.

One of the main causes of resistant bacteria is the abuse of antibiotics. The imprudent and excessive use of antibiotics has resulted in the natural selection of resistant forms of bacteria. The antibiotic kills most of the infecting bacteria, and therefore only the resistant forms remain. These resistant forms reproduce, resulting in an increase in the proportion of resistant forms over non-resistant ones. Another major misuse of antibiotics is in patients with colds or the flu, for which antibiotics are useless. Another problem is the excessive use of antibiotics in livestock. The routine use of antibiotics in animal feed promotes bacterial resistance as well. In the United States, 70 percent of the antibiotics produced are fed to animals. These antibiotics are given to livestock in low doses, which maximizes the probability of resistance developing, and these resistant bacteria are readily transferred to humans.

Footnotes

1. 1 Battistuzzi, FU, Feijao, A, and Hedges, SB. A genomic timescale of prokaryote evolution: Insights into the origin of methanogenesis, phototrophy, and the colonization of land. *BioMed Central: Evolutionary Biology* 4 (2004): 44, doi:10.1186/1471-2148-4-44.

5.3.E: Prokaryotes - Bacteria and Archaea (Exercises)

This page titled 5.3: Prokaryotes - Bacteria and Archaea is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

5.3.E: Prokaryotes - Bacteria and Archaea (Exercises)

22.1: Prokaryotic Diversity

Prokaryotes are ubiquitous. They cover every imaginable surface where there is sufficient moisture, and they live on and inside of other living things. In the typical human body, prokaryotic cells outnumber human body cells by about ten to one. They comprise the majority of living things in all ecosystems. Some prokaryotes thrive in environments that are inhospitable for most living things.

Review Questions

The first forms of life on Earth were thought to be_____.

A. single-celled plants
B. prokaryotes
C. insects
D. large animals such as dinosaurs

Answer

B

Microbial mats _____.

A. are the earliest forms of life on Earth
B. obtained their energy and food from hydrothermal vents
C. are multi-layered sheet of prokaryotes including mostly bacteria but also archaea
D. all of the above

Answer

D

The first organisms that oxygenated the atmosphere were

A. cyanobacteria
B. phototrophic organisms
C. anaerobic organisms
D. all of the above

Answer

A

Halophiles are organisms that require_____.

A. a salt concentration of at least 0.2 M
B. high sugar concentration
C. the addition of halogens
D. all of the above

Answer

A

Free Response

Describe briefly how you would detect the presence of a non-culturable prokaryote in an environmental sample.

Answer

As the organisms are non-culturable, the presence could be detected through molecular techniques, such as PCR.

Why do scientists believe that the first organisms on Earth were extremophiles?

Answer

Because the environmental conditions on Earth were extreme: high temperatures, lack of oxygen, high radiation, and the like.

22.2: Structure of Prokaryotes

There are many differences between prokaryotic and eukaryotic cells. However, all cells have four common structures: the plasma membrane, which functions as a barrier for the cell and separates the cell from its environment; the cytoplasm, a jelly-like substance inside the cell; nucleic acids, the genetic material of the cell; and ribosomes, where protein synthesis takes place.

Review Questions

The presence of a membrane-enclosed nucleus is a characteristic of _____.

A. prokaryotic cells
B. eukaryotic cells
C. all cells
D. viruses

Answer

B

Which of the following consist of prokaryotic cells?

A. bacteria and fungi
B. archaea and fungi
C. protists and animals
D. bacteria and archaea

Answer

D

The cell wall is _____.

A. interior to the cell membrane
B. exterior to the cell membrane
C. a part of the cell membrane
D. interior or exterior, depending on the particular cell

Answer

B

Organisms most likely to be found in extreme environments are _____.

A. fungi
B. bacteria
C. viruses
D. archaea

Answer

B

Prokaryotes stain as Gram-positive or Gram-negative because of differences in the cell _____.

A. wall
B. cytoplasm
C. nucleus
D. chromosome

Answer

A

Pseudopeptidoglycan is a characteristic of the walls of _____.

A. eukaryotic cells
B. bacterial prokaryotic cells
C. archaean prokaryotic cells
D. bacterial and archaean prokaryotic cells

Answer

C

The lipopolysaccharide layer (LPS) is a characteristic of the wall of _____.

A. archaean cells
B. Gram-negative bacteria
C. bacterial prokaryotic cells
D. eukaryotic cells

Answer

B

Free Response

Mention three differences between bacteria and archaea.

Answer

Responses will vary. A possible answer is: Bacteria contain peptidoglycan in the cell wall; archaea do not. The cell membrane in bacteria is a lipid bilayer; in archaea, it can be a lipid bilayer or a monolayer. Bacteria contain fatty acids on the cell membrane, whereas archaea contain phytanyl.

Explain the statement that both types, bacteria and archaea, have the same basic structures, but built from different chemical components.

Answer

Both bacteria and archaea have cell membranes and they both contain a hydrophobic portion. In the case of bacteria, it is a fatty acid; in the case of archaea, it is a hydrocarbon (phytanyl). Both bacteria and archaea have a cell wall that protects them. In the case of bacteria, it is composed of peptidoglycan, whereas in the case of archaea, it is pseudopeptidoglycan, polysaccharides, glycoproteins, or pure protein. Bacterial and archaeal flagella also differ in their chemical structure.

22.3: Prokaryotic Metabolism

Prokaryotes are metabolically diverse organisms. There are many different environments on Earth with various energy and carbon sources, and variable conditions. Prokaryotes have been able to live in every environment by using whatever energy and carbon sources are available. Prokaryotes fill many niches on Earth, including being involved in nutrient cycles such as nitrogen and carbon cycles, decomposing dead organisms, and thriving inside living organisms, including humans.

Review Questions

Which of the following elements is *not* a micronutrient?

A. boron
B. calcium
C. chromium
D. manganese

Answer

B

Prokaryotes that obtain their energy from chemical compounds are called _____.

A. phototrophs
B. auxotrophs
C. chemotrophs
D. lithotrophs

Answer

C

Ammonification is the process by which _____.

A. ammonia is released during the decomposition of nitrogen-containing organic compounds
B. ammonium is converted to nitrite and nitrate in soils
C. nitrate from soil is transformed to gaseous nitrogen compounds such as NO, N_2O, and N_2
D. gaseous nitrogen is fixed to yield ammonia

Answer

A

Plants use carbon dioxide from the air and are therefore called _____.

A. consumers
B. producers
C. decomposer
D. carbon fixers

Answer

B

Free Response

Think about the conditions (temperature, light, pressure, and organic and inorganic materials) that you may find in a deep-sea hydrothermal vent. What type of prokaryotes, in terms of their metabolic needs (autotrophs, phototrophs, chemotrophs, etc.), would you expect to find there?

Answer

Responses will vary. In a deep-sea hydrothermal vent, there is no light, so prokaryotes would be chemotrophs instead of phototrophs. The source of carbon would be carbon dioxide dissolved in the ocean, so they would be autotrophs. There is not a lot of organic material in the ocean, so prokaryotes would probably use inorganic sources, thus they would be chemolitotrophs. The temperatures are very high in the hydrothermal vent, so the prokaryotes would be thermophilic.

22.4: Bacterial Diseases in Humans

Devastating pathogen-borne diseases and plagues, both viral and bacterial in nature, have affected humans since the beginning of human history. The true cause of these diseases was not understood at the time, and some people thought that diseases were a spiritual punishment. Over time, people came to realize that staying apart from afflicted persons, and disposing of the corpses and personal belongings of victims of illness, reduced their own chances of getting sick.

Review Questions

A disease that is constantly present in a population is called _____.

A. pandemic
B. epidemic
C. endemic
D. re-emerging

Answer

C

Which of the statements about biofilms is incorrect?

A. Biofilms are considered responsible for diseases such as cystic fibrosis.
B. Biofilms produce dental plaque, and colonize catheters and prostheses.
C. Biofilms colonize open wounds and burned tissue.
D. All statements are incorrect.

Answer

D

Which of these statements is true?

A. An antibiotic is any substance produced by a organism that is antagonistic to the growth of prokaryotes.
B. An antibiotic is any substance produced by a prokaryote that is antagonistic to the growth of other viruses.
C. An antibiotic is any substance produced by a prokaryote that is antagonistic to the growth of eukaryotic cells.
D. An antibiotic is any substance produced by a prokaryote that prevents growth of the same prokaryote.

Answer

A

Free Response

Explain the reason why the imprudent and excessive use of antibiotics has resulted in a major global problem.

Answer

Antibiotics kill bacteria that are sensitive to them; thus, only the resistant ones will survive. These resistant bacteria will reproduce, and therefore, after a while, there will be only resistant bacteria.

Researchers have discovered that washing spinach with water several times does not prevent foodborne diseases due to *E. coli*. How can you explain this fact?

Answer

E. coli colonizes the surface of the leaf, forming a biofilm that is more difficult to remove than free (planktonic) cells. Additionally, bacteria can be taken up in the water that plants are grown in, thereby entering the plant tissues rather than simply residing on the leaf surface.

22.5: Beneficial Prokaryotes

Not all prokaryotes are pathogenic. On the contrary, pathogens represent only a very small percentage of the diversity of the microbial world. In fact, our life would not be possible without prokaryotes. Just think about the role of prokaryotes in biogeochemical cycles.

Review Questions

Which of these occurs through symbiotic nitrogen fixation?

A. The plant benefits from using an endless source of nitrogen.
B. The soil benefits from being naturally fertilized.
C. Bacteria benefit from using photosynthates from the plant.
D. All of the above occur.

Answer

D

Synthetic compounds found in an organism but not normally produced or expected to be present in that organism are called _____.

A. pesticides
B. bioremediators
C. recalcitrant compounds
D. xenobiotics

Answer

D

Bioremediation includes _____.

A. the use of prokaryotes that can fix nitrogen
B. the use of prokaryotes to clean up pollutants
C. the use of prokaryotes as natural fertilizers
D. All of the above

Answer

B

Free Response

Your friend believes that prokaryotes are always detrimental and pathogenic. How would you explain to them that they are wrong?

Answer

Remind them of the important roles prokaryotes play in decomposition and freeing up nutrients in biogeochemical cycles; remind them of the many prokaryotes that are not human pathogens and that fill very specialized niches. Furthermore, our normal bacterial symbionts are crucial for our digestion and in protecting us from pathogens.

This page titled 5.3.E: Prokaryotes - Bacteria and Archaea (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **22.E: Prokaryotes - Bacteria and Archaea (Exercises)** is licensed CC BY 4.0.

5.4: Protists

Protists

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 3 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe the cell structure characteristics of protists
- Describe the metabolic diversity of protists
- Describe the life cycle diversity of protists
- Describe representative protist organisms from each of the six presently recognized supergroups of eukaryotes
- Identify the evolutionary relationships of plants, animals, and fungi within the six presently recognized supergroups of eukaryotes

Introduction

Humans have been familiar with macroscopic organisms (organisms big enough to see with the unaided eye) since before there was written history, and it is likely that most cultures distinguished between animals and land plants, and most probably included the macroscopic fungi as plants. Therefore, it became an interesting challenge to deal with the world of microorganisms once microscopes were developed a few centuries ago. Many different naming schemes were used over the last couple of centuries, but it has become the most common practice to refer to eukaryotes that are not land plants, animals, or fungi as protists.

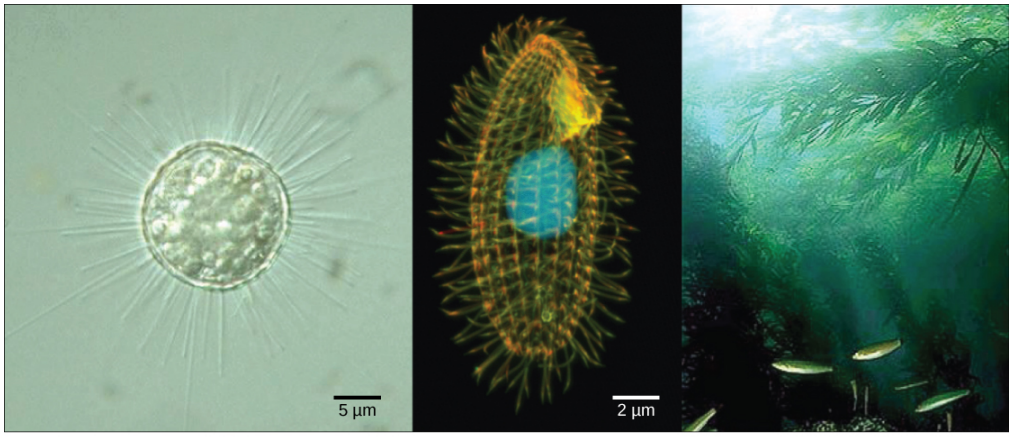


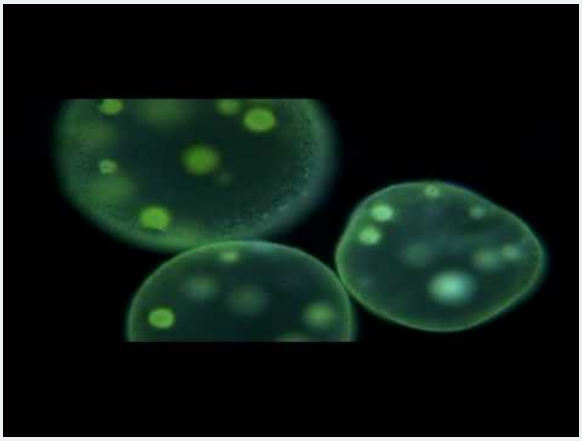
Figure 5.4.1: Protists range from the (a) microscopic, single-celled *canthocystis turfacea* and the (b) ciliate *Tetrahymena thermophila*, both visualized here using light microscopy, to (c) the enormous, multicellular kelp (Chromalveolata) that extend for dozens of meters in underwater "forests" along the Pacific coast (credit a: modification of work by Yuiuji Tsukii; credit b: modification of work by Richard Robinson, Public Library of Science; credit c: modification of work by Kip Evans, NOAA; scale-bar data from Matt Russell).

The name protist was first suggested by Ernst Haeckel in the late nineteenth century. It has been applied in many contexts and has been formally used to represent a kingdom-level taxon called **Protista**. Many modern systematists (biologists who study the relationships among organisms) are naming taxa as groups of organisms thought to include all the descendants of a LCA (monophyletic group). During the past two decades, the field of molecular genetics has demonstrated that some protists are more related to animals, plants, or fungi than they are to other protists. Therefore, not including animals, plants and fungi make the kingdom Protista a **paraphyletic group**, or one that does not include all descendants of its common ancestor Figure 5.4.1. For this

reason, protist lineages originally classified into the kingdom Protista continue to be examined and debated. In the meantime, the term “protist” is still used informally to describe this diverse group of eukaryotes.

Video





This 4-minute video, explore the many varied types of protists and their evolutionary history.
Question after watching: Why are all three types of algae placed in Protista rather than in Kingdom Plantae?

Cell Structure

The cells of protists are among the most elaborate of all cells. Most protists are microscopic and unicellular, but some multicellular forms exist. A few protists live as colonies that behave in some ways as a group of independent free-living cells and in other ways as a multicellular organism. Not all protists are microscopic. Some have huge, macroscopic cells, such as the plasmodia (giant amoebae) of myxomycete slime molds or the marine green alga *Caulerpa*. Some protists are multicellular, such as the red, green, and brown seaweeds. It is among the protists that one finds the wealth of ways that organisms can grow. In fact, many protist cells are multinucleated; in some species, the nuclei are different sizes and have distinct roles in protist cell function.

Single protist cells range in size from less than a micrometer to three meters in length, to hectares in area. Protist cells may be enveloped by animal-like cell membranes or plant-like cell walls. Others are encased in glassy silica-based shells or wound with

pellicles of interlocking protein strips (Figure 5.4.4). The pellicle functions like a flexible coat of armor, preventing the protist from being torn or pierced without compromising its range of motion.



Figure 5.4.4: The pellicle of a euglenid can be seen here as the thread-like structures on the right side of the organism. Deuterostome CC-SA-3.0

Classifying Protists

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This convergent evolution is one reason why protist classification is so challenging.

The emerging classification scheme groups the entire domain Eukaryota into six “supergroups” that contain all the protists as well as animals, plants ("land plants" in the figure), and fungi that evolved from a common ancestor (Figure 5.4.2). The **supergroups** are believed to be monophyletic, meaning that all organisms within each supergroup are believed to have evolved from a single common ancestor, and thus all members are most closely related to each other than to organisms outside that group. There is still evidence lacking for the monophyly of some groups.

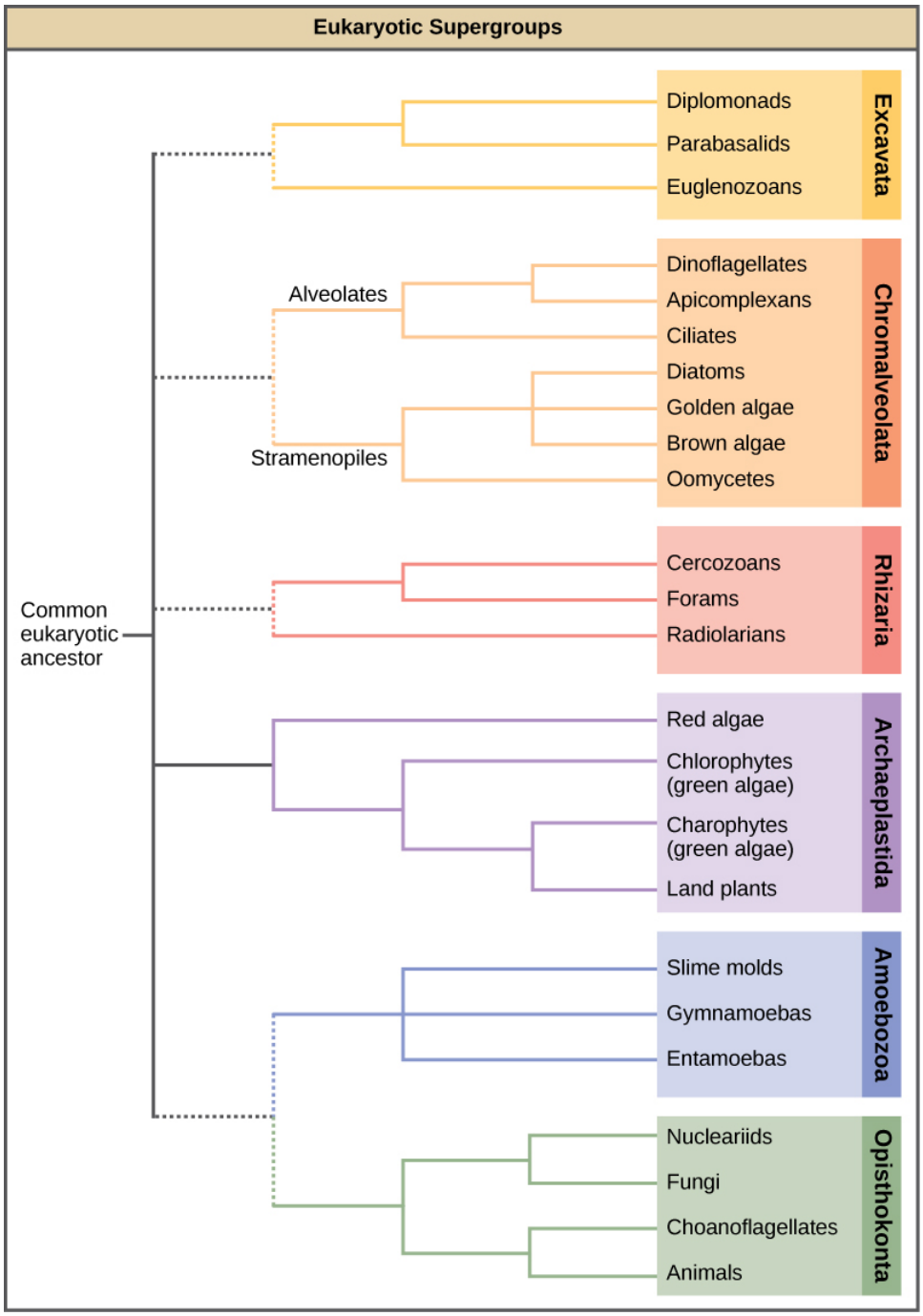


Figure 5.4.2: This diagram shows a proposed classification of the domain Eukarya. Currently, the domain Eukarya is divided into six supergroups. Within each supergroup are multiple kingdoms (note the Animals - *Animalia*, *Fungi*, and Land Plants - *Plantae*; all the rest of the taxa belong to *Protista*). Dotted lines indicate suggested evolutionary relationships that remain under debate.

The classification of eukaryotes is still in flux, and the six supergroups may be modified or replaced by a more appropriate hierarchy as genetic, morphological, and ecological data accumulate. Keep in mind that the classification scheme presented here is just one of several hypotheses, and the true evolutionary relationships are still to be determined. Above all, **eukaryotes** are organisms whose cells have membrane-bound organelles, including nuclei.

Excavata

Many of the protist species classified into the supergroup Excavata are asymmetrical, single-celled organisms with a feeding groove “excavated” from one side. This supergroup includes heterotrophic predators, photosynthetic species, and parasites. Its subgroups are the diplomonads, parabasalids, and euglenozoans.

Diplomonads

Diplomonads exist in anaerobic environments and use alternative pathways, such as glycolysis, to generate energy. Each diplomonad cell has two identical nuclei and uses several flagella for locomotion.

Parabasalids

Parabasalids move with flagella and membrane rippling. *Trichomonas vaginalis*, a parabasalid that causes a sexually transmitted disease in humans, employs these mechanisms to transit through the male and female urogenital tracts. *T. vaginalis* causes trichamoniasis, which appears in an estimated 180 million cases worldwide each year.

Euglenozoans

Euglenozoans includes parasites, heterotrophs, autotrophs, and mixotrophs, ranging in size from 10 to 500 µm. Euglenoids move through their aquatic habitats using two long flagella that guide them toward light sources sensed by a primitive ocular organ called an eyespot. The familiar genus, *Euglena*, encompasses some mixotrophic species that display a photosynthetic capability only when light is present. In the dark, the chloroplasts of *Euglena* shrink up and temporarily cease functioning, and the cells instead take up organic nutrients from their environment.

Video



Euglenoids have had a very, very long time to evolve, and that has led to the things they have evolved into being extremely diverse—so diverse that, combined with the varied shape-shifting abilities of its member species, euglenoids have proven challenging to both identify and classify.

Chromalveolata

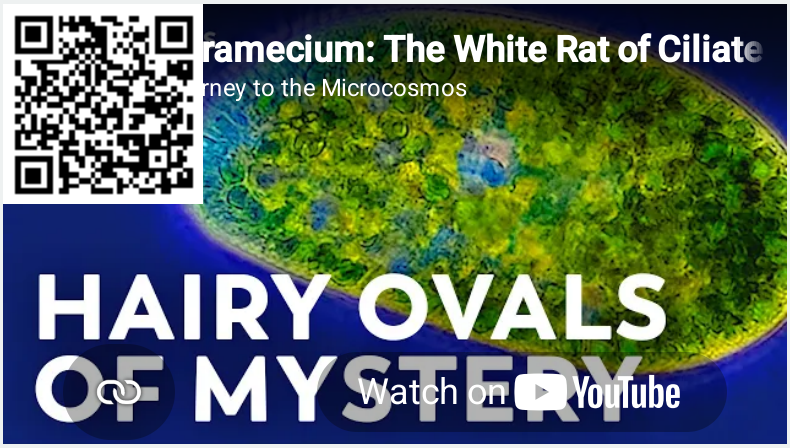
Current evidence suggests that species classified as chromalveolates are derived from a common ancestor that engulfed a photosynthetic red algal cell, which itself had already evolved chloroplasts from an endosymbiotic relationship with a photosynthetic prokaryote. Therefore, the ancestor of chromalveolates is believed to have resulted from a secondary endosymbiotic event. However, some chromalveolates appear to have lost red alga-derived plastid organelles or lack plastid genes altogether. Therefore, this supergroup should be considered a hypothesis-based working group that is subject to change. Chromalveolates include very important photosynthetic organisms, such as diatoms, brown algae, and significant disease agents in animals and plants. The chromalveolates can be subdivided into alveolates and stramenopiles.

Alveolates: Dinoflagellates, Apicomplexians, and Ciliates

A large body of data supports that the alveolates are derived from a shared common ancestor. The alveolates are named for the presence of an alveolus, or membrane-enclosed sac, beneath the cell membrane. The exact function of the alveolus is unknown, but it may be involved in osmoregulation. The alveolates are further categorized into some of the better-known protists: the dinoflagellates, the apicomplexans, and the ciliates.

Dinoflagellates exhibit extensive morphological diversity and can be photosynthetic, heterotrophic, or mixotrophic. Many dinoflagellates are encased in interlocking plates of cellulose. Two perpendicular flagella fit into the grooves between the cellulose plates, with one flagellum extending longitudinally and a second encircling the dinoflagellate. Together, the flagella contribute to the characteristic spinning motion of dinoflagellates. These protists exist in freshwater and marine habitats, and are a component of plankton, the typically microscopic organisms that drift through the water and serve as a crucial food source for larger aquatic organisms.

Video



The apicomplexan protists are so named because their microtubules, fibrin, and vacuoles are asymmetrically distributed at one end of the cell in a structure called an apical complex (Figure 5.4.3*a*). The apical complex is specialized for entry and infection of host cells. Indeed, all apicomplexans are parasitic. This group includes the genus *Plasmodium*, which causes malaria in humans (Figure 5.4.3*b*). Apicomplexan life cycles are complex, involving multiple hosts and stages of sexual and asexual reproduction.

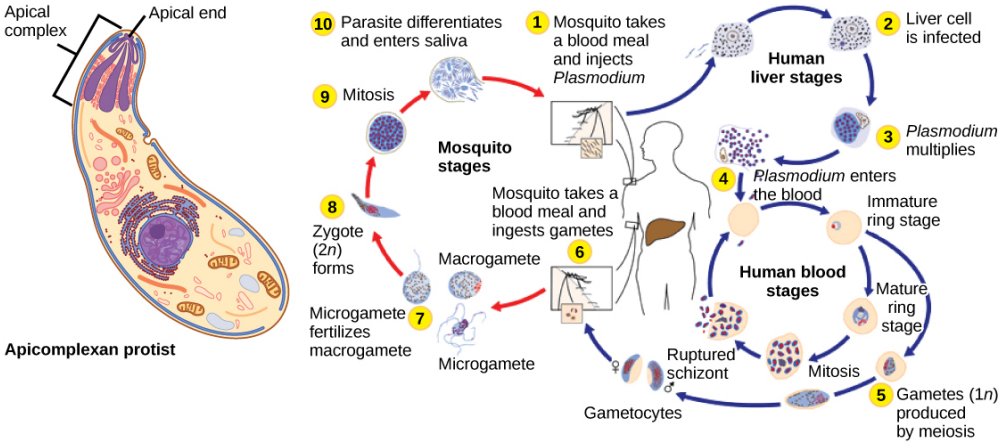


Figure 5.4.3: (a) Apicomplexans are parasitic protists. They have a characteristic apical complex that enables them to infect host cells. (b) *Plasmodium*, the causative agent of malaria, has a complex life cycle typical of apicomplexans. (credit b: modification of work by CDC)

The ciliates, which include *Paramecium* and *Tetrahymena*, are a group of protists 10 to 3,000 micrometers in length that are covered in rows, tufts, or spirals of tiny cilia. By beating their cilia synchronously or in waves, ciliates can coordinate directed movements and ingest food particles. Certain ciliates have fused cilia-based structures that function like paddles, funnels, or fins. Ciliates also are surrounded by a pellicle, providing protection without compromising agility. The genus *Paramecium* includes protists that have organized their cilia into a plate-like primitive mouth, called an oral groove, which is used to capture and digest bacteria.

Stramenopiles: Diatoms, Brown Algae, Golden Algae, and Oomycetes

The other subgroup of chromalveolates, the stramenopiles, includes photosynthetic marine algae and heterotrophic protists. The unifying feature of this group is the presence of a textured, or “hairy,” flagellum. Many stramenopiles also have an additional flagellum that lacks hair-like projections. Members of this subgroup range in size from single-celled diatoms to the massive and multicellular kelp.

The diatoms are unicellular photosynthetic protists that encase themselves in intricately patterned, glassy cell walls composed of silicon dioxide in a matrix of organic particles. These protists are a component of freshwater and marine plankton. Most species of diatoms reproduce asexually, although some instances of sexual reproduction and sporulation also exist.

Video



Like diatoms, golden algae are largely unicellular, although some species can form large colonies. Their characteristic gold color results from their extensive use of carotenoids, a group of photosynthetic pigments that are generally yellow or orange in color. Golden algae are found in both freshwater and marine environments, where they form a major part of the plankton community.

The brown algae are primarily marine, multicellular organisms that are known colloquially as seaweeds. Giant kelps are a type of brown algae. Some brown algae have evolved specialized tissues that resemble terrestrial plants, with root-like holdfasts, stem-like stipes, and leaf-like blades that are capable of photosynthesis. The stipes of giant kelps are enormous, extending in some cases for 60 meters. A variety of algal life cycles exists, but the most complex is alternation of generations, in which both haploid and diploid stages involve multicellularity.

The water molds, oomycetes (“egg fungus”), were so-named based on their fungus-like morphology, but molecular data have shown that the water molds are not closely related to fungi. The oomycetes are characterized by a cellulose-based cell wall and an extensive network of filaments that allow for nutrient uptake. As diploid spores, many oomycetes have two oppositely directed flagella (one hairy and one smooth) for locomotion.

Rhizaria

The Rhizaria supergroup includes many of the amoebas, most of which have threadlike or needle-like pseudopodia (Figure 5.4.3.135.4.3.13). Pseudopodia function to trap and engulf food particles and to direct movement in rhizarian protists. These pseudopods project outward from anywhere on the cell surface and can anchor to a substrate. The protist then transports its cytoplasm into the pseudopod, thereby moving the entire cell. This type of motion, called cytoplasmic streaming, is used by several diverse groups of protists as a means of locomotion or as a method to distribute nutrients and oxygen.

Foraminifera

Foraminiferans, or forams, are unicellular heterotrophic protists, ranging from approximately 20 micrometers to several centimeters in length, and occasionally resembling tiny snails. As a group, the forams exhibit porous shells, called tests that are built from various organic materials and typically hardened with calcium carbonate. The tests may house photosynthetic algae, which the forams can harvest for nutrition. Foram pseudopodia extend through the pores and allow the forams to move, feed, and gather

additional building materials. Typically, forams are associated with sand or other particles in marine or freshwater habitats. Foraminiferans are also useful as indicators of pollution and changes in global weather patterns.

Video



Radiolarians

A second subtype of Rhizaria, the radiolarians, exhibit intricate exteriors of glassy silica with radial or bilateral symmetry. Needle-like pseudopods supported by microtubules radiate outward from the cell bodies of these protists and function to catch food particles. The shells of dead radiolarians sink to the ocean floor, where they may accumulate in 100 meter-thick depths. Preserved, sedimented radiolarians are very common in the fossil record.

Archaeplastida

Red algae and green algae are included in the supergroup Archaeplastida. It was from a common ancestor of these protists that the land plants evolved, since their closest relatives are found in this group. Molecular evidence supports that all Archaeplastida are descendents of an endosymbiotic relationship between a heterotrophic protist and a cyanobacterium. The red and green algae include unicellular, multicellular, and colonial forms.

Red Algae

Red algae, or rhodophytes, are primarily multicellular, lack flagella, and range in size from microscopic, unicellular protists to large, multicellular forms grouped into the informal seaweed category. The red algae life cycle is an alternation of generations. Some species of red algae contain phycoerythrins, photosynthetic accessory pigments that are red in color and outcompete the green tint of chlorophyll, making these species appear as varying shades of red. Other protists classified as red algae lack phycoerythrins and are parasites. Red algae are common in tropical waters where they have been detected at depths of 260 meters. Other red algae exist in terrestrial or freshwater environments.

Video



Green Algae: Chlorophytes and Charophytes

The most abundant group of algae is the green algae. The green algae exhibit similar features to the land plants, particularly in terms of chloroplast structure. That this group of protists shared a relatively recent common ancestor with land plants is well supported. The green algae are subdivided into the chlorophytes and the charophytes. The charophytes are the closest living relatives to land plants and resemble them in morphology and reproductive strategies. Charophytes are common in wet habitats, and their presence often signals a healthy ecosystem.

The chlorophytes exhibit great diversity of form and function. Chlorophytes primarily inhabit freshwater and damp soil, and are a common component of plankton. *Chlamydomonas* is a simple, unicellular chlorophyte with a pear-shaped morphology and two opposing, anterior flagella that guide this protist toward light sensed by its eyespot. More complex chlorophyte species exhibit haploid gametes and spores that resemble *Chlamydomonas*.

Video



True multicellular organisms, such as the sea lettuce, *Ulva*, are represented among the chlorophytes. In addition, some chlorophytes exist as large, multinucleate, single cells. Species in the genus *Caulerpa* exhibit flattened fern-like foliage and can reach lengths of 3 meters. *Caulerpa* species undergo nuclear division, but their cells do not complete cytokinesis, remaining instead as massive and elaborate single cells (Figure 5.4.5).



Figure 5.4.5: *Caulerpa taxifolia* is a chlorophyte consisting of a single cell containing potentially thousands of nuclei. (credit: NOAA)

Amoebozoa

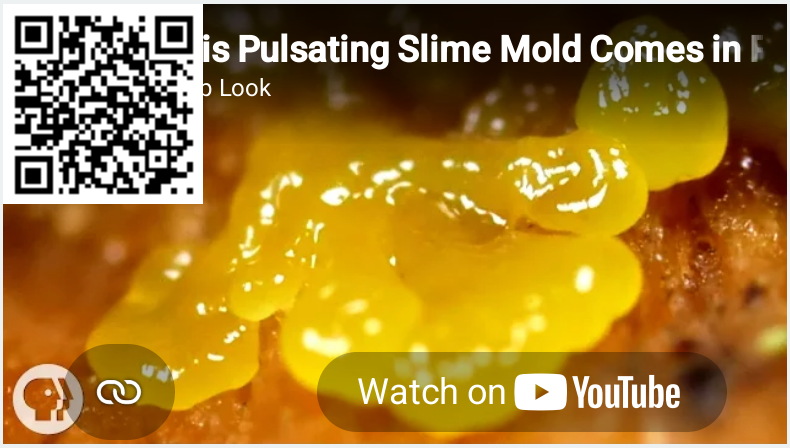
The amoebozoans characteristically exhibit pseudopodia that extend like tubes or flat lobes, rather than the hair-like pseudopodia of rhizarian amoeba. The Amoebozoa include several groups of unicellular amoeba-like organisms that are free-living or parasites.

Slime Molds

A subset of the amoebozoans, the slime molds, has several morphological similarities to fungi that are thought to be the result of convergent evolution. For instance, during times of stress, some slime molds develop into spore-generating fruiting bodies, much like fungi.

The slime molds are categorized on the basis of their life cycles into plasmodial or cellular types. Plasmodial slime molds are composed of large, multinucleate cells and move along surfaces like an amorphous blob of slime during their feeding stage (Figure 5.4.3.195.4.3.19). Food particles are lifted and engulfed into the slime mold as it glides along. Upon maturation, the plasmodium takes on a net-like appearance with the ability to form fruiting bodies, or sporangia, during times of stress. Haploid spores are produced by meiosis within the sporangia, and spores can be disseminated through the air or water to potentially land in more favorable environments. If this occurs, the spores germinate to form ameboid or flagellate haploid cells that can combine with each other and produce a diploid zygotic slime mold to complete the life cycle.

Video



Unlike the cells of other living beings, which have only one nucleus that carries their genetic information, slime molds can organize into something like a cell with thousands of nuclei.
Question after watching:

Opisthokonta

The opisthokonts include the animal-like choanoflagellates, which are believed to resemble the common ancestor of sponges and, in fact, all animals. Choanoflagellates include unicellular and colonial forms, and number about 244 described species. These organisms exhibit a single, apical flagellum that is surrounded by a contractile collar composed of microvilli. The collar uses a similar mechanism to sponges to filter out bacteria for ingestion by the protist. The morphology of choanoflagellates was recognized early on as resembling the collar cells of sponges, and suggesting a possible relationship to animals.

Metabolism

Protists exhibit many forms of nutrition and may be aerobic or anaerobic. Protists that store energy by photosynthesis belong to a group of photoautotrophs and are characterized by the presence of chloroplasts. Other protists are heterotrophic and consume organic materials (such as other organisms) to obtain nutrition. Amoebas and some other heterotrophic protist species ingest particles by a process called **phagocytosis**, in which the cell membrane engulfs a food particle and brings it inward, pinching off an intracellular membranous sac, or vesicle, called a food vacuole (Figure 5.4.6). The food particle is broken down into small molecules that can diffuse into the cytoplasm and be used in cellular metabolism. Undigested materials are expelled from the cell via exocytosis.

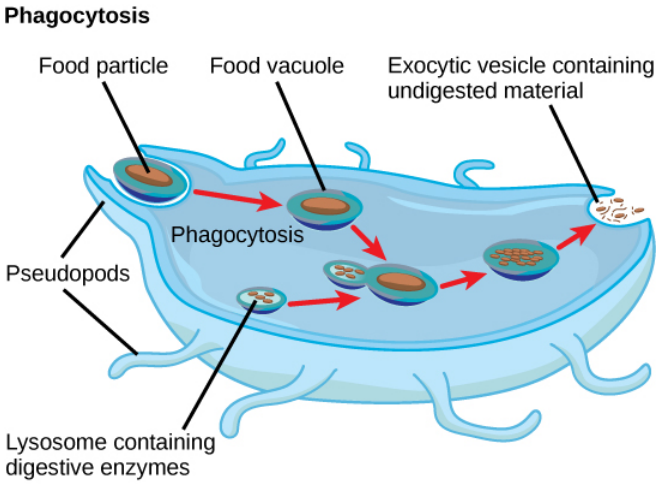


Figure 5.4.6: The stages of phagocytosis include the engulfment of a food particle, the digestion of the particle using hydrolytic enzymes contained within a lysosome, and the expulsion of undigested materials from the cell.

Subtypes of heterotrophs, called **saprobes**, absorb nutrients from dead organisms or their organic wastes. Some protists can function as **mixotrophs**, obtaining nutrition by photoautotrophic or heterotrophic routes, depending on whether sunlight or organic nutrients are available.

Video





In this 11-minute video, the diverse ways that protist extract energy from their environment are explored.
Question after watching: What is the advantage of being a mixotroph in aquatic environments?

Video



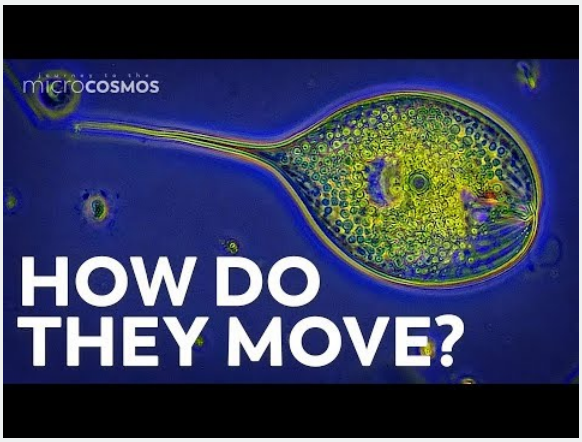
Yes, they might eat your brain, but there's a lot more to amoebas than that!
Question after watching:

Motility

Most protists are motile, but different types of protists have evolved different modes of movement (Figure 5.4.6). Some protists have one or more flagella, which they rotate or whip. Others are covered in rows or tufts of tiny cilia that they coordinately beat to swim. Still others form cytoplasmic extensions called **pseudopodia** anywhere on the cell, anchor the pseudopodia to a substrate, and pull themselves forward. Some protists can move toward or away from a stimulus, a movement referred to as taxis. Movement toward light, termed **phototaxis**, is accomplished by coupling their locomotion strategy with a light-sensing organ.

Video





In this 11-minute video, find out how these single-celled eukaryotes move through their viscous environment. Question after watching: After making a table with the three main types of possible movements, which representative organisms would you include to help you remember each one?

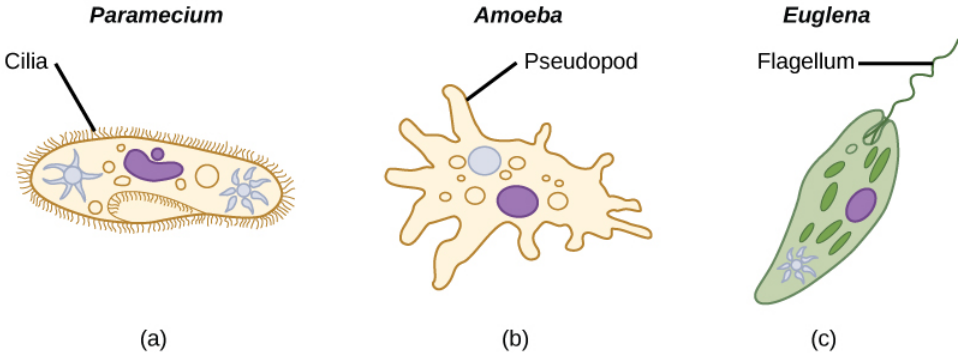


Figure 5.4.6: Protists use one of three methods for locomotion: (a) *Paramecium* waves hair-like appendages called cilia to propel itself. (b) *Amoeba* uses lobe-like pseudopods to anchor itself to a solid surface and pull itself forward. (c) *Euglena* uses a whip-like tail called a flagellum to propel itself.

Life Cycles

Protists reproduce by many mechanisms. Most undergo some form of asexual reproduction, such as binary fission, to produce two daughter cells. In protists, binary fission can occur along the transverse or longitudinal axis of the cell, depending on the axis of orientation. Sometimes *Paramecium* uses binary fission to reproduce. Some protists such as the true slime molds exhibit multiple fission and simultaneously divide into many daughter cells. Others produce tiny buds that go on to divide and grow to the size of the parental protist.

Sexual reproduction, involving meiosis and fertilization, is also found among protists, and many protist species can switch from asexual to sexual reproduction when necessary. Sexual reproduction is often associated with periods of stress such as when nutrients are rare or environmental changes occur. Sexual reproduction may allow the protist to recombine genes and produce new variations in its progeny that may be better suited to surviving in the new environment.

In addition, sexual reproduction is often associated with the creation of resistant **cysts** that are a protective, resting stage of the life cycle of the protist. Depending on their habitat, the cysts may be particularly resistant to temperature extremes, desiccation, or low pH. This strategy also allows certain protists to "wait out" stressors until their environment becomes more favorable for survival or until they are carried (such as by wind, water, or transport on a larger organism) to a different environment because cysts exhibit little cellular metabolism and leave the organism in a sort of suspended animation.

Protist life cycles range from simple to complex. Certain parasitic protists have complicated life cycles and must infect different host species at different developmental stages to complete their life cycle. Some protists are unicellular in the haploid form and multicellular in the diploid form, a strategy employed by animals (gametes are unicellular, but fertilized eggs rapidly develop and divide to form multicellular animals). Other protists have multicellular stages in both haploid and diploid forms, a strategy called alternation of generations that is also used by plants.

Video





In this 8.5-minute video, explore the ways that protists reproduce.
Question after watching: Explain in your own words why sexual reproduction can be useful if a protist's environment changes.

Ecology

Nearly all protists exist in aquatic environments, including freshwater and marine environments, damp soil, and even snow. They are also common in the digestive tracts of animals and in the vascular tissues of plants. Others invade the cells of other protists, animals, and plants. Protists function in diverse ecological niches. Whereas some protist species are essential components of the food chain and generators of biomass, others function in the decomposition of organic materials. Still other protists are dangerous human **pathogens** or causative agents of devastating plant diseases. Several protist species are parasites that infect animals or plants. A few protist species live on dead organisms or their wastes and contribute to their decay.

Primary Producers

Protists are essential sources of nutrition for many other organisms. In some cases, as in plankton, protists are consumed directly. Alternatively, photosynthetic protists serve as producers of nutrition for other organisms. The protists themselves and their products of photosynthesis are essential—directly or indirectly—to the survival of organisms ranging from bacteria to mammals (Figure 5.4.7). As primary producers, protists feed a large proportion of the world's aquatic species. (On land, terrestrial plants serve as primary producers.) In fact, approximately one-quarter of the world's photosynthesis is conducted by protists, particularly dinoflagellates, diatoms, and multicellular algae.

Protists do not create food sources only for sea-dwelling organisms. For instance, certain anaerobic parabasalid species exist in the digestive tracts of termites and wood-eating cockroaches, where they contribute an essential step in the digestion of cellulose ingested by these insects as they bore through wood.



Figure 5.4.7: Virtually all aquatic organisms depend directly or indirectly on protists for food. (credit “mollusks”: modification of work by Craig Stihler, USFWS; credit “crab”: modification of work by David Berkowitz; credit “dolphin”: modification of work by Mike Baird; credit “fish”: modification of work by Tim Sheerman-Chase; credit “penguin”: modification of work by Aaron Logan)

Protists as Bioremediators

Video



Microbes are used for everything from baking to brewing, but wastewater treatment is where they do some of their most important work.

Question after watching:

Human Parasites

The human parasite, *Trypanosoma brucei*, belongs to a subgroup of Euglenozoa, the kinetoplastids. The kinetoplastid subgroup is named after the kinetoplast, a DNA mass carried within the single, oversized mitochondrion possessed by each of these cells. This subgroup includes several parasites, collectively called trypanosomes, which cause devastating human diseases and infect an insect species during a portion of their life cycle. *T. brucei* develops in the gut of the tsetse fly after the fly bites an infected human or other mammalian host. *T. brucei* is responsible for African sleeping sickness, common in central Africa, and confounds the human immune system by changing its thick layer of surface glycoproteins with each infectious cycle.

The glycoproteins are identified by the immune system as foreign antigens, and a specific antibody defense is mounted against the parasite. However, *T. brucei* has thousands of possible antigens, and with each subsequent generation, the protist switches to a

glycoprotein coating with a different molecular structure. In this way, *T. brucei* is capable of replicating continuously without the immune system ever succeeding in clearing the parasite.

T. brucei attacks red blood cells. The parasite then travels to the insect salivary glands to be transmitted to another human or other mammal when the infected tsetse fly consumes another blood meal. The disease is associated with severe chronic fatigue, coma, and without treatment, eventual death. During epidemic periods, mortality from the disease can be high. Greater surveillance and control measures lead to a reduction in reported cases; some of the lowest numbers reported in 50 years (fewer than 10,000 cases in all of sub-Saharan Africa) have happened since 2009.

Video



Plant Parasites

Protist parasites of terrestrial plants include agents that destroy food crops. The oomycete *Plasmopara viticola* parasitizes grape plants, causing a disease called downy mildew (Figure 5.4.8). Grape plants infected with *P. viticola* appear stunted and have discolored, withered leaves. The spread of downy mildew nearly collapsed the French wine industry in the nineteenth century.

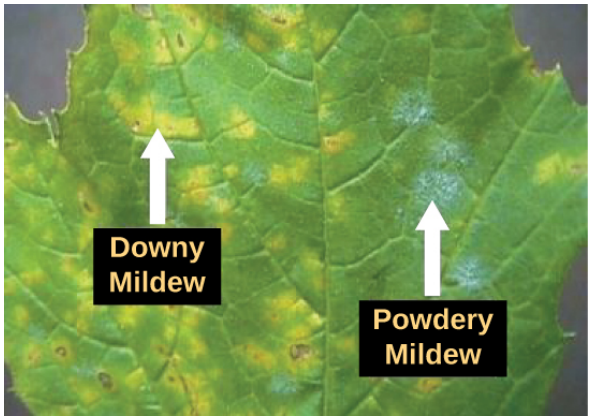


Figure 5.4.8: Both downy and powdery mildews on this grape leaf are caused by an infection of *P. viticola*. (credit: modification of work by USDA)

Phytophthora infestans is an oomycete responsible for potato late blight, which causes potato stalks and stems to decay into black slime (Figure 5.4.9). Widespread potato blight caused by *P. infestans* precipitated the well-known Irish potato famine in the nineteenth century that claimed the lives of approximately 1 million people and led to the emigration of at least 1 million more from Ireland. Late blight continues to plague potato crops in certain parts of the United States and Russia, wiping out as much as 70 percent of crops when no pesticides are applied.



Figure 5.4.9: These unappetizing remnants result from an infection with *P. infestans*, the causative agent of potato late blight. (credit: USDA)

? Optional Activity 5.4.1

Protists with the capabilities to perform photosynthesis and to absorb nutrients from dead organisms are called _____.

A. photoautotrophs
B. mixotrophs
C. saprobes
D. heterotrophs

Answer

B. mixotrophs

? Optional Activity 5.4.2

Which of these locomotor organs would likely be the shortest?

A. a flagellum
B. a cilium
C. an extended pseudopod
D. a pellicle

Answer

B. a cilium

This page titled 5.4: Protists is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **23.0: Prelude to Protists** by OpenStax is licensed CC BY 4.0.
- **23.2: Characteristics of Protists** by OpenStax is licensed CC BY 4.0.
- **23.3: Groups of Protists** by OpenStax is licensed CC BY 4.0.
- **23.4: Ecology of Protists** by OpenStax is licensed CC BY 4.0.

5.4.E: Protists (Exercises)

Characteristics of Protists

There are over 100,000 described living species of protists, and it is unclear how many undescribed species may exist. Since many protists live as commensals or parasites in other organisms and these relationships are often species-specific, there is a huge potential for protist diversity that matches the diversity of hosts. As the catchall term for eukaryotic organisms that are not animal, plant, or fungi, it is not surprising that very few characteristics are common to all protists.

Review Questions

Protists that have a pellicle are surrounded by _____.

A. silica dioxide
B. calcium carbonate
C. carbohydrates
D. proteins

Answer

D

Protists with the capabilities to perform photosynthesis and to absorb nutrients from dead organisms are called _____.

A. photoautotrophs
B. mixotrophs
C. saprobes
D. heterotrophs

Answer

B

Which of these locomotor organs would likely be the shortest?

A. a flagellum
B. a cilium
C. an extended pseudopod
D. a pellicle

Answer

B

Alternation of generations describes which of the following?

A. The haploid form can be multicellular; the diploid form is unicellular.
B. The haploid form is unicellular; the diploid form can be multicellular.
C. Both the haploid and diploid forms can be multicellular.
D. Neither the haploid nor the diploid forms can be multicellular.

Answer

C

Free Response

Explain in your own words why sexual reproduction can be useful if a protist's environment changes.

Answer

The ability to perform sexual reproduction allows protists to recombine their genes and produce new variations of progeny that may be better suited to the new environment. In contrast, asexual reproduction generates progeny that are clones of the parent.

Giardia lamblia is a cyst-forming protist parasite that causes diarrhea if ingested. Given this information, against what type(s) of environments might *G. lamblia* cysts be particularly resistant?

Answer

As an intestinal parasite, *Giardia* cysts would be exposed to low pH in the stomach acids of its host. To survive this environment and reach the intestine, the cysts would have to be resistant to acidic conditions.

Groups of Protists

In the span of several decades, the Kingdom Protista has been disassembled because sequence analyses have revealed new genetic (and therefore evolutionary) relationships among these eukaryotes. Moreover, protists that exhibit similar morphological features may have evolved analogous structures because of similar selective pressures—rather than because of recent common ancestry. This phenomenon, called convergent evolution, is one reason why protist classification is so challenging.

Review Questions

Which protist group exhibits mitochondrial remnants with reduced functionality?

A. slime molds
B. diatoms
C. parabasalids
D. dinoflagellates

Answer

C

Conjugation between two *Paramecia* produces _____ total daughter cells.

A. 2
B. 4
C. 8
D. 16

Answer

C

What is the function of the raphe in diatoms?

A. locomotion
B. defense
C. capturing food
D. photosynthesis

Answer

A

What genus of protists appears to contradict the statement that unicellularity restricts cell size?

A. *Dictyostelium*
B. *Ulva*
C. *Plasmodium*
D. *Caulerpa*

Answer

D

Free Response

The chlorophyte (green algae) genera *Ulva* and *Caulerpa* both have macroscopic leaf-like and stem-like structures, but only *Ulva* species are considered truly multicellular. Explain why.

Answer

Unlike *Ulva*, protists in the genus *Caulerpa* actually are large, multinucleate, single cells. Because these organisms undergo mitosis without cytokinesis and lack cytoplasmic divisions, they cannot be considered truly multicellular.

Why might a light-sensing eyespot be ineffective for an obligate saprobe? Suggest an alternative organ for a saprobic protist.

Answer

By definition, an obligate saprobe lacks the ability to perform photosynthesis, so it cannot directly obtain nutrition by searching for light. Instead, a chemotactic mechanism that senses the odors released during decay might be a more effective sensing organ for a saprobe.

Ecology of Protists

Protists function in various ecological niches. Whereas some protist species are essential components of the food chain and generators of biomass, others function in the decomposition of organic materials. Still other protists are dangerous human pathogens or causative agents of devastating plant diseases.

Review Questions

An example of carbon fixation is _____.

A. photosynthesis
B. decomposition
C. phagocytosis
D. parasitism

Answer

A

Which parasitic protist evades the host immune system by altering its surface proteins with each generation?

A. *Paramecium caudatum*
B. *Trypanosoma brucei*
C. *Plasmodium falciparum*
D. *Phytophthora infestans*

Answer

B

Free Response

How does killing *Anopheles* mosquitoes affect the *Plasmodium* protists?

Answer

Plasmodium parasites infect humans and cause malaria. However, they must complete part of their life cycle within *Anopheles* mosquitoes, and they can only infect humans via the bite wound of a mosquito. If the mosquito population is decreased, then fewer *Plasmodium* would be able to develop and infect humans, thereby reducing the incidence of human infections with this parasite.

Without treatment, why does African sleeping sickness invariably lead to death?

Answer

The trypanosomes that cause this disease are capable of expressing a glycoprotein coat with a different molecular structure with each generation. Because the immune system must respond to specific antigens to raise a meaningful defense, the changing nature of trypanosome antigens prevents the immune system from ever clearing this infection. Massive trypanosome infection eventually leads to host organ failure and death.

This page titled 5.4.E: Protists (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **23.E: Protists (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

5.5: Fungi

Kingdom Fungi

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 90 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- List the characteristics of fungi
- Describe the composition of the mycelium
- Describe the mode of nutrition of fungi
- Explain sexual and asexual reproduction in fungi
- Describe the role of fungi in the ecosystem

Introduction to Fungi

Video





This 2.5-minute video introduces organisms in the kingdom Fungi.
Question after watching: Are fungi unicellular or multicellular?

The word ***fungus*** comes from the Latin word for mushrooms. Indeed, the familiar mushroom is a reproductive structure used by many types of fungi. However, there are also many fungi species that do not produce mushrooms at all (Figure 5.5.1). Being eukaryotes, a typical fungal cell contains a nucleus and many membrane-bound organelles. The kingdom Fungi (pronounced either *fun-guy* or *fun-jie*) includes an wide variety of living organisms collectively referred to as Eucomycota, or true Fungi. While scientists have identified about 100,000 species of fungi, this is only a fraction of the 1.5 million species of fungus likely present on Earth. Edible mushrooms, yeasts, black mold, and the producer of the antibiotic penicillin, *Penicillium notatum*, are all members of the kingdom Fungi, which belongs to the domain Eukarya.



Figure 5.5.1: Many species of fungus produce (a) the familiar mushroom (basidiocarp), which is a reproductive structure visible to the naked eye. (b) This coral fungus displays brightly colored fruiting bodies. (c) This electron micrograph shows the spore-bearing structures of *Aspergillus*, a type of toxic fungi found mostly in soil and plants. (credit "mushroom": modification of work by Chris Wee; credit "coral fungus": modification of work by Cory Zanker; credit "*Aspergillus*": modification of work by Janice Haney Carr, Robert Simmons, CDC; scale-bar data from Matt Russell)

Although humans have used yeasts and multicellular fungi since prehistoric times. Until recently, the biology of fungi was poorly understood. Up until the mid-20th century, many scientists classified fungi as plants. Fungi, like plants, are **sessile**, meaning they are seemingly rooted in place. Their mode of nutrition was poorly understood. Then came the field of **mycology**: the scientific study of fungi.

Most fungi are multicellular organisms. They display two distinct morphological stages: vegetative and reproductive. The vegetative stage consists of a tangle of slender thread-like structures called **hyphae** (singular, hypha), whereas the reproductive stage can be more conspicuous (such as what is seen in (Figure 5.5.1). The mass of hyphae is a **mycelium** (Figure 5.5.2). It can grow on a surface, in soil or decaying material, in a liquid, or even on living tissue.

The vegetative body of a fungus is a unicellular or multicellular **thallus**, meaning a collection of cells or tissues not structured into organs. Dimorphic fungi can change from a unicellular to multicellular state depending on environmental conditions. Unicellular fungi are generally referred to as **yeasts**, including *Saccharomyces cerevisiae* (baker's yeast) and *Candida* species (the agents of thrush, a common fungal infection) (Figure 5.5.3).

Although individual hyphae must be observed under a microscope, the mycelium of a fungus can be very large. The giant *Armillaria solidipes* (honey mushroom) is considered the largest organism on Earth, spreading across more than 2,000 acres of underground soil in eastern Oregon; it is estimated to be at least 2,400 years old.

Based on fossil evidence, fungi appeared in the pre-Cambrian era, about 450 million years ago. Molecular biology analysis of the fungal genome suggests that fungi are more closely related to animals than plants. They are a polyphyletic group of organisms that share characteristics, rather than sharing a single common ancestor.

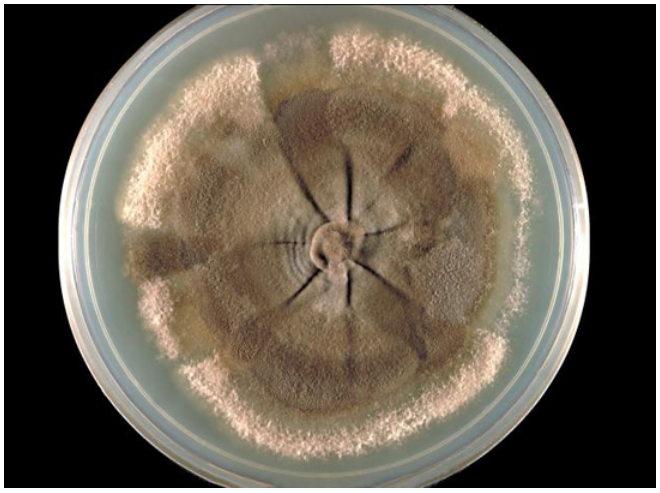


Figure 5.5.2: The mycelium of the fungus *Neotestudina rosati* can be pathogenic to humans. The fungus enters through a cut or scrape and develops a mycetoma, a chronic subcutaneous infection. (credit: CDC)

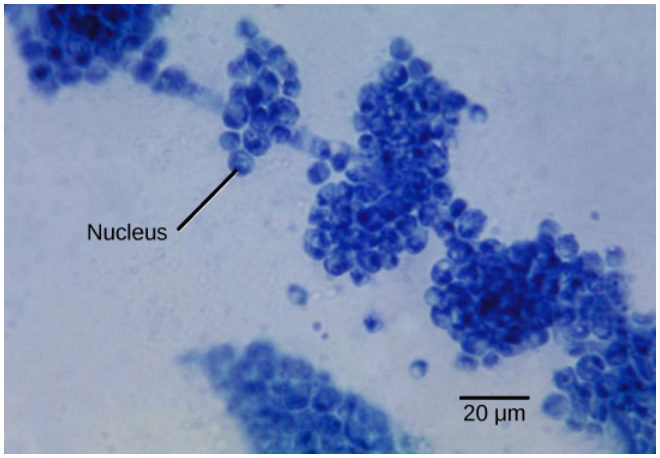


Figure 5.5.3: Candida albicans is a yeast cell and the agent of candidiasis and thrush. This organism has a similar morphology to coccus bacteria; however, yeast is a eukaryotic organism (note the nucleus). (credit: modification of work by Dr. Godon Roberstad, CDC; scale-bar data from Matt Russell)

Evolutionary History of Fungi

The kingdom Fungi contains five major phyla that were established using molecular data or information about their mode of sexual reproduction. Fungi that reproduce without a sexual cycle, and that are hard to classify according to their DNA, are placed for

convenience in a sixth group called a “form phylum.” The form phylum is sort of like a placeholder bin where fungi that don’t seem to fit anywhere else can be categorized until we learn more about them. Not all mycologists agree with this scheme.

The five true phyla of fungi are the **Chytridiomycota** (Chytrids), the **Zygomycota** (conjugated fungi), the **Ascomycota** (sac fungi), the **Basidiomycota** (club fungi) and the recently described Phylum **Glomeromycota** (Figure 5.5.4). An older classification scheme grouped fungi that strictly use asexual reproduction into Deuteromycota, a group that is no longer in use.

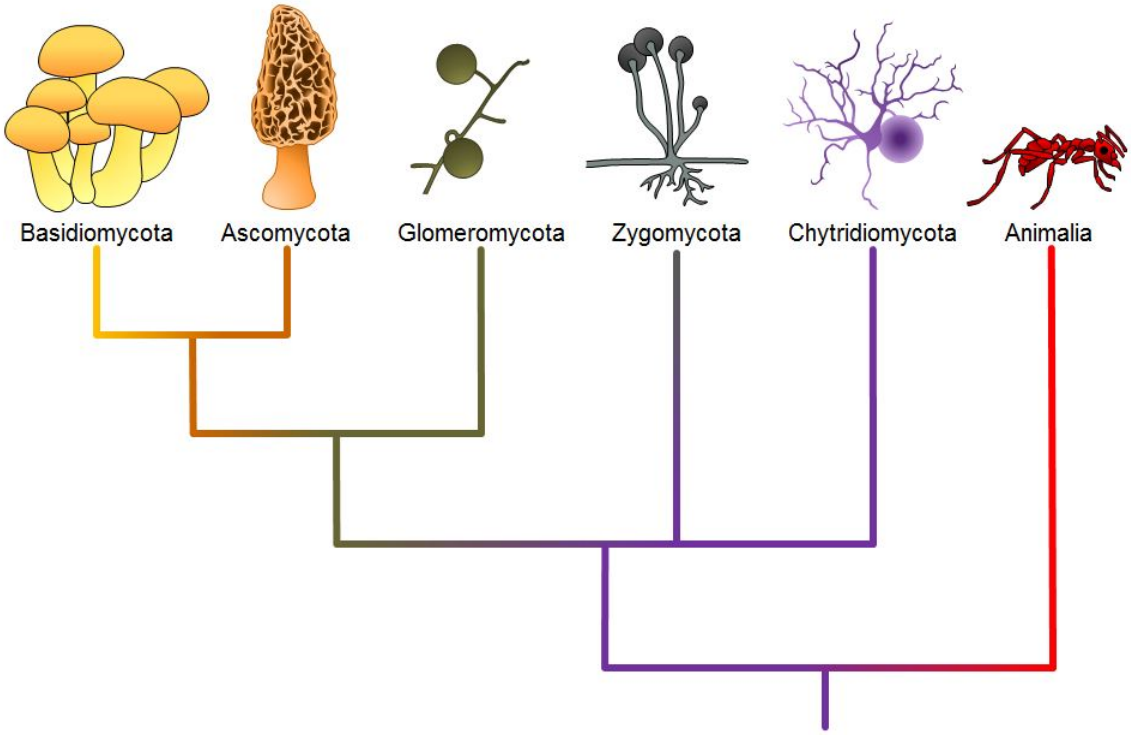


Figure 5.5.4: Cladogram of the Fungi. (OpenStax Biology 2e; CC-BY 4.0)

Note

Note: “-mycota” is used to designate a phylum while “-mycetes” formally denotes a class or is used informally to refer to all members of the phylum.

Chytridiomycota - The Chytrids

Chytridiomycota (chytrids) are considered the most primitive group of fungi. The ecological habitat and cell structure of chytrids have much in common with protists. The evolutionary record shows that the first recognizable chytrids appeared during the late pre-Cambrian period, more than 500 million years ago. Like all fungi, chytrids have chitin in their cell walls, but one group of chytrids has both cellulose and chitin in the cell wall. Most chytrids are unicellular; a few form multicellular organisms and hyphae, which have no septa between cells (coenocytic). They are mostly aquatic, and their gametes are the only fungal cells known to have flagella. They reproduce both sexually and asexually; the asexual spores are called **zoospores**.

Zygomycota - The Conjugated Fungi

Zygomycota (conjugated fungi) produce non-septated hyphae with many nuclei. Hyphae are the primary cell bodies of fungal organisms. Zygomycetes have a thallus of coenocytic hyphae in which the nuclei are haploid when the organism is in the vegetative stage. The fungi usually reproduce asexually by producing sporangiospores (Figure 5.5.5). The black tips of bread mold are the swollen sporangia packed with black spores (Figure 5.5.6). When spores land on a suitable substrate, they germinate and produce a new mycelium. Their hyphae fuse during sexual reproduction, under unfavorable conditions to produce a **zygospore** in a **zygosporangium**.

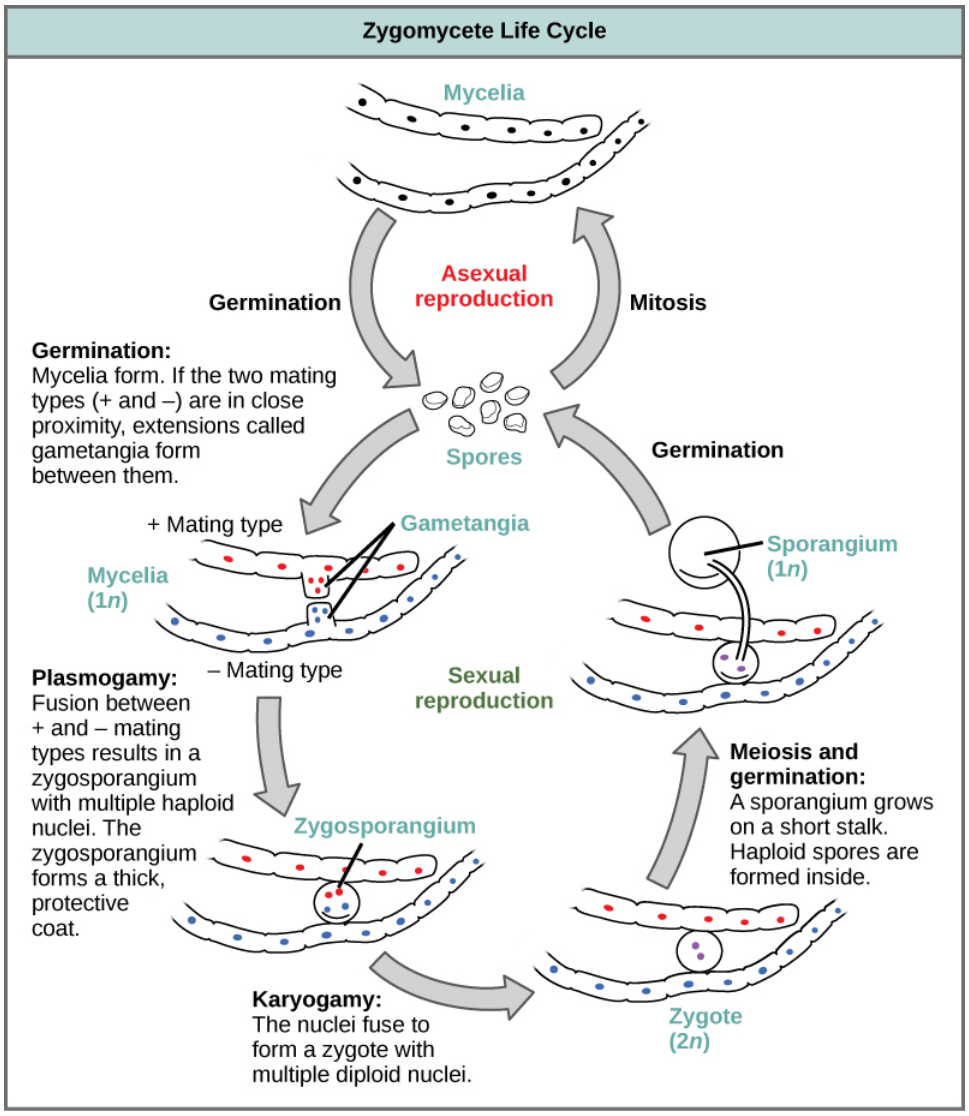
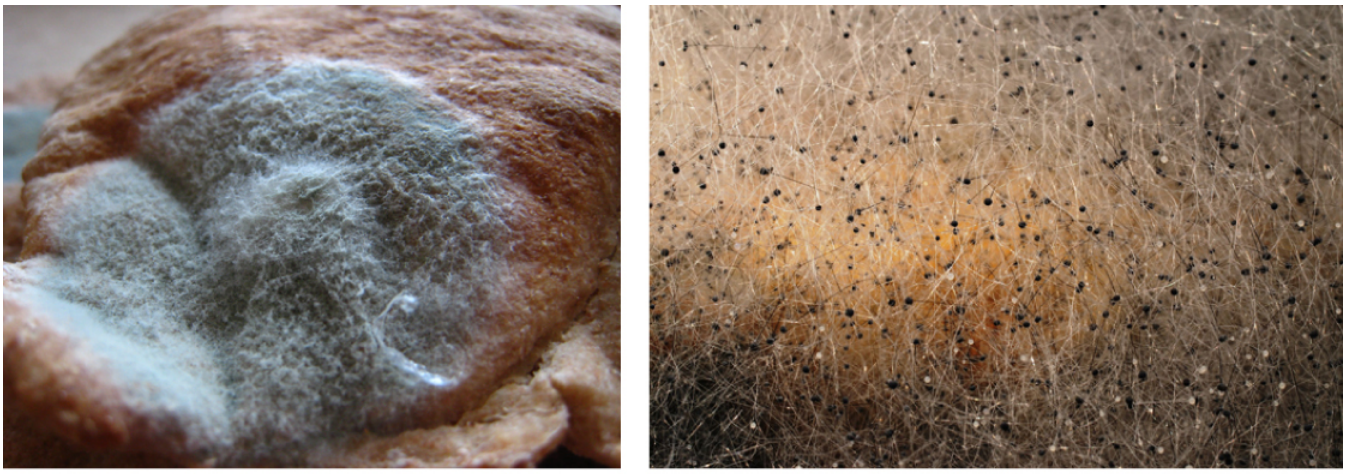


Figure 5.5.5: Zygomycetes have asexual and asexual life cycles. In the sexual life cycle, plus and minus mating types conjugate to form a zygosporangium.



(a) (b)

Figure 5.5.6: Sporangia grow at the end of stalks, which appear as (a) white fuzz seen on this bread mold, *Rhizopus stolonifer*. The (b) tips of bread mold are the spore-containing sporangia. (credit b: modification of work by "polandeze"/Flickr)

They include the familiar bread mold, *Rhizopus stolonifer*, which rapidly propagates on the surfaces of breads, fruits, and vegetables. Most species are saprobes, living off decaying organic material; a few are parasites, particularly of insects. Zygomycetes play a considerable commercial role. The metabolic products of other species of *Rhizopus* are intermediates in the synthesis of semi-synthetic steroid hormones.

Ascomycota - The Sac Fungi

The majority of known fungi belong to the Phylum Ascomycota, which is characterized by the formation of an ascus (plural, asci), a sac-like structure that contains haploid ascospores. Many ascomycetes are of commercial importance. Some play a beneficial role, such as the yeasts used in baking, brewing, and wine fermentation, plus truffles and morels, which are held as gourmet delicacies. *Aspergillus oryzae* is used in the fermentation of rice to produce sake. Other ascomycetes parasitize plants and animals, including humans. For example, fungal pneumonia poses a significant threat to AIDS patients who have a compromised immune system. Ascomycetes not only infest and destroy crops directly; they also produce poisonous secondary metabolites that make crops unfit for consumption. Filamentous ascomycetes produce hyphae divided by perforated septa, allowing streaming of cytoplasm from one cell to the other. Conidia and asci, which are used respectively for asexual and sexual reproductions, are usually separated from the vegetative hyphae by blocked (non-perforated) septa.

Ascomycota (sac fungi) form spores in sacs called **asci** (millions of which fuse together into **ascocarps**) during sexual reproduction (Figure 5.5.7). However, this name was obtained because the sexual form attracted the human eye. Asexual reproduction is their most common form of reproduction.

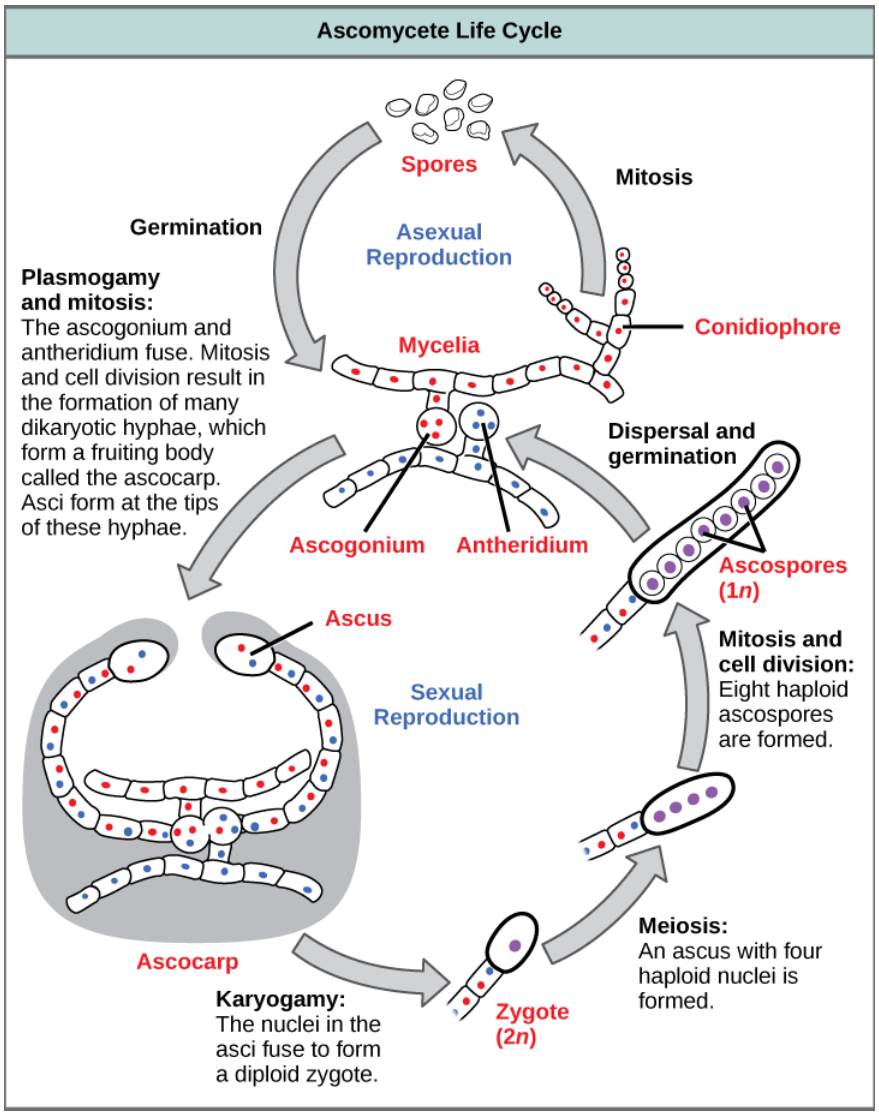


Figure 5.5.7: The lifecycle of an ascomycete is characterized by the production of asci during the sexual phase. The haploid phase is the predominant phase of the life cycle.

Basidiomycota - The Club Fungi

Basidiomycota (club fungi) produce showy fruiting bodies that contain **basidia** in the form of clubs known as **basiciocarps** (the clubs under the mushroom bell shape in what looks like gills or sheets. Magnified, these sheets have club-like protrusions). These mushroom-producing basidiomyces are sometimes referred to as “gill fungi” because of the presence of gill-like structures on the underside of the cap. The “gills” are actually compacted hyphae on which the basidia are borne. Spores are stored in the basidia.

This group also includes shelf fungus, which cling to the bark of trees like small shelves. In addition, the basidiomycota includes smuts and rusts, which are important plant pathogens; toadstools, and shelf fungi stacked on tree trunks. Most edible fungi belong to the Phylum Basidiomycota; however, some basidiomycetes produce deadly toxins. For example, *Cryptococcus neoformans* causes severe respiratory illness.

The lifecycle of basidiomycetes includes alternation of generations (Figure 5.5.8). Spores are generally produced through sexual reproduction, rather than asexual reproduction. The club-shaped basidium carries spores called basidiospores. In the basidium, nuclei of two different mating strains fuse (karyogamy), giving rise to a diploid zygote that then undergoes meiosis. The haploid nuclei migrate into basidiospores, which germinate and generate monokaryotic hyphae. The mycelium that results is called a primary mycelium. Mycelia of different mating strains can combine and produce a secondary mycelium that contains haploid nuclei of two different mating strains. This is the dikaryotic stage of the basidiomyces lifecyle and and it is the dominant stage.

Eventually, the secondary mycelium generates a basidiocarp, which is a fruiting body that protrudes from the ground—this is what we think of as a mushroom. The basidiocarp bears the developing basidia on the gills under its cap.

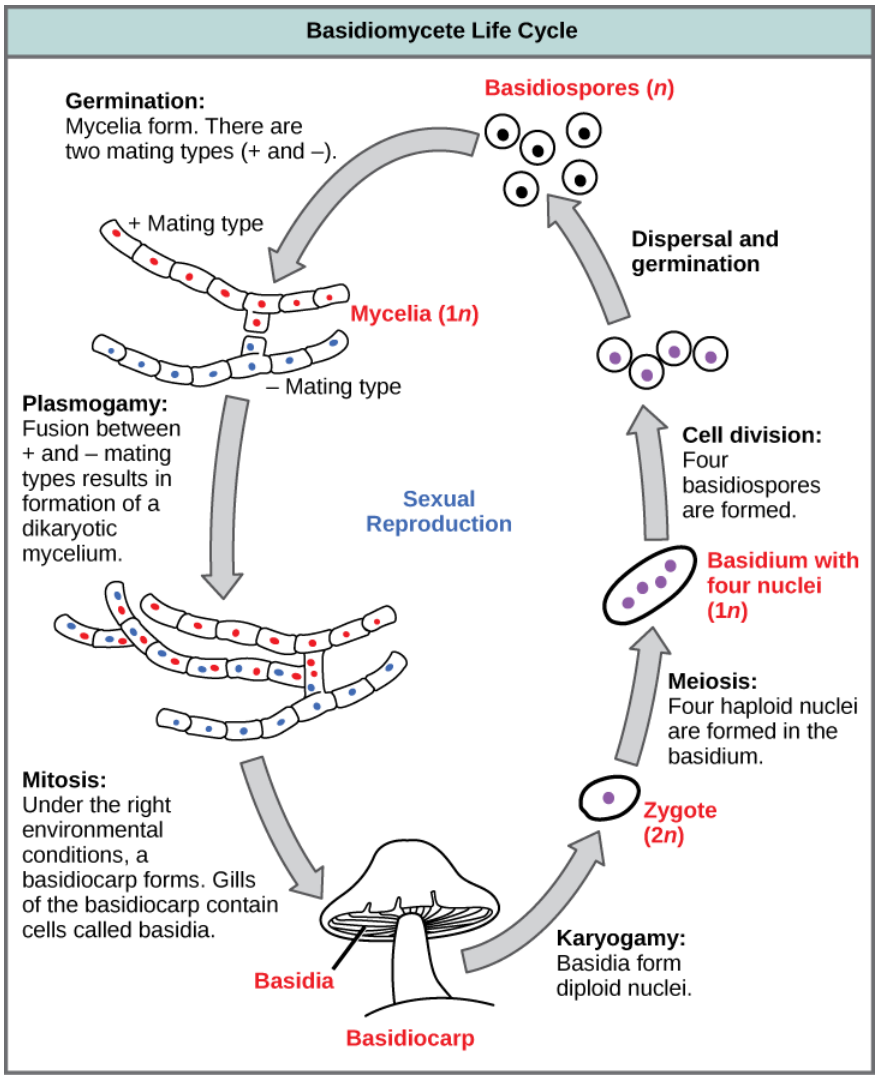


Figure 5.5.8: The lifecycle of a basidiomycete alternates generation with a prolonged stage in which two nuclei (dikaryon) are present in the hyphae.

Glomeromycota

The Glomeromycota is a newly established phylum which comprises about 230 species that all form **mycorrhizal** relationships with the roots of plants. Fossil records indicate that trees and their root symbionts share a long evolutionary history. It appears that all members of this family form arbuscular mycorrhizae: the hyphae interact with the root cells forming a mutually beneficial association where the plants supply the carbon source and energy in the form of carbohydrates to the fungus, and the fungus supplies essential minerals from the soil to the plant.

The glomeromycetes do not reproduce sexually and do not survive without the presence of plant roots. Although they have coenocytic hyphae like the zygomycetes, they do not form zygospores. DNA analysis shows that all glomeromycetes probably descended from a common ancestor, making them a monophyletic lineage.

Asexual Ascomycota and Basidiomycota

Fungi that have no known sexual cycle were classified in the form phylum Deuteromycota. That phylum no longer exists. Present classification now puts these fungi into the phyla Ascomycota and Basidiomycota based on evolutionary relationships.

Video





In this 9-minute lecture, the characteristics, reproduction, and categories of the kingdom Fungi are explained. Question after watching: Mr. Anderson says that we probably have more in common in our lifestyle with fungi than with plants. What sort of evidence can you find to support this assertion?

Video





This 6.5-minute video provides an evolutionary history of fungi.
Question after watching: This video suggests that fungi were critical to the evolution of plants and animals. How?

Career Connection: Mycologist

Mycologists are biologists who study fungi. Mycology is a branch of microbiology, and many mycologists start their careers with a degree in microbiology. To become a mycologist, a bachelor's degree in a biological science (preferably majoring in microbiology) and a master's degree in mycology are minimally necessary. Mycologists can specialize in taxonomy and fungal genomics, molecular and cellular biology, plant pathology, biotechnology, or biochemistry. Some medical microbiologists concentrate on the study of infectious diseases caused by fungi (mycoses). Mycologists collaborate with zoologists and plant pathologists to identify and control difficult fungal infections, such as the devastating chestnut blight, the mysterious decline in frog populations in many areas of the world, or the deadly epidemic called white-nose syndrome, which has decimated bats in eastern North America and spreading west at a rapid rate.

Government agencies hire mycologists as research scientists and technicians to monitor the health of crops, national parks, and national forests. Mycologists are also employed in the private sector by companies that develop chemical and biological control products or new agricultural products, and by companies that provide disease control services. Because of the key role played by fungi in the fermentation of alcohol and the preparation of many important foods, scientists with a good

understanding of fungal physiology routinely work in the food technology industry. **Oenology**, the science of winemaking, relies not only on the knowledge of grape varietals and soil composition but also on an understanding of the characteristics of the wild yeasts that thrive in different winemaking regions. It is possible to purchase yeast strains isolated from specific grape-growing regions. The great French chemist and microbiologist, Louis Pasteur, made many of his essential discoveries working on the humble brewer's yeast, thus discovering the process of fermentation.

Cell Structure and Function

Fungi are eukaryotes, and as such, have a complex cellular organization. Unlike plant cells, fungal cells do not have chloroplasts or chlorophyll. Many fungi display bright colors arising from other cellular pigments, ranging from red, to green, to black. The poisonous *Amanita muscaria* (fly agaric) is recognizable by its bright red cap with white patches (Figure 5.5.9). Pigments in fungi are associated with the cell wall and play a protective role against ultraviolet radiation. Some fungal pigments are toxic.



Figure 5.5.9: The poisonous *Amanita muscaria* is native to temperate and boreal regions of North America, including British Columbia. (credit: Christine Majul)

Like plant cells, fungal cells have a thick cell wall. The rigid layers of fungal cell walls contain complex polysaccharides called chitin and glucans. Chitin, also found in the exoskeleton of insects, gives structural strength to the cell walls of fungi. The wall protects the cell from desiccation and predators. Fungi have plasma membranes like other eukaryotes, except that the structure is stabilized by ergosterol: a steroid molecule that replaces the cholesterol found in animal cell membranes. Most members of the kingdom Fungi are nonmotile. Flagella are produced only by the gametes in the primitive Phylum Chytridiomycota.

? Optional Activity 5.5.1

Which polysaccharide is usually found in the cell wall of fungi?

A. starch
B. glycogen
C. chitin
D. cellulose

Answer

C. chitin

? Optional Activity 5.5.2

Which of these organelles is not found in a fungal cell?

A. chloroplast
B. nucleus

C. mitochondrion
D. Golgi apparatus

Answer

A. chloroplast

Growth

Most fungal hyphae are divided into separate cells by endwalls called **septa** (singular, septum) (Figure 5.5.6). In most phyla of fungi, tiny holes in the septa allow for the rapid flow of nutrients and small molecules from cell to cell along the hypha. They are described as perforated septa. The hyphae in bread molds (which belong to the Phylum Zygomycota) are not separated by septa. Instead, they are formed by large cells containing many nuclei, an arrangement described as **coenocytic hyphae** Figure 5.5.10. Thus, hyphae can be formed by one unicellular (multi-nuclear) fungal cell or by a multicellular assortment of fungi cells.

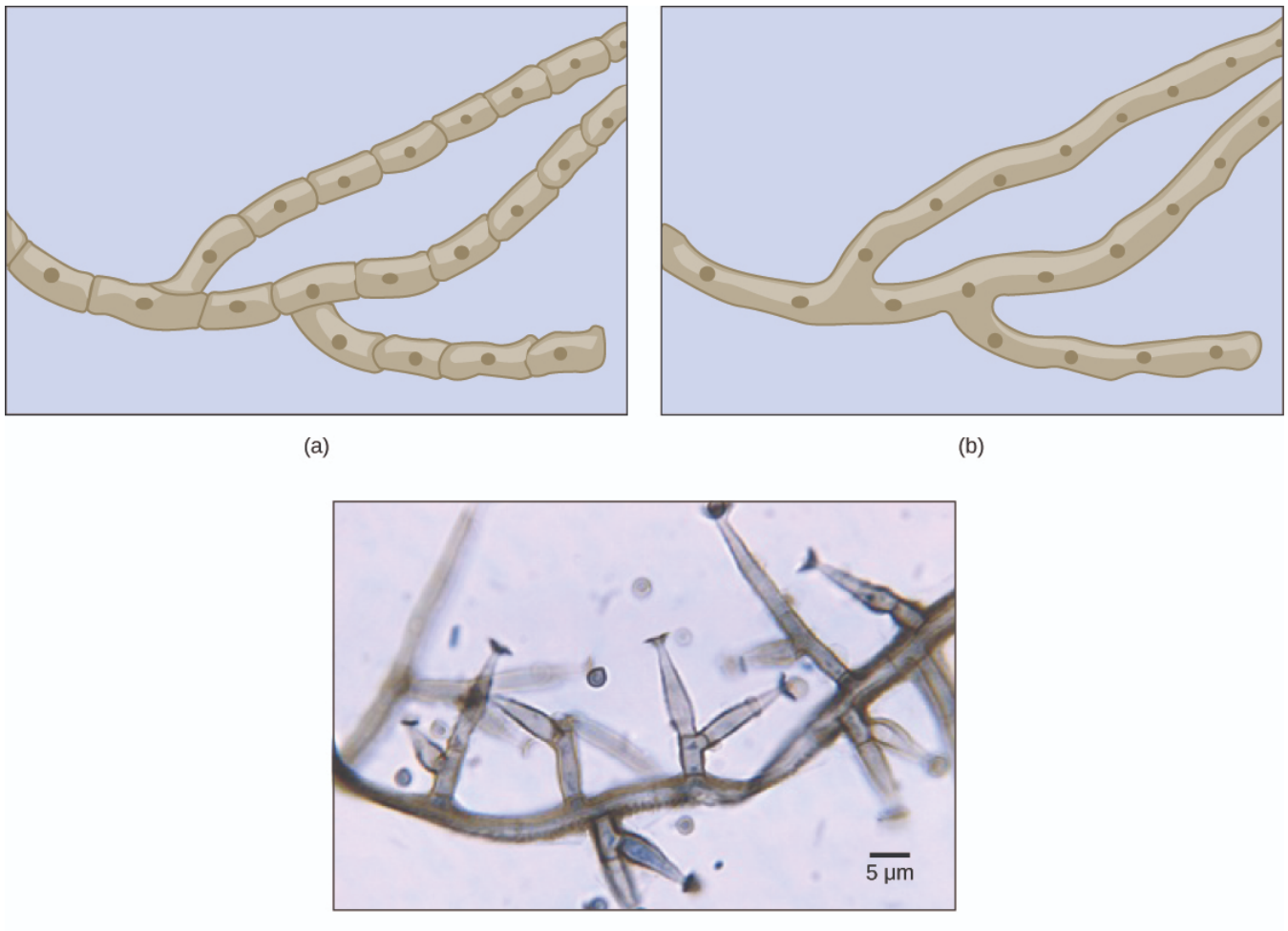


Figure 5.5.10: Fungal hyphae may be (a) septated or (b) coenocytic (coeno- = "common"; -cytic = "cell") with many nuclei present in a single hypha. A bright field light micrograph of (c) *Phialophora richardsiae* shows septa that divide the hyphae. (credit c: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Fungi thrive in environments that are moist and slightly acidic and can grow with or without light. They vary in their oxygen requirement. Most fungi are **obligate aerobes**, requiring oxygen to survive. Other species, such as the Chytridiomycota that reside in the rumen of cattle, are **obligate anaerobes**, in that they only use anaerobic respiration because oxygen will disrupt their metabolism or kill them. Yeasts are intermediate, being **facultative anaerobes**. This means that they grow best in the presence of oxygen using aerobic respiration but can survive using anaerobic respiration when oxygen is not available. The alcohol produced from yeast fermentation is used in wine and beer production.

? Optional Activity 5.5.3

The wall dividing individual cells in a fungal filament is called a

A. thallus
B. hypha
C. mycelium
D. septum

Answer

D. septum

Nutrition

Like animals, fungi are heterotrophs; they use complex organic compounds as a source of carbon, rather than fix carbon dioxide from the atmosphere as do some bacteria and most plants. In addition, fungi do not fix nitrogen from the atmosphere. Like animals, they must obtain it from their diet. However, unlike most animals, which ingest food and then digest it internally in specialized organs, fungi perform these steps in the reverse order; digestion precedes ingestion. Fungi are **decomposers**. First, **exoenzymes** are transported out of the hyphae, where they process nutrients in the environment. Then, the smaller molecules produced by this external digestion are absorbed through the large surface area of the mycelium. As with animal cells, the polysaccharide of storage is glycogen, rather than starch, as found in plants.

Fungi are mostly saprobes: organisms that derive nutrients from decaying organic matter. They obtain their nutrients from dead or decomposing organic matter: mainly plant material. Fungal exoenzymes break down insoluble polysaccharides, such as the cellulose and lignin of dead wood, into readily absorbable glucose molecules. The carbon, nitrogen, and other elements are thus released into the environment.

Because of their varied metabolic pathways, fungi fulfill an important ecological role and are being investigated as potential tools in bioremediation. For example, some species of fungi can be used to break down diesel oil and **polycyclic aromatic hydrocarbons (PAHs)** that are often released by industrial processes as environmental pollutants. Other species take up heavy metals, such as cadmium and lead. Some fungi are parasitic, infecting either plants or animals. Smut and Dutch elm disease affect plants, whereas athlete’s foot and candidiasis (thrush) are medically important fungal infections in humans.

Reproduction

Fungi reproduce sexually and/or asexually. **Perfect fungi** reproduce both sexually and asexually, while the so-called **imperfect fungi** reproduce only asexually (by mitosis).

In both sexual and asexual reproduction, fungi produce spores that disperse from the parent organism by either floating on the wind, a liquid medium, or attaching to an animal. Fungal spores are smaller and lighter than plant seeds. The giant puffball mushroom bursts open and releases trillions of spores. The huge number of spores released increases the likelihood of landing in an environment that will support growth (Figure 5.5.11).



Figure 5.5.11: The (a) giant puffball mushroom (b) releases a cloud of spores when it reaches maturity. (credit a: modification of work by Roger Griffith; credit b: modification of work by Pearson Scott Foresman, donated to the Wikimedia Foundation)

Asexual Reproduction

Fungi reproduce asexually by fragmentation, budding, or producing spores. Fragments of hyphae can grow new colonies. Somatic cells in yeast form buds. During budding (a type of cytokinesis), a bulge forms on the side of the cell, the nucleus divides mitotically, and the bud ultimately detaches itself from the mother cell (Figure 5.5.12).

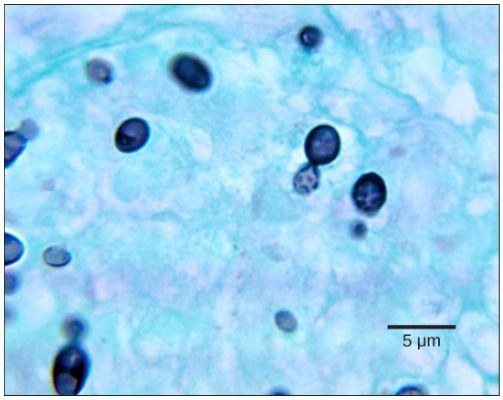


Figure 5.5.12: The dark cells in this bright field light micrograph are the pathogenic yeast *Histoplasma capsulatum*, seen against a backdrop of light blue tissue. Histoplasma primarily infects lungs but can spread to other tissues, causing histoplasmosis, a potentially fatal disease. The cell in the top right quadrant is in the process of budding, with the larger bodu pinching off a smaller round daughter cell. (credit: modification of work by Dr. Libero Ajello, CDC; scale-bar data from Matt Russell)

The most common mode of asexual reproduction is through the formation of asexual **spores**, which are produced by one parent only (through mitosis) and are genetically identical to that parent (Figure 5.5.13). Spores allow fungi to expand their distribution and colonize new environments. They may be released from the parent thallus either outside or within a special reproductive sac called a **sporangium**.

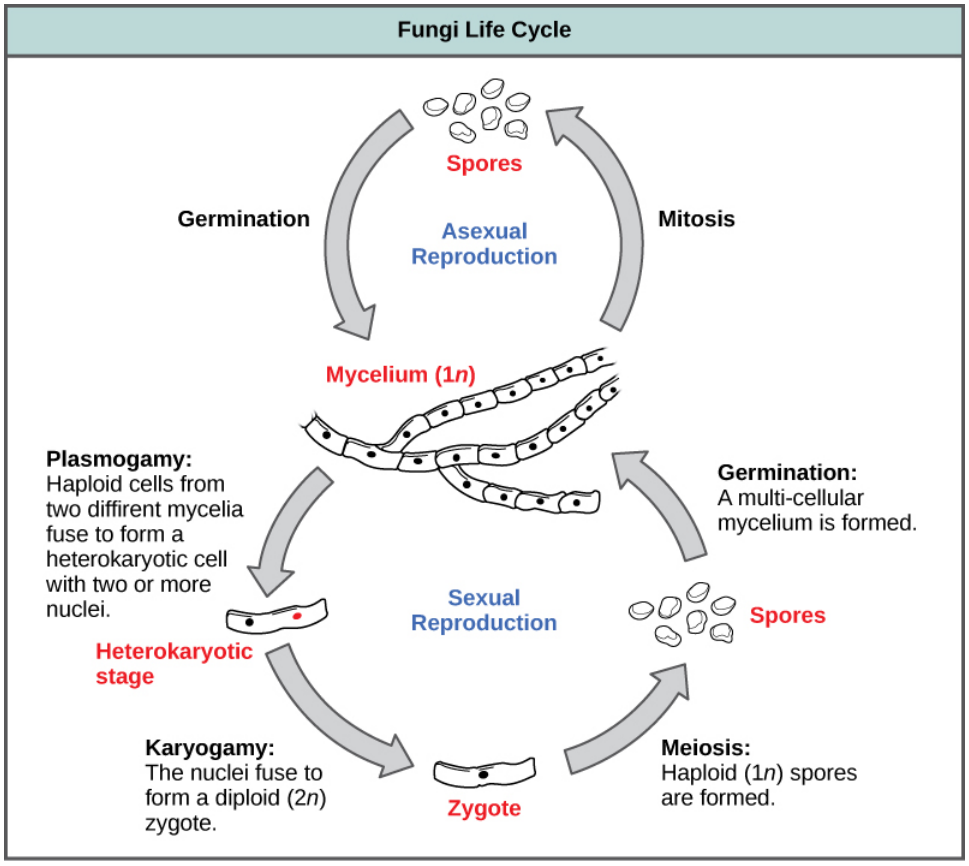


Figure 5.5.9: Fungi may have both asexual and sexual stages of reproduction.

There are many types of asexual spores. **Conidiospores** are unicellular or multicellular spores that are released directly from the tip or side of the hypha. Other asexual spores originate in the fragmentation of a hypha to form single cells that are released as spores; some of these have a thick wall surrounding the fragment. Yet others bud off the vegetative parent cell. **Sporangiospores** are produced in a sporangium (Figure 5.5.14).

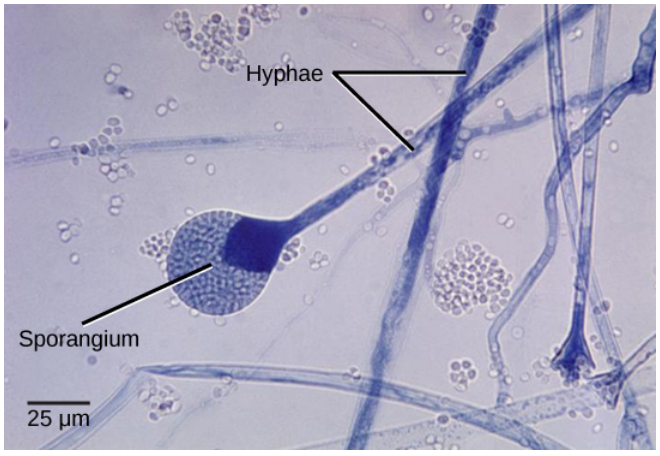


Figure 5.5.14: This bright field light micrograph shows the release of spores from a sporangium at the end of a hypha called a sporangiophore. The organism is a *Mucor* sp. fungus, a mold often found indoors. (credit: modification of work by Dr. Lucille Georg, CDC; scale-bar data from Matt Russell)

Sexual Reproduction

Sexual reproduction introduces genetic variation into a population of fungi. In fungi, sexual reproduction often occurs in response to adverse environmental conditions. During sexual reproduction, two mating types are produced. When both mating types are

present in the same mycelium, it is called **homothallic**, or self-fertile. **Heterothallic** mycelia require two different, but compatible, mycelia to reproduce sexually.

Although there are many variations in fungal sexual reproduction, all include the following three stages (Figure 5.5.9). First, during **plasmogamy** (literally, “marriage or union of cytoplasm”), two haploid cells fuse, leading to a dikaryotic stage where two haploid nuclei coexist in a single cell. During **karyogamy** (“nuclear marriage”), the haploid nuclei fuse to form a diploid zygote nucleus. Finally, meiosis takes place in the gametangia (singular, gametangium) organs, in which gametes of different mating types are generated. At this stage, spores are disseminated into the environment.

Niche and Habitat

Fungi have colonized nearly all environments on Earth, but are frequently found in cool, dark, moist places with a supply of decaying material. Fungi are saprobes that decompose organic matter. Fungi often interact with other organisms, forming beneficial or mutualistic associations. Many successful mutualistic relationships involve a fungus and another organism.

For example most terrestrial plants form symbiotic relationships with fungi. The roots of the plant connect with the underground parts of the fungus forming mycorrhizae. Through mycorrhizae, the fungus and plant exchange nutrients and water, greatly aiding the survival of both species Alternatively, lichens are an association between a fungus and its photosynthetic partner (usually an alga). More on this is discussed below.

Fungi also cause serious infections in plants and animals. For example, Dutch elm disease, which is caused by the fungus *Ophiostoma ulmi*, is a particularly devastating type of fungal infestation that destroys many native species of elm (*Ulmus* sp.) by infecting the tree’s vascular system. The elm bark beetle acts as a vector, transmitting the disease from tree to tree. Accidentally introduced in the 1900s, the fungus decimated elm trees across the continent. Many European and Asiatic elms are less susceptible to Dutch elm disease than American elms.

Decomposers and Recyclers

The food web would be incomplete without organisms that decompose organic matter (Figure 5.5.15). Some elements—such as nitrogen and phosphorus—are required in large quantities by biological systems, and yet are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.



Figure 5.5.15: Fungi are an important part of ecosystem nutrient cycles. These bracket fungi growing on the side of a tree are the fruiting structures of a basidiomycete. They receive their nutrients through their hyphae, which invade and decay the tree trunk. (credit: Cory Zanker)

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and

enzymes is dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways (Figure 5.5.16).

Video



This 4-minute TedEd introduces concepts of energy flow in an ecosystem, including the role of decomposers. Question after watching: Do humans sometimes eat detritus directly? Provide an example.



Figure 5.5.16: Shelf fungi, so called because they grow on trees in a stack, attack and digest the trunk or branches of a tree. While some shelf fungi are found only on dead trees, others can parasitize living trees and cause eventual death, so they are considered serious tree pathogens. (credit: Cory Zanker)

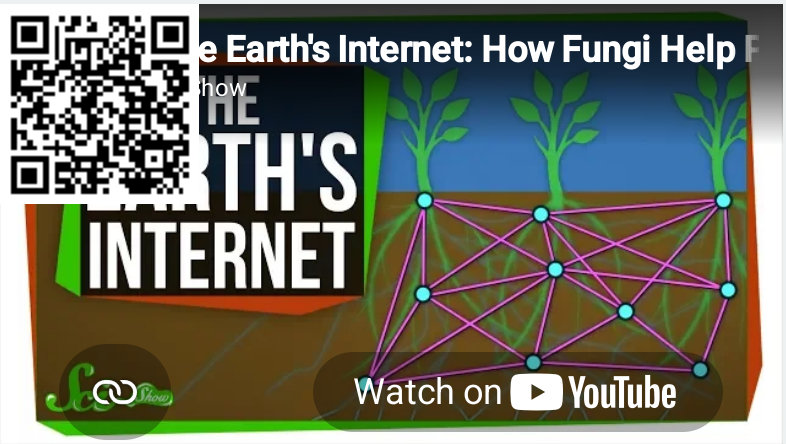
Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. The definition does not describe the quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

One of the most remarkable associations between fungi and plants is the establishment of **mycorrhizae**. Mycorrhiza, which comes from the Greek words *myco* meaning fungus and *rhizo* meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Somewhere between 80 and 90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae 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.

Lichens are not a single organism, but rather another example of mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota phyla) lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium) (Figure 5.5.17). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship.

Video



This 5-minute video provides an overview of mycorrhiza.
Question after watching: What are some of the functions of the common mycelium network?



Figure 5.5.17: Lichens have many forms. They may be (a) crust-like, (b) hair-like, or (c) leaf-like. (credit a: modification of work by Jo Naylor; credit b: modification of work by "djpmapleferryman"/Flickr; credit c: modification of work by Cory Zanker)

Optional Activity 5.5.3

What term describes the close association of a fungus with the root of a tree?

A. a rhizoid
B. a lichen
C. a mycorrhiza
D. an endophyte

Answer

C. a mycorrhiza

Evolution Connection: Coevolution of Land Plants and Mycorrhizae

Mycorrhizae are the mutually beneficial symbiotic association between roots of vascular plants and fungi. A well-accepted theory proposes that fungi were instrumental in the evolution of the root system in plants and contributed to the success of Angiosperms. The bryophytes (mosses and liverworts), which are considered the most primitive plants and the first to survive on dry land, do not have a true root system; some have mycorrhizae and some do not. They depend on a simple **rhizoid** (an underground organ) and cannot survive in dry areas. True roots appeared in vascular plants. Vascular plants that developed a system of thin extensions from the rhizoids (found in mosses) are thought to have had a selective advantage because they had a

greater surface area of contact with the fungal partners than the mosses and liverworts, thus availing themselves of more nutrients in the ground.

Fossil records indicate that fungi preceded plants on dry land. The first association between fungi and photosynthetic organisms on land involved moss-like plants and endophytes. These early associations developed before roots appeared in plants. Slowly, the benefits of the endophyte and rhizoid interactions for both partners led to present-day mycorrhizae; up to about 90 percent of today's vascular plants have associations with fungi in their rhizosphere. The fungi involved in mycorrhizae display many characteristics of primitive fungi; they produce simple spores, show little diversification, do not have a sexual reproductive cycle, and cannot live outside of a mycorrhizal association. The plants benefited from the association because mycorrhizae allowed them to move into new habitats because of increased uptake of nutrients, and this gave them a selective advantage over plants that did not establish symbiotic relationships.

Fungal Parasites and Pathogens

The production of sufficient good-quality crops is essential to human existence. Plant diseases have ruined crops, bringing widespread famine. Many plant pathogens are fungi that cause tissue decay and eventual death of the host (Figure 5.5.18). In addition to destroying plant tissue directly, some plant pathogens spoil crops by producing potent toxins. Fungi are also responsible for food spoilage and the rotting of stored crops. For example, the fungus *Claviceps purpurea* causes ergot, a disease of cereal crops (especially of rye). Although the fungus reduces the yield of cereals, the effects of ergot's alkaloid toxins on humans and animals are of much greater significance. In animals, the disease is referred to as ergotism. The most common signs and symptoms are convulsions, hallucination, gangrene, and loss of milk in cattle. The active ingredient of ergot is lysergic acid, which is a precursor of the drug LSD. Smuts, rusts, and powdery or downy mildew are other examples of common fungal pathogens that affect crops. Aflatoxins are toxic, carcinogenic compounds released by fungi of the genus *Aspergillus*. Periodically, harvests of nuts and grains are tainted by aflatoxins, leading to a massive recall of produce. This sometimes ruins producers and causes food shortages in developing countries.

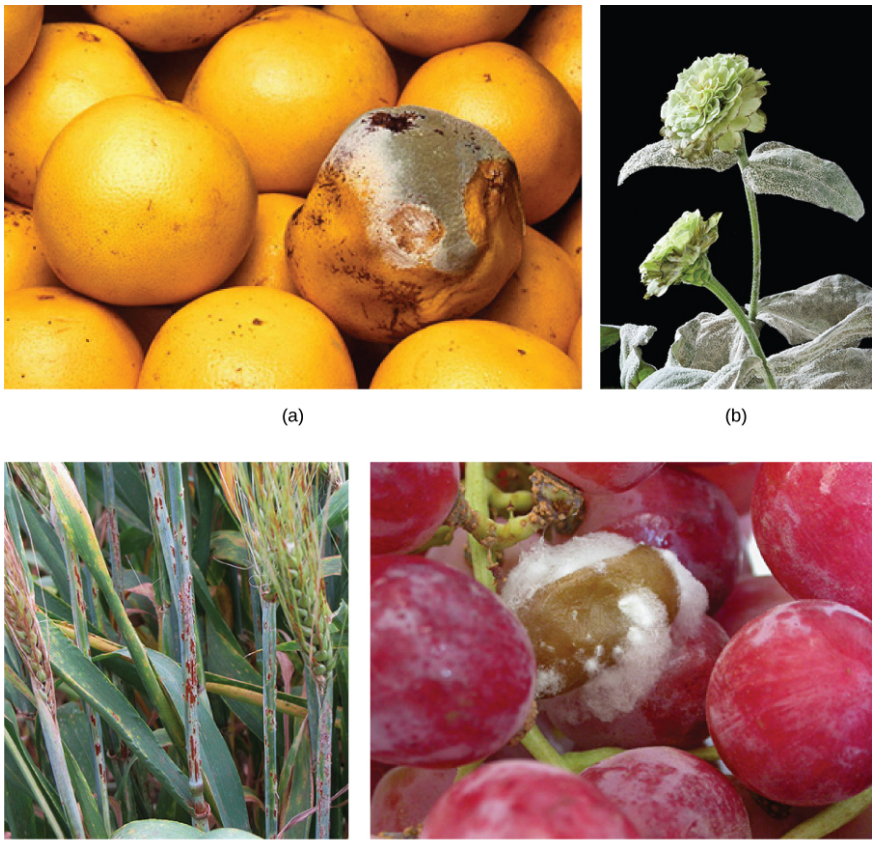


Figure 5.5.18: Some fungal pathogens include (a) green mold on grapefruit, (b) powdery mildew on a zinnia, (c) stem rust on a sheaf of barley, and (d) grey rot on grapes. In wet conditions *Botrytis cinerea*, the fungus that causes grey rot, can destroy a grape crop. However, controlled infection of grapes by *Botrytis* results in noble rot, a condition that produces strong and much-prized dessert wines. (credit a: modification of work by Scott Bauer, USDA-ARS; credit b: modification of work by Stephen Ausmus, USDA-ARS; credit c: modification of work by David Marshall, USDA-ARS; credit d: modification of work by Joseph Smilanick, USDA-ARS)

Animal and Human Parasites and Pathogens

Fungi can affect animals, including humans, in several ways. A mycosis is a fungal disease that results from infection and direct damage. Fungi attack animals directly by colonizing and destroying tissues. Mycotoxicosis is the poisoning of humans (and other animals) by foods contaminated by fungal toxins (mycotoxins). Mycetismus describes the ingestion of preformed toxins in poisonous mushrooms. In addition, individuals who display hypersensitivity to molds and spores develop strong and dangerous allergic reactions. Fungal infections are generally very difficult to treat because, unlike bacteria, fungi are eukaryotes. Antibiotics only target prokaryotic cells, whereas compounds that kill fungi also harm the eukaryotic animal host.

Many fungal infections are superficial; that is, they occur on the animal's skin. Termed cutaneous ("skin") mycoses, they can have devastating effects. For example, the decline of the world's frog population in recent years may be caused by the chytrid fungus *Batrachochytrium dendrobatidis*, which infects the skin of frogs and presumably interferes with gaseous exchange. Similarly, more than a million bats in the United States have been killed by white-nose syndrome, which appears as a white ring around the mouth of the bat. It is caused by the cold-loving fungus *Geomyces destructans*, which disseminates its deadly spores in caves where bats hibernate. Mycologists are researching the transmission, mechanism, and control of *G. destructans* to stop its spread.

Video



The true story of *Cordyceps.*

Importance of Fungi

Note



Engineers, medical researchers, and designers are utilizing the natural abilities of various fungi for antibiotics, building materials, water filtration, toxic waste cleanup, pest abatement, textiles, and other purposes.

Although we often think of fungi as organisms that cause disease and rot food, fungi are important to human life on many levels. As we have seen, they influence the well-being of human populations on a large scale because they are part of the nutrient cycle in ecosystems. They have other ecosystem roles as well. As animal pathogens, fungi help to control the population of damaging pests. These fungi are very specific to the insects they attack, and do not infect animals or plants. Fungi are currently under investigation as potential microbial insecticides, with several already on the market. For example, the fungus *Beauveria bassiana* is a pesticide being tested as a possible biological control agent for the recent spread of emerald ash borer.

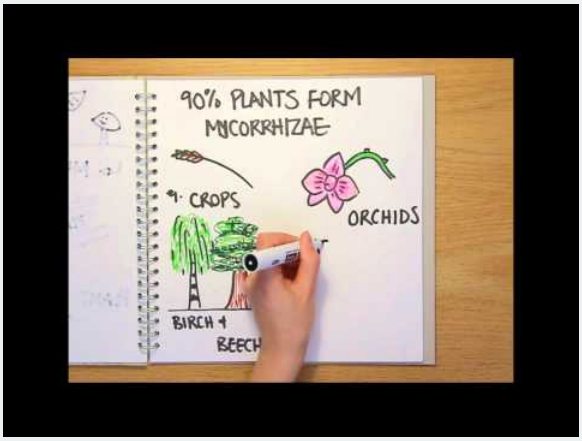
Fermentation—of grains to produce beer, and of fruits to produce wine—is an ancient art that humans in most cultures have practiced for millennia. Wild yeasts are acquired from the environment and used to ferment sugars into CO_2 and ethyl alcohol under anaerobic conditions. It is now possible to purchase isolated strains of wild yeasts from different wine-making regions. Louis Pasteur was instrumental in developing a reliable strain of brewer's yeast, *Saccharomyces cerevisiae*, for the French brewing industry in the late 1850s. This was one of the first examples of biotechnology patenting.

Many secondary metabolites of fungi are of great commercial importance. Antibiotics are naturally produced by fungi to kill or inhibit the growth of bacteria, limiting their competition in the natural environment. Important antibiotics, such as penicillin and the cephalosporins, are isolated from fungi. Valuable drugs isolated from fungi include the immunosuppressant drug cyclosporine

(which reduces the risk of rejection after organ transplant), the precursors of steroid hormones, and ergot alkaloids used to stop bleeding. Psilocybin is a compound found in fungi such as *Psilocybe semilanceata* and *Gymnopilus junonius*, which have been used for their hallucinogenic properties by various cultures for thousands of years.

Video





This 5.5-minute video provides a review of the kingdom Fungi.
Question after watching: What are three things you learned in this section, two things you still have questions about, and one visual you created to summarize your learning?

Exercise 5.5.4

If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth?

Answer

Without mycorrhiza, plants cannot absorb adequate nutrients, which stunts their growth. The addition of fungal spores to sterile soil can alleviate this problem.

This page titled 5.5: Fungi is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

5.5.E: Fungi (Exercises)

5.5.2: Characteristics of Fungi

Review Questions

Which polysaccharide is usually found in the cell wall of fungi?

A. starch
B. glycogen
C. chitin
D. cellulose

Answer

C

Which of these organelles is not found in a fungal cell?

A. chloroplast
B. nucleus
C. mitochondrion
D. Golgi apparatus

Answer

A

The wall dividing individual cells in a fungal filament is called a

A. thallus
B. hypha
C. mycelium
D. septum

Answer

D

During sexual reproduction, a homothallic mycelium contains

A. all septated hyphae
B. all haploid nuclei
C. both mating types
D. none of the above

Answer

C

Free Response

What are the evolutionary advantages for an organism to reproduce both asexually and sexually?

Answer

Asexual reproduction is fast and best under favorable conditions. Sexual reproduction allows the recombination of genetic traits and increases the odds of developing new adaptations better suited to a changed environment.

Compare plants, animals, and fungi, considering these components: cell wall, chloroplasts, plasma membrane, food source, and polysaccharide storage. Be sure to indicate fungi's similarities and differences to plants and animals.

Answer

Animals have no cell walls; fungi have cell walls containing chitin; plants have cell walls containing cellulose. Chloroplasts are absent in both animals and fungi but are present in plants. Animal plasma membranes are stabilized with cholesterol, while fungi plasma membranes are stabilized with ergosterol, and plant plasma membranes are stabilized with phytosterols. Animals obtain N and C from food sources via internal digestion. Fungi obtain N and C from food sources via external digestion. Plants obtain organic N from the environment or through symbiotic N-fixing bacteria; they obtain C from photosynthesis. Animals and fungi store polysaccharides as glycogen, while plants store them as starch.

5.5.3: Classifications of Fungi

Review Questions

The most primitive phylum of fungi is the _____.

A. Chytridiomycota
B. Zygomycota
C. Glomeromycota
D. Ascomycota

Answer

A

Members of which phylum produce a club-shaped structure that contains spores?

A. Chytridiomycota
B. Basidiomycota
C. Glomeromycota
D. Ascomycota

Answer

B

Members of which phylum establish a successful symbiotic relationship with the roots of trees?

A. Ascomycota
B. Deuteromycota
C. Basidiomycota
D. Glomeromycota

Answer

D

The fungi that do not reproduce sexually use to be classified as _____.

A. Ascomycota
B. Deuteromycota

C. Basidiomycota
D. Glomeromycota

Answer

B

Free Response

What is the advantage for a basidiomycete to produce a showy and fleshy fruiting body?

Answer

By ingesting spores and disseminating them in the environment as waste, animals act as agents of dispersal. The benefit to the fungus outweighs the cost of producing fleshy fruiting bodies.

For each of the four groups of perfect fungi (Chytridiomycota, Zygomycota, Ascomycota, and Basidiomycota), compare the body structure and features, and provide an example.

Answer

Chytridiomycota (Chytrids) may have a unicellular or multicellular body structure; some are aquatic with motile spores with flagella; an example is the *Allomyces*. Zygomycota (conjugated fungi) have a multicellular body structure; features include zygospores and presence in soil; examples are bread and fruit molds. Ascomycota (sac fungi) may have unicellular or multicellular body structure; a feature is sexual spores in sacs (asci); examples include the yeasts used in bread, wine, and beer production. Basidiomycota (club fungi) have multicellular bodies; features includes sexual spores in the basidiocarp (mushroom) and that they are mostly decomposers; mushroom-producing fungi are an example.

5.5.4: Ecology of Fungi

Review Questions

What term describes the close association of a fungus with the root of a tree?

A. a rhizoid
B. a lichen
C. a mycorrhiza
D. an endophyte

Answer

C

Why are fungi important decomposers?

A. They produce many spores.
B. They can grow in many different environments.
C. They produce mycelia.
D. They recycle carbon and inorganic minerals by the process of decomposition.

Answer

D

Free Response

Why does protection from light actually benefit the photosynthetic partner in lichens?

Answer

Protection from excess light that may bleach photosynthetic pigments allows the photosynthetic partner to survive in environments unfavorable to plants.

5.5.5: Fungal Parasites and Pathogens

Review Questions

A fungus that climbs up a tree reaching higher elevation to release its spores in the wind and does not receive any nutrients from the tree or contribute to the tree's welfare is described as a _____.

A. commensal
B. mutualist
C. parasite
D. pathogen

Answer

A

A fungal infection that affects nails and skin is classified as _____.

A. systemic mycosis
B. mycetismus
C. superficial mycosis
D. mycotoxicosis

Answer

C

Free Response

Why can superficial mycoses in humans lead to bacterial infections?

Answer

Dermatophytes that colonize skin break down the keratinized layer of dead cells that protects tissues from bacterial invasion. Once the integrity of the skin is breached, bacteria can enter the deeper layers of tissues and cause infections.

5.5.6: Importance of Fungi in Human Life

Review Questions

Yeast is a facultative anaerobe. This means that alcohol fermentation takes place only if:

A. the temperature is close to 37°C
B. the atmosphere does not contain oxygen
C. sugar is provided to the cells
D. light is provided to the cells

Answer

B

The advantage of yeast cells over bacterial cells to express human proteins is that:

A. yeast cells grow faster
B. yeast cells are easier to manipulate genetically
C. yeast cells are eukaryotic and modify proteins similarly to human cells
D. yeast cells are easily lysed to purify the proteins

Answer

C

Free Response

Historically, artisanal breads were produced by capturing wild yeasts from the air. Prior to the development of modern yeast strains, the production of artisanal breads was long and laborious because many batches of dough ended up being discarded. Can you explain this fact?

Answer

The dough is often contaminated by toxic spores that float in the air. It was one of Louis Pasteur's achievements to purify reliable strains of baker's yeast to produce bread consistently.

This page titled 5.5.E: Fungi (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **24.E: Fungi (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

5.6: Introduction to Animal Diversity

5.6.1: Introduction

5.6.2: The Evolutionary History of the Animal Kingdom

5.6.3: Features of the Animal Kingdom

5.6.4: Features Used to Classify Animals

5.6.5: Animal Phylogeny

5.6.E: Introduction to Animal Diversity (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 5.6: Introduction to Animal Diversity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

5.6.1: Introduction



Figure 5.6.1.1: The leaf chameleon (*Brookesia micra*) was discovered in northern Madagascar in 2012. At just over one inch long, it is the smallest known chameleon. (credit: modification of work by Frank Glaw, et al., PLOS)

Animal evolution began in the ocean over 600 million years ago with tiny creatures that probably do not resemble any living organism today. Since then, animals have evolved into a highly diverse kingdom. Although over one million extant (currently living) species of animals have been identified, scientists are continually discovering more species as they explore ecosystems around the world. The number of extant species is estimated to be between 3 and 30 million.

But what is an animal? While we can easily identify dogs, birds, fish, spiders, and worms as animals, other organisms, such as corals and sponges, are not as easy to classify. Animals vary in complexity—from sea sponges to crickets to chimpanzees—and scientists are faced with the difficult task of classifying them within a unified system. They must identify traits that are common to all animals as well as traits that can be used to distinguish among related groups of animals. The animal classification system characterizes animals based on their anatomy, morphology, evolutionary history, features of embryological development, and genetic makeup. This classification scheme is constantly developing as new information about species arises. Understanding and classifying the great variety of living species help us better understand how to conserve the diversity of life on earth.





This page titled 5.6.1: Introduction is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **27.0: Introduction** by OpenStax is licensed CC BY 4.0.

5.6.2: The Evolutionary History of the Animal Kingdom

Skills to Develop

- Describe the features that characterized the earliest animals and when they appeared on earth
- Explain the significance of the Cambrian period for animal evolution and the changes in animal diversity that took place during that time
- Describe some of the unresolved questions surrounding the Cambrian explosion
- Discuss the implications of mass animal extinctions that have occurred in evolutionary history

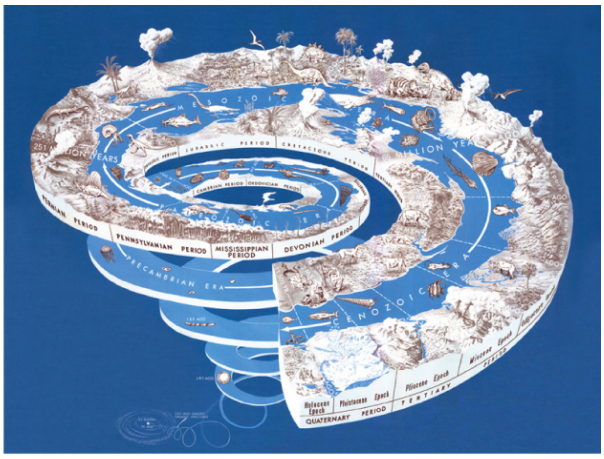
Many questions regarding the origins and evolutionary history of the animal kingdom continue to be researched and debated, as new fossil and molecular evidence change prevailing theories. Some of these questions include the following: How long have animals existed on Earth? What were the earliest members of the animal kingdom, and what organism was their common ancestor? While animal diversity increased during the Cambrian period of the Paleozoic era, 530 million years ago, modern fossil evidence suggests that primitive animal species existed much earlier.

Pre-Cambrian Animal Life

The time before the Cambrian period is known as the Ediacaran period (from about 635 million years ago to 543 million years ago), the final period of the late Proterozoic Neoproterozoic Era (Figure 5.6.2.1). It is believed that early animal life, termed Ediacaran biota, evolved from protists at this time. Some protest species called choanoflagellates closely resemble the choanocyte cells in the simplest animals, sponges. In addition to their morphological similarity, molecular analyses have revealed similar sequence homologies in their DNA.

EON	ERA	PERIOD	MILLIONS OF YEARS AGO
Phanerozoic	Cenozoic	Quaternary	1.6
		Tertiary	66
	Mesozoic	Cretaceous	138
		Jurassic	205
		Triassic	240
	Paleozoic	Permian	290
		Pennsylvanian	330
		Mississippian	360
		Devonian	410
		Silurian	435
		Ordovician	500
		Cambrian	540
Proterozoic	Late Proterozoic Middle Proterozoic Early Proterozoic	Ediacaran 635-543 MYA	2500
Archean	Late Archean Middle Archean Early Archean		3800?
Pre-Archean			

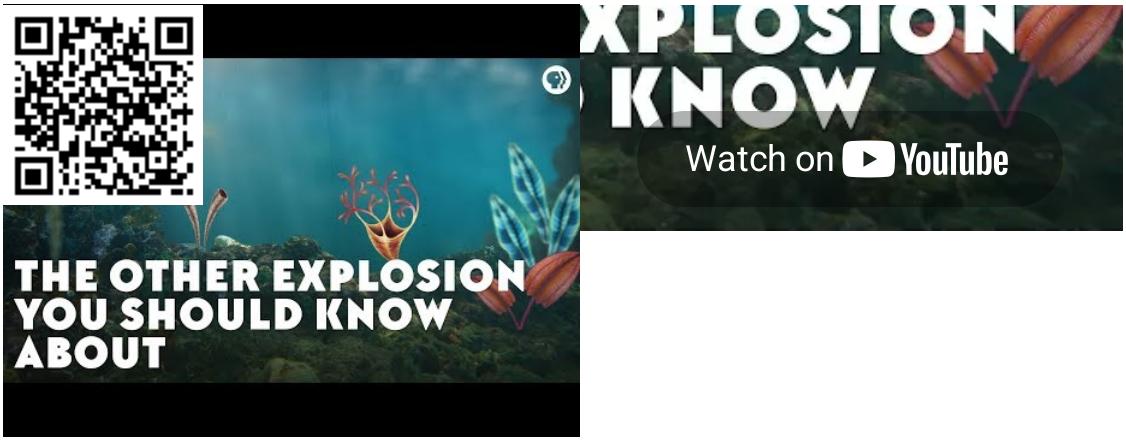
(a)



(b)

Figure 5.6.2.1: (a) Earth's history is divided into eons, eras, and periods. Note that the Ediacaran period starts in the Proterozoic eon and ends in the Cambrian period of the Phanerozoic eon. (b) Stages on the geological time scale are represented as a spiral. (credit: modification of work by USGS)





The earliest life comprising Ediacaran biota was long believed to include only tiny, sessile, soft-bodied sea creatures. However, recently there has been increasing scientific evidence suggesting that more varied and complex animal species lived during this time, and possibly even before the Ediacaran period.

Fossils believed to represent the oldest animals with hard body parts were recently discovered in South Australia. These sponge-like fossils, named *Coronacollina acula*, date back as far as 560 million years, and are believed to show the existence of hard body parts and spicules that extended 20–40 cm from the main body (estimated about 5 cm long). Other fossils from the Ediacaran period are shown in Figure 5.6.2.2.







(a) (b)

Figure 5.6.2.2: Fossils of (a) *Cyclomedusa* and (b) *Dickinsonia* date to 650 million years ago, during the Ediacaran period. (credit: modification of work by "Smith609"/Wikimedia Commons)

Another recent fossil discovery may represent the earliest animal species ever found. While the validity of this claim is still under investigation, these primitive fossils appear to be small, one-centimeter long, sponge-like creatures. These fossils from South Australia date back 650 million years, actually placing the putative animal before the great ice age extinction event that marked the transition between the Cryogenian period and the Ediacaran period. Until this discovery, most scientists believed that there was no animal life prior to the Ediacaran period. Many scientists now believe that animals may in fact have evolved during the Cryogenian period.

The Cambrian Explosion of Animal Life

The Cambrian period, occurring between approximately 542–488 million years ago, marks the most rapid evolution of new animal phyla and animal diversity in Earth's history. It is believed that most of the animal phyla in existence today had their origins during this time, often referred to as the Cambrian explosion (Figure 27.4.3). Echinoderms, mollusks, worms, arthropods, and chordates arose during this period. One of the most dominant species during the Cambrian period was the trilobite, an arthropod that was among the first animals to exhibit a sense of vision (Figure 5.6.2.4).







Figure 5.6.2.3: An artist's rendition depicts some organisms from the Cambrian period.

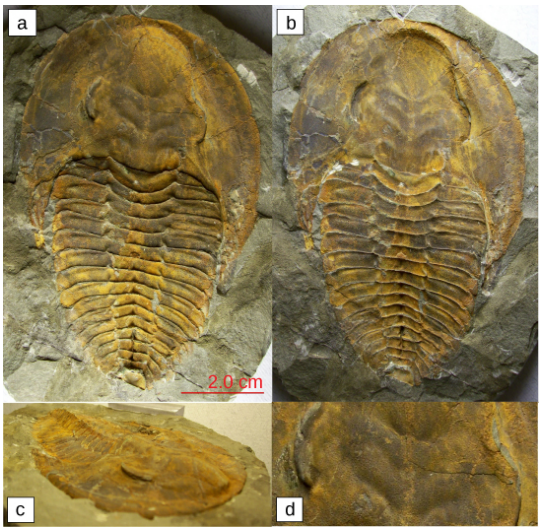


Figure 5.6.2.4: These fossils (a–d) belong to trilobites, extinct arthropods that appeared in the early Cambrian period, 525 million years ago, and disappeared from the fossil record during a mass extinction at the end of the Permian period, about 250 million years ago.

The cause of the Cambrian explosion is still debated. There are many theories that attempt to answer this question. Environmental changes may have created a more suitable environment for animal life. Examples of these changes include rising atmospheric oxygen levels and large increases in oceanic calcium concentrations that preceded the Cambrian period (Figure 5.6.2.5). Some scientists believe that an expansive, continental shelf with numerous shallow lagoons or pools provided the necessary living space for larger numbers of different types of animals to co-exist. There is also support for theories that argue that ecological relationships between species, such as changes in the food web, competition for food and space, and predator-prey relationships, were primed to promote a sudden massive coevolution of species. Yet other theories claim genetic and developmental reasons for the Cambrian explosion. The morphological flexibility and complexity of animal development afforded by the evolution of *Hox* control genes may have provided the necessary opportunities for increases in possible animal morphologies at the time of the Cambrian period. Theories that attempt to explain why the Cambrian explosion happened must be able to provide valid reasons for the massive animal diversification, as well as explain why it happened *when* it did. There is evidence that both supports and refutes each of the theories described above, and the answer may very well be a combination of these and other theories.

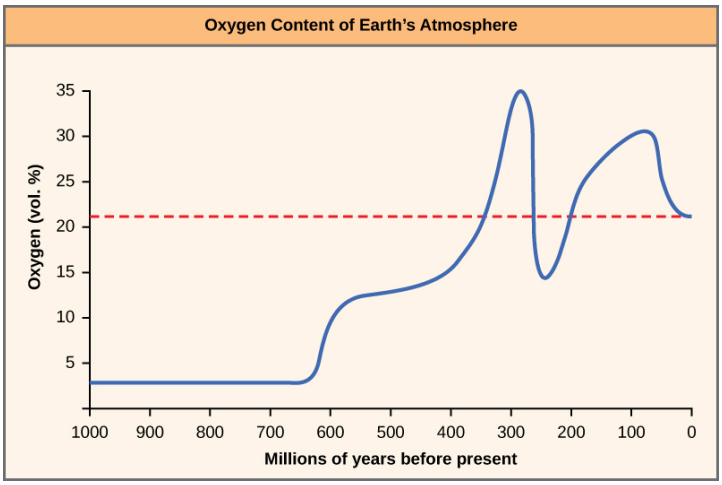


Figure 5.6.2.5: The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago.

However, unresolved questions about the animal diversification that took place during the Cambrian period remain. For example, we do not understand how the evolution of so many species occurred in such a short period of time. Was there really an "explosion" of life at this particular time? Some scientists question the validity of the this idea, because there is increasing evidence to suggest that more animal life existed prior to the Cambrian period and that other similar species' so-called explosions (or radiations) occurred later in history as well. Furthermore, the vast diversification of animal species that appears to have begun

during the Cambrian period continued well into the following Ordovician period. Despite some of these arguments, most scientists agree that the Cambrian period marked a time of impressively rapid animal evolution and diversification that is unmatched elsewhere during history.

Post-Cambrian Evolution and Mass Extinctions

The periods that followed the Cambrian during the Paleozoic Era are marked by further animal evolution and the emergence of many new orders, families, and species. As animal phyla continued to diversify, new species adapted to new ecological niches. During the Ordovician period, which followed the Cambrian period, plant life first appeared on land. This change allowed formerly aquatic animal species to invade land, feeding directly on plants or decaying vegetation. Continual changes in temperature and moisture throughout the remainder of the Paleozoic Era due to continental plate movements encouraged the development of new adaptations to terrestrial existence in animals, such as limbed appendages in amphibians and epidermal scales in reptiles.

Changes in the environment often create new niches (living spaces) that contribute to rapid speciation and increased diversity. On the other hand, cataclysmic events, such as volcanic eruptions and meteor strikes that obliterate life, can result in devastating losses of diversity. Such periods of mass extinction (Figure 5.6.2.6) have occurred repeatedly in the evolutionary record of life, erasing some genetic lines while creating room for others to evolve into the empty niches left behind. The end of the Permian period (and the Paleozoic Era) was marked by the largest mass extinction event in Earth's history, a loss of roughly 95 percent of the extant species at that time. Some of the dominant phyla in the world's oceans, such as the trilobites, disappeared completely. On land, the disappearance of some dominant species of Permian reptiles made it possible for a new line of reptiles to emerge, the dinosaurs. The warm and stable climatic conditions of the ensuing Mesozoic Era promoted an explosive diversification of dinosaurs into every conceivable niche in land, air, and water. Plants, too, radiated into new landscapes and empty niches, creating complex communities of producers and consumers, some of which became very large on the abundant food available.





Another mass extinction event occurred at the end of the Cretaceous period, bringing the Mesozoic Era to an end. Skies darkened and temperatures fell as a large meteor impact and tons of volcanic ash blocked incoming sunlight. Plants died, herbivores and carnivores starved, and the mostly cold-blooded dinosaurs ceded their dominance of the landscape to more warm-blooded mammals. In the following Cenozoic Era, mammals radiated into terrestrial and aquatic niches once occupied by dinosaurs, and birds, the warm-blooded offshoots of one line of the ruling reptiles, became aerial specialists. The appearance and dominance of flowering plants in the Cenozoic Era created new niches for insects, as well as for birds and mammals. Changes in animal species diversity during the late Cretaceous and early Cenozoic were also promoted by a dramatic shift in Earth's geography, as continental plates slid over the crust into their current positions, leaving some animal groups isolated on islands and continents, or separated by mountain ranges or inland seas from other competitors. Early in the Cenozoic, new ecosystems appeared, with the evolution of grasses and coral reefs. Late in the Cenozoic, further extinctions followed by speciation occurred during ice ages that covered high latitudes with ice and then retreated, leaving new open spaces for colonization.

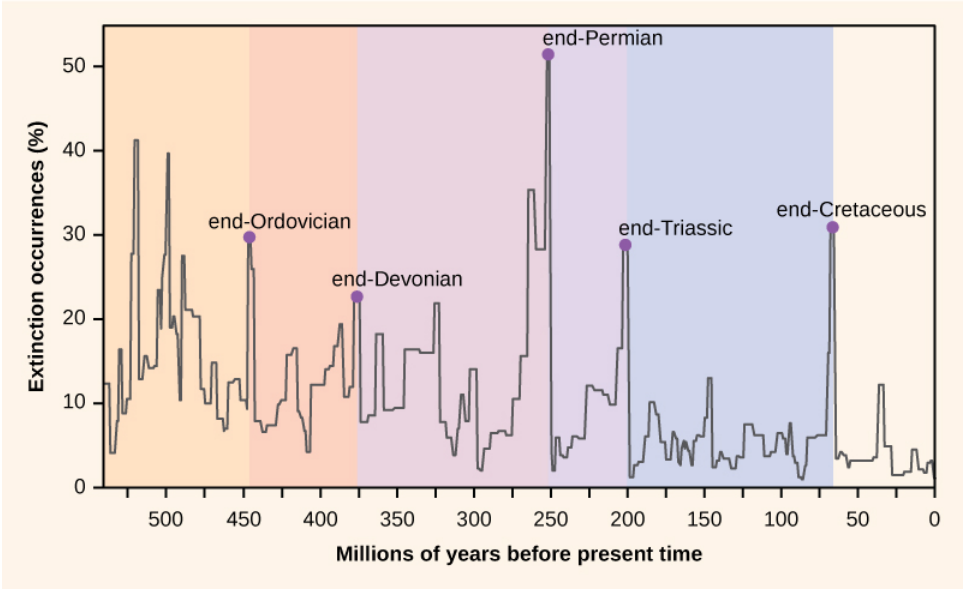


Figure 5.6.2.6: Mass extinctions have occurred repeatedly over geological time.

Career Connection: Paleontologist

Natural history museums contain the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontogists are scientists who study prehistoric life. They use fossils to observe and explain how life evolved on Earth and how species interacted with each other and with the environment. A paleontologist needs to be knowledgeable in biology, ecology, chemistry, geology, and many other scientific disciplines. A paleontologist's work may involve field studies: searching for and studying fossils. In addition to digging for and finding fossils, paleontologists also prepare fossils for further

study and analysis. Although dinosaurs are probably the first animals that come to mind when thinking about paleontology, paleontologists study everything from plant life, fungi, and fish to sea animals and birds.

An undergraduate degree in earth science or biology is a good place to start toward the career path of becoming a paleontologist. Most often, a graduate degree is necessary. Additionally, work experience in a museum or in a paleontology lab is useful.

Summary

The most rapid diversification and evolution of animal species in all of history occurred during the Cambrian period of the Paleozoic Era, a phenomenon known as the Cambrian explosion. Until recently, scientists believed that there were only very few tiny and simplistic animal species in existence before this period. However, recent fossil discoveries have revealed that additional, larger, and more complex animals existed during the Ediacaran period, and even possibly earlier, during the Cryogenian period. Still, the Cambrian period undoubtedly witnessed the emergence of the majority of animal phyla that we know today, although many questions remain unresolved about this historical phenomenon.

The remainder of the Paleozoic Era is marked by the growing appearance of new classes, families, and species, and the early colonization of land by certain marine animals. The evolutionary history of animals is also marked by numerous major extinction events, each of which wiped out a majority of extant species. Some species of most animal phyla survived these extinctions, allowing the phyla to persist and continue to evolve into species that we see today.

Glossary

Cambrian explosion
: time during the Cambrian period (542–488 million years ago) when most of the animal phyla in existence today evolved

Cryogenian period
: geologic period (850–630 million years ago) characterized by a very cold global climate

Ediacaran period
: geological period (630–542 million years ago) when the oldest definite multicellular organisms with tissues evolved

mass extinction
: event that wipes out the majority of species within a relatively short geological time period

---

This page titled 5.6.2: The Evolutionary History of the Animal Kingdom is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **27.4: The Evolutionary History of the Animal Kingdom** by OpenStax is licensed CC BY 4.0.

5.6.3: Features of the Animal Kingdom

Skills to Develop

- List the features that distinguish the kingdom Animalia from other kingdoms
- Explain the processes of animal reproduction and embryonic development
- Describe the roles that Hox genes play in development

Even though members of the animal kingdom are incredibly diverse, most animals share certain features that distinguish them from organisms in other kingdoms. All animals are eukaryotic, multicellular organisms, and almost all animals have a complex tissue structure with differentiated and specialized tissues. Most animals are motile, at least during certain life stages. All animals require a source of food and are therefore heterotrophic, ingesting other living or dead organisms; this feature distinguishes them from autotrophic organisms, such as most plants, which synthesize their own nutrients through photosynthesis. As heterotrophs, animals may be carnivores, herbivores, omnivores, or parasites (Figure 5.6.3.1). Most animals reproduce sexually, and the offspring pass through a series of developmental stages that establish a determined and fixed body plan. The body plan refers to the morphology of an animal, determined by developmental cues.



(a) (b)

Figure 5.6.3.1: All animals are heterotrophs that derive energy from food. The (a) black bear is an omnivore, eating both plants and animals. The (b) heartworm *Dirofilaria immitis* is a parasite that derives energy from its hosts. It spends its larval stage in mosquitoes and its adult stage infesting the heart of dogs and other mammals, as shown here. (credit a: modification of work by USDA Forest Service; credit b: modification of work by Clyde Robinson)

Complex Tissue Structure

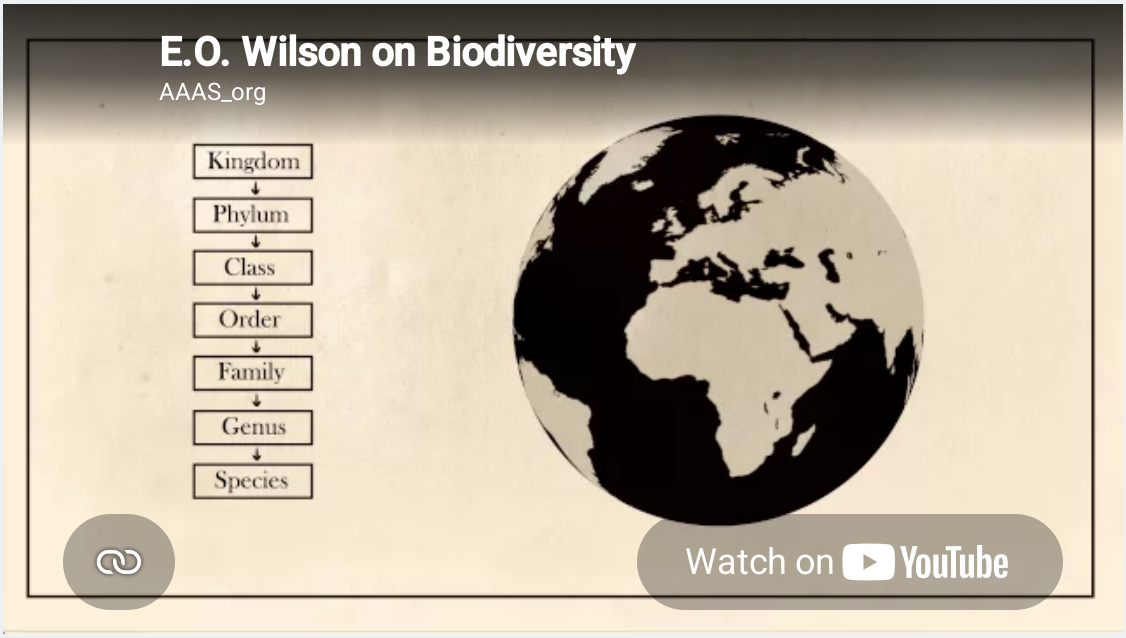
As multicellular organisms, animals differ from plants and fungi because their cells don't have cell walls, their cells may be embedded in an extracellular matrix (such as bone, skin, or connective tissue), and their cells have unique structures for intercellular communication (such as gap junctions). In addition, animals possess unique tissues, absent in fungi and plants, which allow coordination (nerve tissue) of motility (muscle tissue). Animals are also characterized by specialized connective tissues that provide structural support for cells and organs. This connective tissue constitutes the extracellular surroundings of cells and is made up of organic and inorganic materials. In vertebrates, bone tissue is a type of connective tissue that supports the entire body structure. The complex bodies and activities of vertebrates demand such supportive tissues. Epithelial tissues cover, line, protect, and secrete. Epithelial tissues include the epidermis of the integument, the lining of the digestive tract and trachea, and make up the ducts of the liver and glands of advanced animals.

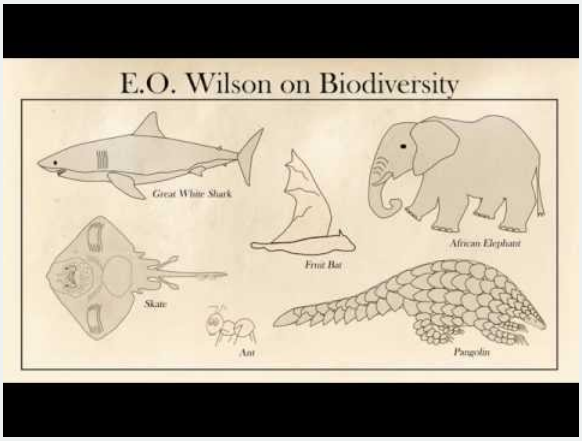
The animal kingdom is divided into Parazoa (sponges) and Eumetazoa (all other animals). As very simple animals, the organisms in group Parazoa ("beside animal") do not contain true specialized tissues; although they do possess specialized cells that perform different functions, those cells are not organized into tissues. These organisms are considered animals since they lack the ability to make their own food. Animals with true tissues are in the group Eumetazoa ("true animals"). When we think of animals, we usually think of Eumetazoans, since most animals fall into this category.

The different types of tissues in true animals are responsible for carrying out specific functions for the organism. This differentiation and specialization of tissues is part of what allows for such incredible animal diversity. For example, the evolution of nerve tissues and muscle tissues has resulted in animals' unique ability to rapidly sense and respond to changes in their

environment. This allows animals to survive in environments where they must compete with other species to meet their nutritional demands.

Link to Learning





Watch a short presentation by biologist E.O. Wilson on the importance of diversity.

Animal Reproduction and Development

Most animals are diploid organisms, meaning that their body (somatic) cells are diploid and haploid reproductive (gamete) cells are produced through meiosis. Some exceptions exist: For example, in bees, wasps, and ants, the male is haploid because it develops from unfertilized eggs. Most animals undergo sexual reproduction: This fact distinguishes animals from fungi, protists, and bacteria, where asexual reproduction is common or exclusive. However, a few groups, such as cnidarians, flatworm, and roundworms, undergo asexual reproduction, although nearly all of those animals also have a sexual phase to their life cycle.

Processes of Animal Reproduction and Embryonic Development

During sexual reproduction, the haploid gametes of the male and female individuals of a species combine in a process called fertilization. Typically, the small, motile male sperm fertilizes the much larger, sessile female egg. This process produces a diploid fertilized egg called a zygote.

Some animal species—including sea stars and sea anemones, as well as some insects, reptiles, and fish—are capable of asexual reproduction. The most common forms of asexual reproduction for stationary aquatic animals include budding and fragmentation, where part of a parent individual can separate and grow into a new individual. In contrast, a form of asexual reproduction found in certain insects and vertebrates is called parthenogenesis (or “virgin beginning”), where unfertilized eggs can develop into new male offspring. This type of parthenogenesis is called haplodiploidy. These types of asexual reproduction produce genetically identical offspring, which is disadvantageous from the perspective of evolutionary adaptability because of the potential buildup of deleterious mutations. However, for animals that are limited in their capacity to attract mates, asexual reproduction can ensure genetic propagation.

After fertilization, a series of developmental stages occur during which primary germ layers are established and reorganize to form an embryo. During this process, animal tissues begin to specialize and organize into organs and organ systems, determining their future morphology and physiology. Some animals, such as grasshoppers, undergo incomplete metamorphosis, in which the young resemble the adult. Other animals, such as some insects, undergo complete metamorphosis where individuals enter one or more larval stages that may in differ in structure and function from the adult (Figure 5.6.3.2). For the latter, the young and the adult may have different diets, limiting competition for food between them. Regardless of whether a species undergoes complete or incomplete metamorphosis, the series of developmental stages of the embryo remains largely the same for most members of the animal kingdom.

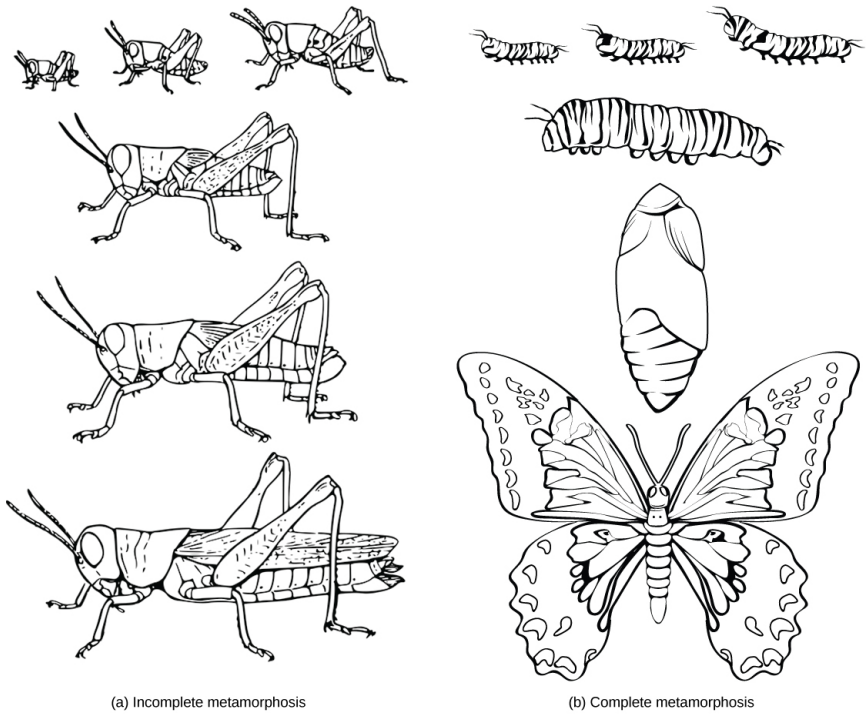


Figure 5.6.3.2: (a) The grasshopper undergoes incomplete metamorphosis. (b) The butterfly undergoes complete metamorphosis. (credit: S.E. Snodgrass, USDA)

The process of animal development begins with the cleavage, or series of mitotic cell divisions, of the zygote (Figure 5.6.3.3). Three cell divisions transform the single-celled zygote into an eight-celled structure. After further cell division and rearrangement of existing cells, a 6–32-celled hollow structure called a blastula is formed. Next, the blastula undergoes further cell division and cellular rearrangement during a process called gastrulation. This leads to the formation of the next developmental stage, the gastrula, in which the future digestive cavity is formed. Different cell layers (called germ layers) are formed during gastrulation. These germ layers are programmed to develop into certain tissue types, organs, and organ systems during a process called organogenesis.

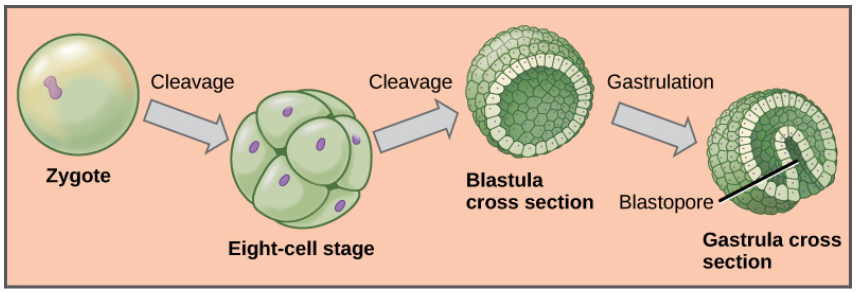


Figure 5.6.3.3: During embryonic development, the zygote undergoes a series of mitotic cell divisions, or cleavages, to form an eight-cell stage, then a hollow blastula. During a process called gastrulation, the blastula folds inward to form a cavity in the gastrula.

Link to Learning



Watch the following video to see how human embryonic development (after the blastula and gastrula stages of development) reflects evolution.

The Role of Homeobox (*Hox*) Genes in Animal Development

Since the early 19th century, scientists have observed that many animals, from the very simple to the complex, shared similar embryonic morphology and development. Surprisingly, a human embryo and a frog embryo, at a certain stage of embryonic development, look remarkably alike. For a long time, scientists did not understand why so many animal species looked similar during embryonic development but were very different as adults. They wondered what dictated the developmental direction that a fly, mouse, frog, or human embryo would take. Near the end of the 20th century, a particular class of genes was discovered that had this very job. These genes that determine animal structure are called “homeotic genes,” and they contain DNA sequences called homeoboxes. The animal genes containing homeobox sequences are specifically referred to as *Hox* genes. This family of genes is responsible for determining the general body plan, such as the number of body segments of an animal, the number and placement of appendages, and animal head-tail directionality. The first *Hox* genes to be sequenced were those from the fruit fly (*Drosophila melanogaster*). A single *Hox* mutation in the fruit fly can result in an extra pair of wings or even appendages growing from the “wrong” body part.

While there are a great many genes that play roles in the morphological development of an animal, what makes *Hox* genes so powerful is that they serve as master control genes that can turn on or off large numbers of other genes. *Hox* genes do this by coding transcription factors that control the expression of numerous other genes. *Hox* genes are homologous in the animal kingdom, that is, the genetic sequences of *Hox* genes and their positions on chromosomes are remarkably similar across most animals because of their presence in a common ancestor, from worms to flies, mice, and humans (Figure 5.6.3.4). One of the contributions to increased animal body complexity is that *Hox* genes have undergone at least two duplication events during animal evolution, with the additional genes allowing for more complex body types to evolve.

Art Connection

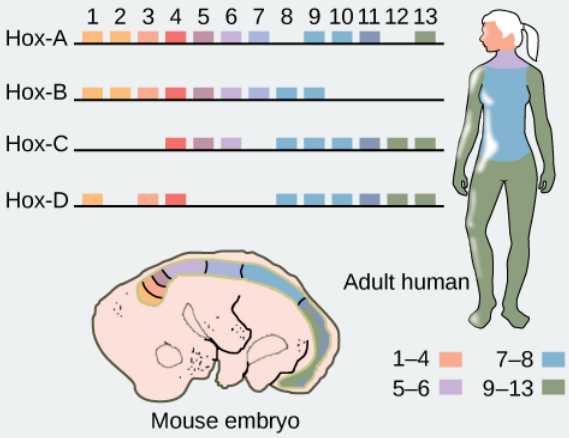


Figure 5.6.3.4: Hox genes are highly conserved genes encoding transcription factors that determine the course of embryonic development in animals. In vertebrates, the genes have been duplicated into four clusters: *Hox-A*, *Hox-B*, *Hox-C*, and *Hox-D*. Genes within these clusters are expressed in certain body segments at certain stages of development. Shown here is the homology between *Hox* genes in mice and humans. Note how Hox gene expression, as indicated with orange, pink, blue and green shading, occurs in the same body segments in both the mouse and the human.

If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

Summary

Animals constitute an incredibly diverse kingdom of organisms. Although animals range in complexity from simple sea sponges to human beings, most members of the animal kingdom share certain features. Animals are eukaryotic, multicellular, heterotrophic organisms that ingest their food and usually develop into motile creatures with a fixed body plan. A major characteristic unique to the animal kingdom is the presence of differentiated tissues, such as nerve, muscle, and connective tissues, which are specialized to perform specific functions. Most animals undergo sexual reproduction, leading to a series of developmental embryonic stages that are relatively similar across the animal kingdom. A class of transcriptional control genes called *Hox* genes directs the organization of the major animal body plans, and these genes are strongly homologous across the animal kingdom.

Art Connections

Figure 5.6.3.4: If a *Hox 13* gene in a mouse was replaced with a *Hox 1* gene, how might this alter animal development?

Answer

The animal might develop two heads and no tail.

Glossary

blastula
16–32 cell stage of development of an animal embryo

body plan
morphology or constant shape of an organism

cleavage
cell division of a fertilized egg (zygote) to form a multicellular embryo

gastrula
stage of animal development characterized by the formation of the digestive cavity

germ layer

collection of cells formed during embryogenesis that will give rise to future body tissues, more pronounced in vertebrate embryogenesis

Hox gene

(also, homeobox gene) master control gene that can turn on or off large numbers of other genes during embryogenesis

organogenesis

formation of organs in animal embryogenesis

This page titled 5.6.3: Features of the Animal Kingdom is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **27.1: Features of the Animal Kingdom** by OpenStax is licensed CC BY 4.0.

5.6.4: Features Used to Classify Animals

Skills to Develop

- Explain the differences in animal body plans that support basic animal classification
- Compare and contrast the embryonic development of protostomes and deuterostomes

Scientists have developed a classification scheme that categorizes all members of the animal kingdom, although there are exceptions to most "rules" governing animal classification (Figure 5.6.4.1). Animals are primarily classified according to morphological and developmental characteristics, such as a body plan. One of the most prominent features of the body plan of true animals is that they are morphologically symmetrical. This means that their distribution of body parts is balanced along an axis. Additional characteristics include the number of tissue layers formed during development, the presence or absence of an internal body cavity, and other features of embryological development, such as the origin of the mouth and anus.

Art Connection

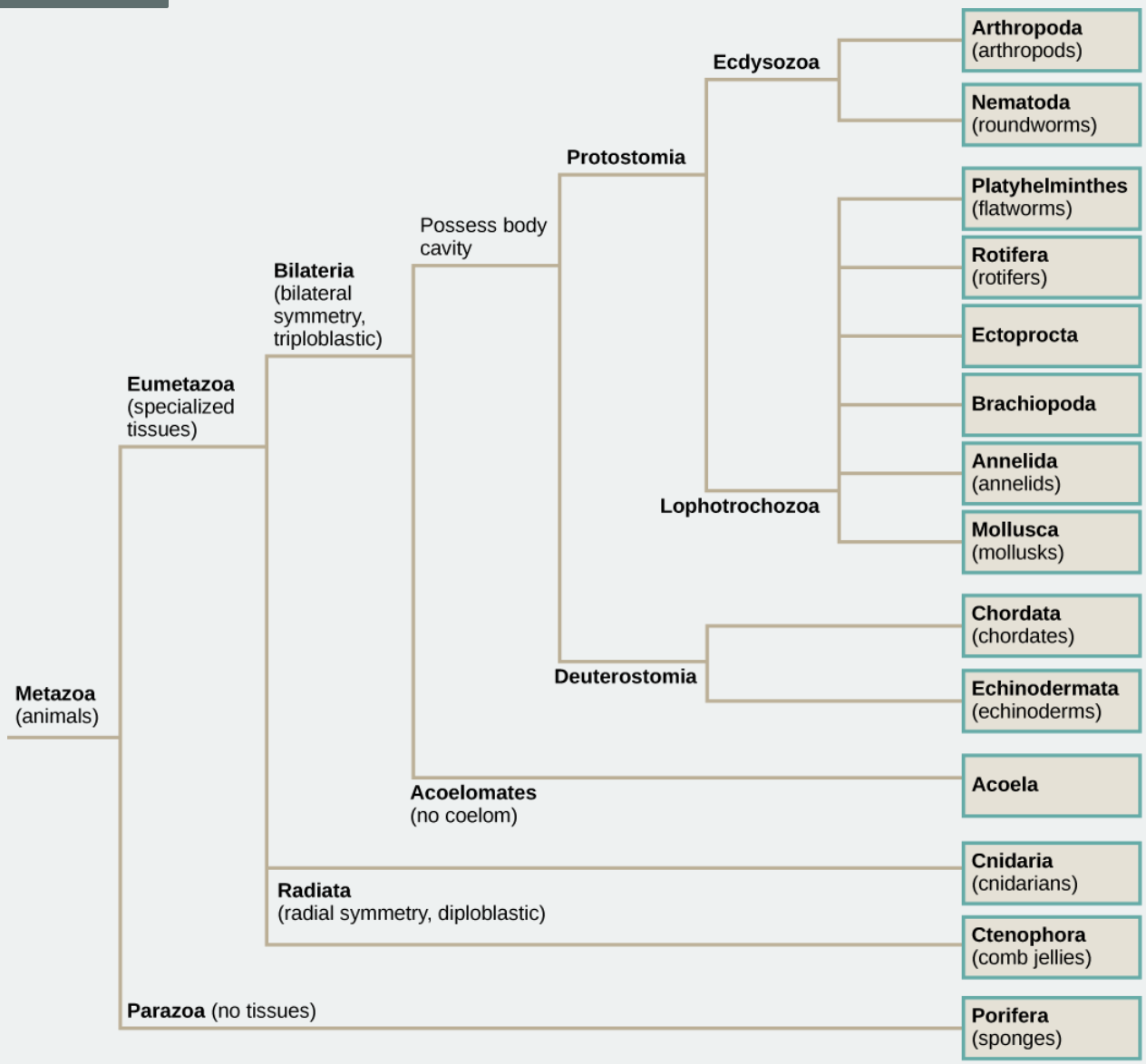


Figure 5.6.4.1: The phylogenetic tree of animals is based on morphological, fossil, and genetic evidence.

Which of the following statements is false?

B. Lophotrochozoa and Ecdysozoa are both Protostomia.
C. Acoela and Cnidaria both possess radial symmetry.
D. Arthropods are more closely related to nematodes than they are to annelids.

Animal Characterization Based on Body Symmetry





At a very basic level of classification, true animals can be largely divided into three groups based on the type of symmetry of their body plan: radially symmetrical, bilaterally symmetrical, and asymmetrical. Asymmetry is a unique feature of Parazoa (Figure 5.6.4.2). Only a few animal groups display radial symmetry. All types of symmetry are well suited to meet the unique demands of a particular animal's lifestyle.

Radial symmetry is the arrangement of body parts around a central axis, as is seen in a drinking glass or pie. It results in animals having top and bottom surfaces but no left and right sides, or front or back. The two halves of a radially symmetrical animal may be described as the side with a mouth or "oral side," and the side without a mouth (the "aboral side"). This form of symmetry marks the body plans of animals in the phyla Ctenophora and Cnidaria, including jellyfish and adult sea anemones (Figure 27.2.2). Radial symmetry equips these sea creatures (which may be sedentary or only capable of slow movement or floating) to experience the environment equally from all directions.

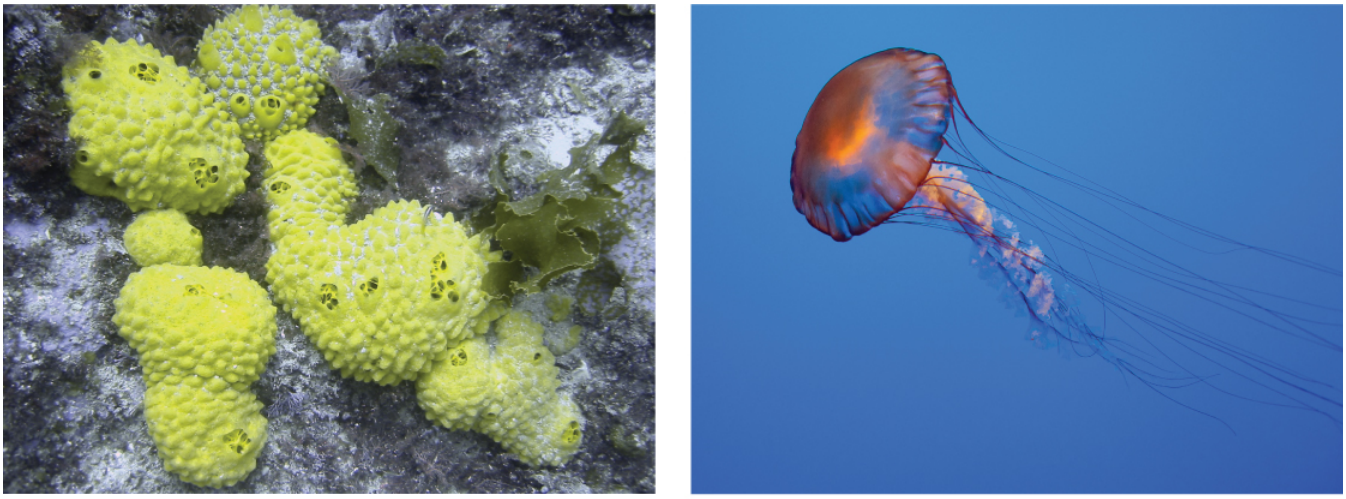


Figure 5.6.4.2: The (a) sponge is asymmetrical. The (b) jellyfish and (c) anemone are radially symmetrical, and the (d) butterfly is bilaterally symmetrical. (credit a: modification of work by Andrew Turner; credit b: modification of work by Robert Freiburger; credit c: modification of work by Samuel Chow; credit d: modification of work by Cory Zanker)

Bilateral symmetry involves the division of the animal through a sagittal plane, resulting in two mirror image, right and left halves, such as those of a butterfly (Figure 5.6.4.2), crab, or human body. Animals with bilateral symmetry have a “head” and “tail” (anterior vs. posterior), front and back (dorsal vs. ventral), and right and left sides (Figure 5.6.4.3). All true animals except those with radial symmetry are bilaterally symmetrical. The evolution of bilateral symmetry that allowed for the formation of anterior and posterior (head and tail) ends promoted a phenomenon called cephalization, which refers to the collection of an organized nervous system at the animal’s anterior end. In contrast to radial symmetry, which is best suited for stationary or limited-motion lifestyles, bilateral symmetry allows for streamlined and directional motion. In evolutionary terms, this simple form of symmetry promoted active mobility and increased sophistication of resource-seeking and predator-prey relationships.

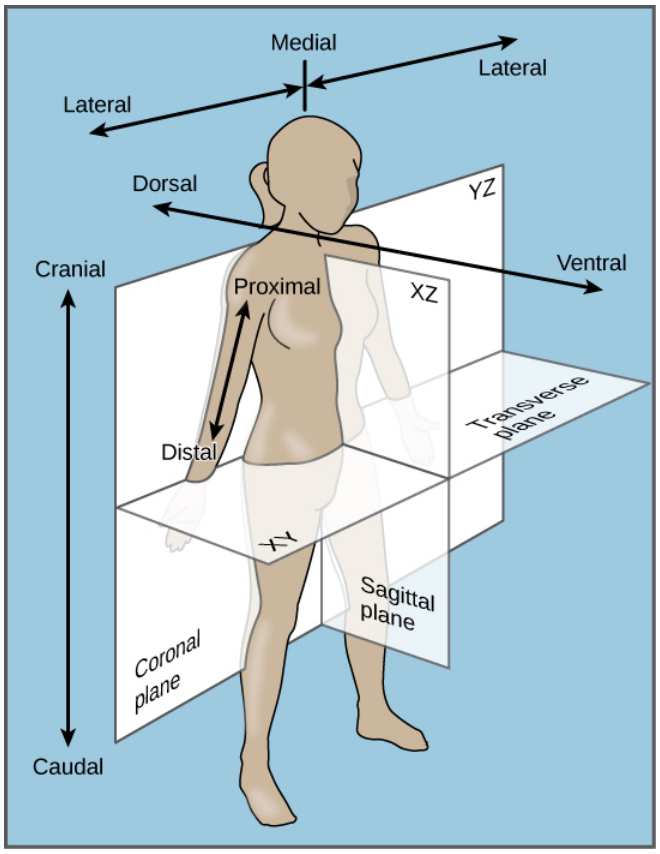
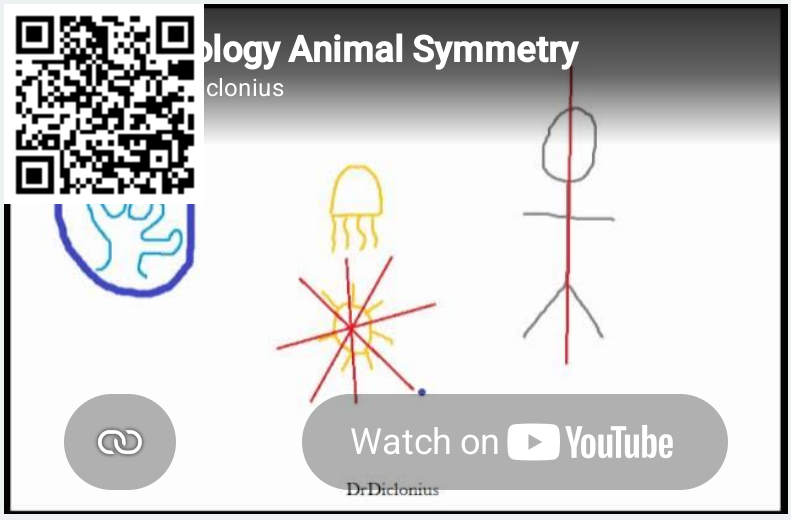


Figure 5.6.4.3: The bilaterally symmetrical human body can be divided into planes.

Animals in the phylum Echinodermata (such as sea stars, sand dollars, and sea urchins) display radial symmetry as adults, but their larval stages exhibit bilateral symmetry. This is termed secondary radial symmetry. They are believed to have evolved from bilaterally symmetrical animals; thus, they are classified as bilaterally symmetrical.

Link to Learning



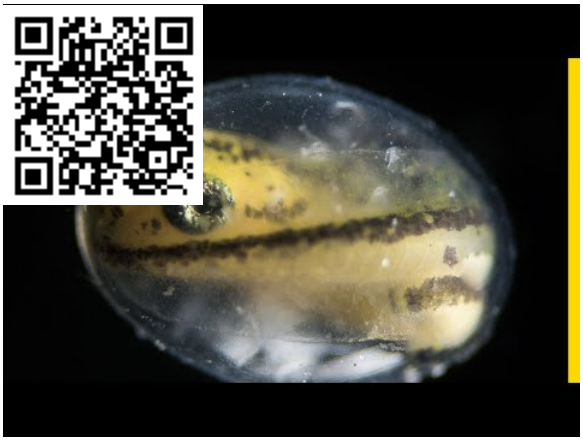
Watch this video to see a quick sketch of the different types of body symmetry.

Animal Characterization Based on Features of Embryological Development

Most animal species undergo a separation of tissues into germ layers during embryonic development. Recall that these germ layers are formed during gastrulation, and that they are predetermined to develop into the animal's specialized tissues and organs. Animals

develop either two or three embryonic germs layers (Figure 5.6.4.4). The animals that display radial symmetry develop two germ layers, an inner layer (endoderm) and an outer layer (ectoderm). These animals are called diploblasts. Diploblasts have a non-living layer between the endoderm and ectoderm. More complex animals (those with bilateral symmetry) develop three tissue layers: an inner layer (endoderm), an outer layer (ectoderm), and a middle layer (mesoderm). Animals with three tissue layers are called triploblasts.







Art Connection

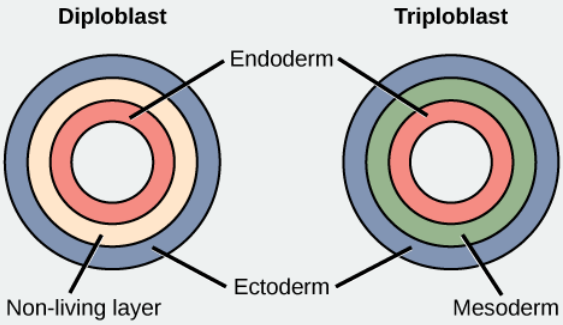


Figure 5.6.4.4: During embryogenesis, diploblasts develop two embryonic germ layers: an ectoderm and an endoderm. Triploblasts develop a third layer—the mesoderm—between the endoderm and ectoderm.

Which of the following statements about diploblasts and triploblasts is false?

A. Animals that display radial symmetry are diploblasts.
B. Animals that display bilateral symmetry are triploblasts.
C. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.
D. The mesoderm gives rise to the central nervous system.

Each of the three germ layers is programmed to give rise to particular body tissues and organs. The endoderm gives rise to the lining of the digestive tract (including the stomach, intestines, liver, and pancreas), as well as to the lining of the trachea, bronchi, and lungs of the respiratory tract, along with a few other structures. The ectoderm develops into the outer epithelial covering of the body surface, the central nervous system, and a few other structures. The mesoderm is the third germ layer; it forms between the endoderm and ectoderm in triploblasts. This germ layer gives rise to all muscle tissues (including the cardiac tissues and muscles of the intestines), connective tissues such as the skeleton and blood cells, and most other visceral organs such as the kidneys and the spleen.

Presence or Absence of a Coelom

Further subdivision of animals with three germ layers (triploblasts) results in the separation of animals that may develop an internal body cavity derived from mesoderm, called a coelom, and those that do not. This epithelial cell-lined coelomic cavity represents a space, usually filled with fluid, which lies between the visceral organs and the body wall. It houses many organs such as the digestive system, kidneys, reproductive organs, and heart, and contains the circulatory system. In some animals, such as mammals, the part of the coelom called the pleural cavity provides space for the lungs to expand during breathing. The evolution of the coelom is associated with many functional advantages. Primarily, the coelom provides cushioning and shock absorption for the major organ systems. Organs housed within the coelom can grow and move freely, which promotes optimal organ development and placement. The coelom also provides space for the diffusion of gases and nutrients, as well as body flexibility, promoting improved animal motility.

Triploblasts that do not develop a coelom are called acoelomates, and their mesoderm region is completely filled with tissue, although they do still have a gut cavity. Examples of acoelomates include animals in the phylum Platyhelminthes, also known as flatworms. Animals with a true coelom are called eucoelomates (or coelomates) (Figure 5.6.4.5). A true coelom arises entirely within the mesoderm germ layer and is lined by an epithelial membrane. This membrane also lines the organs within the coelom, connecting and holding them in position while allowing them some free motion. Annelids, mollusks, arthropods, echinoderms, and chordates are all eucoelomates. A third group of triploblasts has a slightly different coelom derived partly from mesoderm and partly from endoderm, which is found between the two layers. Although still functional, these are considered false coeloms, and those animals are called pseudocoelomates. The phylum Nematoda (roundworms) is an example of a pseudocoelomate. True coelomates can be further characterized based on certain features of their early embryological development.

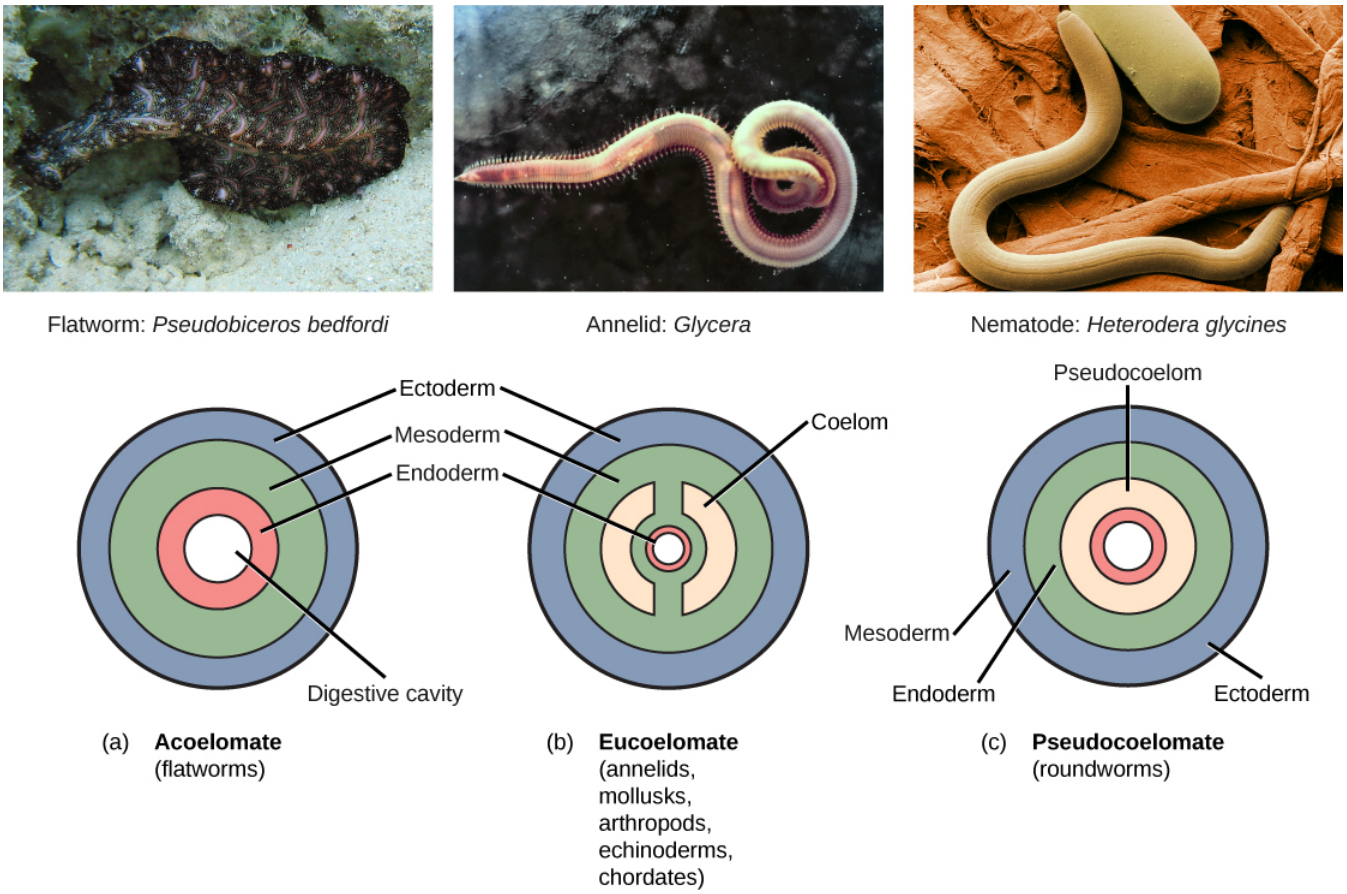


Figure 5.6.4.5: Triploblasts may be (a) acoelomates, (b) eucoelomates, or (c) pseudocoelomates. Acoelomates have no body cavity. Eucoelomates have a body cavity within the mesoderm, called a coelom, which is lined with mesoderm. Pseudocoelomates also have a body cavity, but it is sandwiched between the endoderm and mesoderm. (credit a: modification of work by Jan Derk; credit b: modification of work by NOAA; credit c: modification of work by USDA, ARS)

Embryonic Development of the Mouth

Bilaterally symmetrical, tribloblastic eucoelomates can be further divided into two groups based on differences in their early embryonic development. Protostomes include arthropods, mollusks, and annelids. Deuterostomes include more complex animals such as chordates but also some simple animals such as echinoderms. These two groups are separated based on which opening of the digestive cavity develops first: mouth or anus. The word protostome comes from the Greek word meaning “mouth first,” and deuterostome originates from the word meaning “mouth second” (in this case, the anus develops first). The mouth or anus develops from a structure called the blastopore (Figure 5.6.4.6). The blastopore is the indentation formed during the initial stages of gastrulation. In later stages, a second opening forms, and these two openings will eventually give rise to the mouth and anus (Figure 5.6.4.6). It has long been believed that the blastopore develops into the mouth of protostomes, with the second opening developing into the anus; the opposite is true for deuterostomes. Recent evidence has challenged this view of the development of the blastopore of protostomes, however, and the theory remains under debate.

Another distinction between protostomes and deuterostomes is the method of coelom formation, beginning from the gastrula stage. The coelom of most protostomes is formed through a process called schizocoely, meaning that during development, a solid mass of the mesoderm splits apart and forms the hollow opening of the coelom. Deuterostomes differ in that their coelom forms through a process called enterocoely. Here, the mesoderm develops as pouches that are pinched off from the endoderm tissue. These pouches eventually fuse to form the mesoderm, which then gives rise to the coelom.

The earliest distinction between protostomes and deuterostomes is the type of cleavage undergone by the zygote. Protostomes undergo spiral cleavage, meaning that the cells of one pole of the embryo are rotated, and thus misaligned, with respect to the cells of the opposite pole. This is due to the oblique angle of the cleavage. Deuterostomes undergo radial cleavage, where the cleavage axes are either parallel or perpendicular to the polar axis, resulting in the alignment of the cells between the two poles.

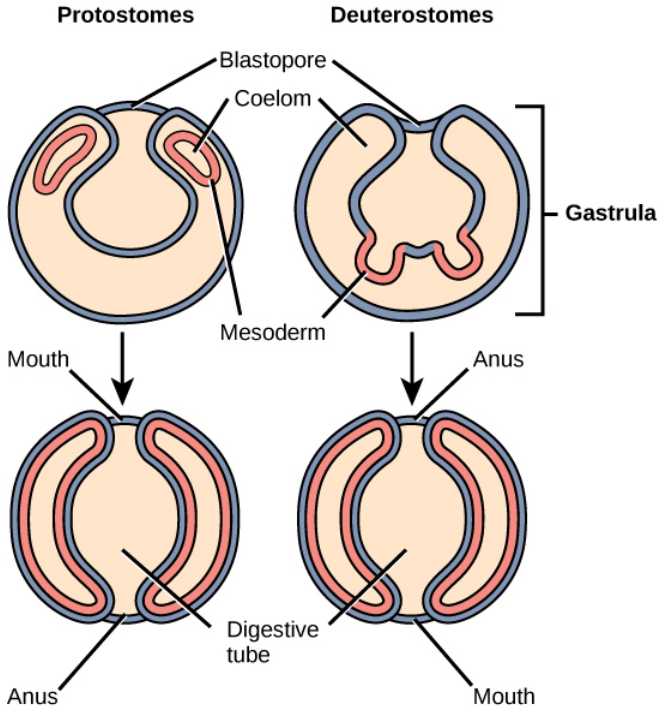


Figure 5.6.4.6: Eucoelomates can be divided into two groups based on their early embryonic development. In protostomes, part of the mesoderm separates to form the coelom in a process called schizocoely. In deuterostomes, the mesoderm pinches off to form the coelom in a process called enterocoely. It was long believed that the blastopore developed into the mouth in protostomes and into the anus in deuterostomes, but recent evidence challenges this belief.

There is a second distinction between the types of cleavage in protostomes and deuterostomes. In addition to spiral cleavage, protostomes also undergo determinate cleavage. This means that even at this early stage, the developmental fate of each embryonic cell is already determined. A cell does not have the ability to develop into any cell type. In contrast, deuterostomes undergo indeterminate cleavage, in which cells are not yet pre-determined at this early stage to develop into specific cell types. These cells

are referred to as undifferentiated cells. This characteristic of deuterostomes is reflected in the existence of familiar embryonic stem cells, which have the ability to develop into any cell type until their fate is programmed at a later developmental stage.

Evolution Connection: The Evolution of the Coelom

One of the first steps in the classification of animals is to examine the animal's body. Studying the body parts tells us not only the roles of the organs in question but also how the species may have evolved. One such structure that is used in classification of animals is the coelom. A coelom is a body cavity that forms during early embryonic development. The coelom allows for compartmentalization of the body parts, so that different organ systems can evolve and nutrient transport is possible. Additionally, because the coelom is a fluid-filled cavity, it protects the organs from shock and compression. Simple animals, such as worms and jellyfish, do not have a coelom. All vertebrates have a coelom that helped them evolve complex organ systems.

Animals that do not have a coelom are called acoelomates. Flatworms and tapeworms are examples of acoelomates. They rely on passive diffusion for nutrient transport across their body. Additionally, the internal organs of acoelomates are not protected from crushing.

Animals that have a true coelom are called eucoelomates; all vertebrates are eucoelomates. The coelom evolves from the mesoderm during embryogenesis. The abdominal cavity contains the stomach, liver, gall bladder, and other digestive organs. Another category of invertebrates animals based on body cavity is pseudocoelomates. These animals have a pseudo-cavity that is not completely lined by mesoderm. Examples include nematode parasites and small worms. These animals are thought to have evolved from coelomates and may have lost their ability to form a coelom through genetic mutations. Thus, this step in early embryogenesis—the formation of the coelom—has had a large evolutionary impact on the various species of the animal kingdom.

Summary

Organisms in the animal kingdom are classified based on their body morphology and development. True animals are divided into those with radial versus bilateral symmetry. Generally, the simpler and often non-motile animals display radial symmetry. Animals with radial symmetry are also generally characterized by the development of two embryological germ layers, the endoderm and ectoderm, whereas animals with bilateral symmetry are generally characterized by the development of a third embryological germ layer, the mesoderm. Animals with three germ layers, called triploblasts, are further characterized by the presence or absence of an internal body cavity called a coelom. The presence of a coelom affords many advantages, and animals with a coelom may be termed true coelomates or pseudocoelomates, depending on which tissue gives rise to the coelom. Coelomates are further divided into one of two groups called protostomes and deuterostomes, based on a number of developmental characteristics, including differences in zygote cleavage and method of coelom formation.

Art Connections

Figure 5.6.4.1: Which of the following statements is false?

A. Eumetazoans have specialized tissues and parazoans don't.
B. Lophotrochozoa and Ecdysozoa are both Bilataria.
C. Acoela and Cnidaria both possess radial symmetry.
D. Arthropods are more closely related to nematodes than they are to annelids.

Answer

C

Figure 5.6.4.4: Which of the following statements about diploblasts and triploblasts is false?

A. Animals that display radial symmetry are diploblasts.
B. Animals that display bilateral symmetry are triploblasts.
C. The endoderm gives rise to the lining of the digestive tract and the respiratory tract.

D. The mesoderm gives rise to the central nervous system.

Answer

D

Glossary

acoelomate
animal without a body cavity

bilateral symmetry
type of symmetry in which there is only one plane of symmetry, so the left and right halves of an animal are mirror images

blastopore
indentation formed during gastrulation, evident in the gastrula stage

coelom
lined body cavity

determinate cleavage
developmental tissue fate of each embryonic cell is already determined

deuterostome
blastopore develops into the anus, with the second opening developing into the mouth

diploblast
animal that develops from two germ layers

enterocoely
mesoderm of deuterostomes develops as pouches that are pinched off from endodermal tissue, cavity contained within the pouches becomes coelom

eucoelomate
animal with a body cavity completely lined with mesodermal tissue

indeterminate cleavage
early stage of development when germ cells or “stem cells” are not yet pre-determined to develop into specific cell types

protostome
blastopore develops into the mouth of protostomes, with the second opening developing into the anus

pseudocoelomate
animal with a body cavity located between the mesoderm and endoderm

radial cleavage
cleavage axes are parallel or perpendicular to the polar axis, resulting in the alignment of cells between the two poles

radial symmetry
type of symmetry with multiple planes of symmetry, with body parts (rays) arranged around a central disk

schizocoely
during development of protostomes, a solid mass of mesoderm splits apart and forms the hollow opening of the coelom

spiral cleavage

cells of one pole of the embryo are rotated or misaligned with respect to the cells of the opposite pole

triploblast

animal that develops from three germ layers

This page titled 5.6.4: Features Used to Classify Animals is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **27.2: Features Used to Classify Animals** by OpenStax is licensed CC BY 4.0.

5.6.5: Animal Phylogeny

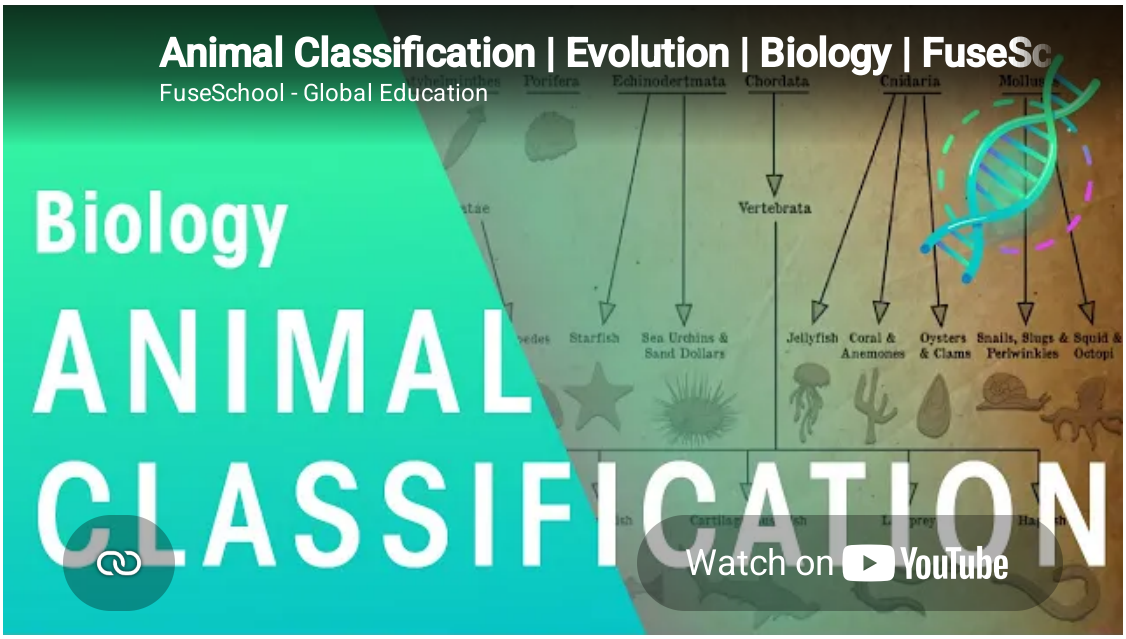
Skills to Develop

- Interpret the metazoan phylogenetic tree
- Describe the types of data that scientists use to construct and revise animal phylogeny
- List some of the relationships within the modern phylogenetic tree that have been discovered as a result of modern molecular data

Biologists strive to understand the evolutionary history and relationships of members of the animal kingdom, and all of life, for that matter. The study of phylogeny aims to determine the evolutionary relationships between phyla. Currently, most biologists divide the animal kingdom into 35 to 40 phyla. Scientists develop phylogenetic trees, which serve as hypotheses about which species have evolved from which ancestors

Recall that until recently, only morphological characteristics and the fossil record were used to determine phylogenetic relationships among animals. Scientific understanding of the distinctions and hierarchies between anatomical characteristics provided much of this knowledge. Used alone, however, this information can be misleading. Morphological characteristics may evolve multiple times, and independently, through evolutionary history. Analogous characteristics may appear similar between animals, but their underlying evolution may be very different. With the advancement of molecular technologies, modern phylogenetics is now informed by genetic and molecular analyses, in addition to traditional morphological and fossil data. With a growing understanding of genetics, the animal evolutionary tree has changed substantially and continues to change as new DNA and RNA analyses are performed on additional animal species.

Constructing an Animal Phylogenetic Tree





The current understanding of evolutionary relationships between animal, or Metazoa, phyla begins with the distinction between “true” animals with true differentiated tissues, called Eumetazoa, and animal phyla that do not have true differentiated tissues (such as the sponges), called Parazoa. Both Parazoa and Eumetazoa evolved from a common ancestral organism that resembles the modern-day protists called choanoflagellates. These protist cells strongly resemble the sponge choanocyte cells today (Figure 5.6.5.1).

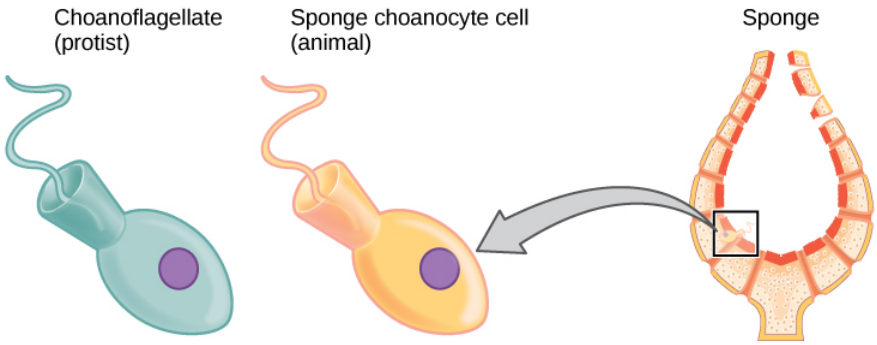


Figure 5.6.5.1: Cells of the protist choanoflagellate resemble sponge choanocyte cells. Beating of choanocyte flagella draws water through the sponge so that nutrients can be extracted and waste removed.

Eumetazoa are subdivided into radially symmetrical animals and bilaterally symmetrical animals, and are thus classified into clade Bilateria or Radiata, respectively. As mentioned earlier, the cnidarians and ctenophores are animal phyla with true radial symmetry. All other Eumetazoa are members of the Bilateria clade. The bilaterally symmetrical animals are further divided into deuterostomes (including chordates and echinoderms) and two distinct clades of protostomes (including ecdysozoans and lophotrochozoans) (Figure 5.6.5.2). Ecdysozoa includes nematodes and arthropods; they are so named for a commonly found characteristic among the group: exoskeletal molting (termed ecdysis). Lophotrochozoa is named for two structural features, each common to certain phyla within the clade. Some lophotrochozoan phyla are characterized by a larval stage called trochophore larvae, and other phyla are characterized by the presence of a feeding structure called a lophophore.



(a) (b)

Figure 5.6.5.2: Animals that molt their exoskeletons, such as these (a) Madagascar hissing cockroaches, are in the clade Ecdysozoa. (b) Phoronids are in the clade Lophotrochozoa. The tentacles are part of a feeding structure called a lophophore. (credit a: modification of work by Whitney Cranshaw, Colorado State University, Bugwood.org; credit b: modification of work by NOAA)

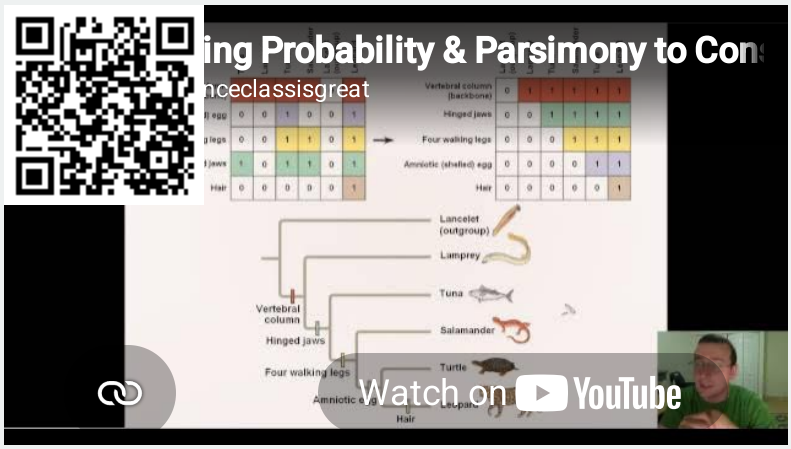
Link to Learning

Explore an interactive tree of life here. Zoom and click to learn more about the organisms and their evolutionary relationships.

Modern Advances in Phylogenetic Understanding Come from Molecular Analyses

The phylogenetic groupings are continually being debated and refined by evolutionary biologists. Each year, new evidence emerges that further alters the relationships described by a phylogenetic tree diagram.

Link to Learning



Watch the following video to learn how biologists use genetic data to determine relationships among organisms.

Nucleic acid and protein analyses have greatly informed the modern phylogenetic animal tree. These data come from a variety of molecular sources, such as mitochondrial DNA, nuclear DNA, ribosomal RNA (rRNA), and certain cellular proteins. Many

evolutionary relationships in the modern tree have only recently been determined due to molecular evidence. For example, a previously classified group of animals called lophophorates, which included brachiopods and bryozoans, were long-thought to be primitive deuterostomes. Extensive molecular analysis using rRNA data found these animals to be protostomes, more closely related to annelids and mollusks. This discovery allowed for the distinction of the protostome clade, the lophotrochozoans. Molecular data have also shed light on some differences within the lophotrochozoan group, and some scientists believe that the phyla Platyhelminthes and Rotifera within this group should actually belong to their own group of protostomes termed Platyzoa.

Molecular research similar to the discoveries that brought about the distinction of the lophotrochozoan clade has also revealed a dramatic rearrangement of the relationships between mollusks, annelids, arthropods, and nematodes, and a new ecdysozoan clade was formed. Due to morphological similarities in their segmented body types, annelids and arthropods were once thought to be closely related. However, molecular evidence has revealed that arthropods are actually more closely related to nematodes, now comprising the ecdysozoan clade, and annelids are more closely related to mollusks, brachiopods, and other phyla in the lophotrochozoan clade. These two clades now make up the protostomes.

Another change to former phylogenetic groupings because of molecular analyses includes the emergence of an entirely new phylum of worm called Acoelomorpha. These acoel flatworms were long thought to belong to the phylum Platyhelminthes because of their similar “flatworm” morphology. However, molecular analyses revealed this to be a false relationship and originally suggested that acoels represented living species of some of the earliest divergent bilaterians. More recent research into the acoelomorphs has called this hypothesis into question and suggested a closer relationship with deuterostomes. The placement of this new phylum remains disputed, but scientists agree that with sufficient molecular data, their true phylogeny will be determined.

Summary

Scientists are interested in the evolutionary history of animals and the evolutionary relationships among them. There are three main sources of data that scientists use to create phylogenetic evolutionary tree diagrams that illustrate such relationships: morphological information (which includes developmental morphologies), fossil record data, and, most recently, molecular data. The details of the modern phylogenetic tree change frequently as new data are gathered, and molecular data has recently contributed to many substantial modifications of the understanding of relationships between animal phyla.

Glossary

Ecdysozoa
clade of protostomes that exhibit exoskeletal molting (ecdysis)

Eumetazoa
group of animals with true differentiated tissues

Lophotrochozoa
clade of protostomes that exhibit a trochophore larvae stage or a lophophore feeding structure

Metazoa
group containing all animals

Parazoa
group of animals without true differentiated tissues

This page titled 5.6.5: Animal Phylogeny is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **27.3: Animal Phylogeny** by OpenStax is licensed CC BY 4.0.

5.6.E: Introduction to Animal Diversity (Exercises)

5.6.1: The Evolutionary History of the Animal Kingdom

Review Questions

Which of the following periods is the earliest during which animals may have appeared?

A. Ordovician period
B. Cambrian period
C. Ediacaran period
D. Cryogenian period

Answer

D

What type of data is primarily used to determine the existence and appearance of early animal species?

A. molecular data
B. fossil data
C. morphological data
D. embryological development data

Answer

B

The time between 542–488 million years ago marks which period?

A. Cambrian period
B. Silurian period
C. Ediacaran period
D. Devonian period

Answer

A

Until recent discoveries suggested otherwise, animals existing before the Cambrian period were believed to be:

A. small and ocean-dwelling
B. small and non-motile
C. small and soft-bodied
D. small and radially symmetrical or asymmetrical

Answer

C

Plant life first appeared on land during which of the following periods?

A. Cambrian period
B. Ordovician period
C. Silurian period
D. Devonian period

Answer

B

Approximately how many mass extinction events occurred throughout the evolutionary history of animals?

A. 3
B. 4
C. 5
D. more than 5

Answer

D

Free Response

Briefly describe at least two theories that attempt to explain the cause of the Cambrian explosion.

Answer

One theory states that environmental factors led to the Cambrian explosion. For example, the rise in atmospheric oxygen and oceanic calcium levels helped to provide the right environmental conditions to allow such a rapid evolution of new animal phyla. Another theory states that ecological factors such as competitive pressures and predator-prey relationships reached a threshold that supported the rapid animal evolution that took place during the Cambrian period.

How is it that most, if not all, of the extant animal phyla today evolved during the Cambrian period if so many massive extinction events have taken place since then?

Answer

It is true that multiple mass extinction events have taken place since the Cambrian period, when most currently existing animal phyla appeared, and the majority of animal species were commonly wiped out during these events. However, a small number of animal species representing each phylum were usually able to survive each extinction event, allowing the phylum to continue to evolve rather than become altogether extinct.

5.6.2: Features of the Animal Kingdom

Review Questions

Which of the following is not a feature common to *most* animals?

A. development into a fixed body plan
B. asexual reproduction
C. specialized tissues
D. heterotrophic nutrient sourcing

Answer

B

During embryonic development, unique cell layers develop and distinguish during a stage called _____.

A. the blastula stage
B. the germ layer stage
C. the gastrula stage
D. the organogenesis stage

Answer

C

Which of the following phenotypes would most likely be the result of a *Hox* gene mutation?

A. abnormal body length or height
B. two different eye colors
C. the contraction of a genetic illness
D. two fewer appendages than normal

Answer

D

Free Response

Why might the evolution of specialized tissues be important for animal function and complexity?

Answer

The development of specialized tissues affords more complex animal anatomy and physiology because differentiated tissue types can perform unique functions and work together in tandem to allow the animal to perform more functions. For example, specialized muscle tissue allows directed and efficient movement, and specialized nervous tissue allows for multiple sensory modalities as well as the ability to respond to various sensory information; these functions are not necessarily available to other non-animal organisms.

Describe and give examples of how humans display all of the features common to the animal kingdom.

Answer

Humans are multicellular organisms. They also contain differentiated tissues, such as epithelial, muscle, and nervous tissue, as well as specialized organs and organ systems. As heterotrophs, humans cannot produce their own nutrients and must obtain them by ingesting other organisms, such as plants, fungi, and animals. Humans undergo sexual reproduction, as well as the same embryonic developmental stages as other animals, which eventually lead to a fixed and motile body plan controlled in large part by *Hox* genes.

How have *Hox* genes contributed to the diversity of animal body plans?

Answer

Altered expression of homeotic genes can lead to major changes in the morphology of the individual. *Hox* genes can affect the spatial arrangements of organs and body parts. If a *Hox* gene was mutated or duplicated, it could affect where a leg might be on a fruit fly or how far apart a person's fingers are.

5.6.3: Features Used to Classify Animals

Review Questions

Which of the following organism is most likely to be a diploblast?

A. sea star
B. shrimp
C. jellyfish
D. insect

Answer

C

Which of the following is not possible?

A. radially symmetrical diploblast
B. diploblastic eucoelomate
C. protostomic coelomate
D. bilaterally symmetrical deuterostome

Answer

B

An animal whose development is marked by radial cleavage and enterocoely is _____.

A. a deuterostome
B. an annelid or mollusk
C. either an acoelomate or eucoelomate
D. none of the above

Answer

A

Free Response

Using the following terms, explain what classifications and groups humans fall into, from the most general to the most specific: symmetry, germ layers, coelom, cleavage, embryological development.

Answer

Humans have body plans that are bilaterally symmetrical and are characterized by the development of three germ layers, making them triploblasts. Humans have true coeloms and are thus eucoelomates. As deuterostomes, humans are characterized by radial and indeterminate cleavage.

Explain some of the advantages brought about through the evolution of bilateral symmetry and coelom formation.

Answer

The evolution of bilateral symmetry led to designated head and tail body regions, and promoted more efficient mobility for animals. This improved mobility allowed for more skillful seeking of resources and prey escaping from predators. The appearance of the coelom in coelomates provides many internal organs with shock absorption, making them less prone to physical damage from bodily assault. A coelom also gives the body greater flexibility, which promotes more efficient movement. The relatively loose placement of organs within the coelom allows them to develop and grow with some spatial freedom, which promoted the evolution of optimal organ arrangement. The coelom also provides space for a circulatory system, which is an advantageous way to distribute body fluids and gases.

5.6.4: Animal Phylogeny

Review Questions

Consulting the modern phylogenetic tree of animals, which of the following would not constitute a clade?

A. deuterostomes
B. lophotrochozoans
C. Parazoa

D. Bilateria

Answer

C

Which of the following is thought to be the most closely related to the common animal ancestor?

A. fungal cells
B. protist cells
C. plant cells
D. bacterial cells

Answer

B

As with the emergence of the Acoelomorpha phylum, it is common for ____ data to misplace animals in close relation to other species, whereas ____ data often reveals a different and more accurate evolutionary relationship.

A. molecular : morphological
B. molecular : fossil record
C. fossil record : morphological
D. morphological : molecular

Answer

D

Free Response

Describe at least two major changes to the animal phylogenetic tree that have come about due to molecular or genetic findings.

Answer

Two new clades that comprise the two major groups of protostomes are called the lophotrochozoans and the ecdysozoans. The formation of these two clades came about through molecular research from DNA and protein data. Also, the novel phylum of worm called Acoelomorpha was determined due to molecular data that distinguished them from other flatworms.

How is it that morphological data alone might lead scientists to group animals into erroneous evolutionary relationships?

Answer

In many cases, morphological similarities between animals may be only superficial similarities and may not indicate a true evolutionary relationship. One of the reasons for this is that certain morphological traits can evolve along very different evolutionary branches of animals for similar ecological reasons.

This page titled 5.6.E: Introduction to Animal Diversity (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **27.E: Introduction to Animal Diversity (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

5.7: Invertebrates

Invertebrate animals are those without a cranium and defined vertebral column or spine. In addition to lacking a spine, most invertebrates also lack an endoskeleton. A large number of invertebrates are aquatic animals, and scientific research suggests that many of the world's species are aquatic invertebrates that have not yet been documented.

5.7.1: Prelude to Invertebrates
5.7.2: Phylum Porifera
5.7.3: Phylum Cnidaria
5.7.4: Superphylum Lophotrochozoa
5.7.5: Superphylum Ecdysozoa
5.7.6: Superphylum Deuterostomia
5.7.E: Invertebrates (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 5.7: Invertebrates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

5.7.1: Prelude to Invertebrates



Figure 5.7.1.1: Nearly 97 percent of animal species are invertebrates, including this sea star (*Astropecten articulates*) common to the eastern and southern coasts of the United States (credit: modification of work by Mark Walz)

A brief look at any magazine pertaining to our natural world, such as *National Geographic*, would show a rich variety of vertebrates, especially mammals and birds. To most people, these are the animals that attract our attention. Concentrating on vertebrates, however, gives us a rather biased and limited view of biodiversity, because it ignores nearly 97 percent of the animal kingdom, namely the invertebrates. Invertebrate animals are those without a cranium and defined vertebral column or spine. In addition to lacking a spine, most invertebrates also lack an endoskeleton. A large number of invertebrates are aquatic animals, and scientific research suggests that many of the world's species are aquatic invertebrates that have not yet been documented.

This page titled 5.7.1: Prelude to Invertebrates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.0: Prelude to Invertebrates** by OpenStax is licensed CC BY 4.0.

5.7.2: Phylum Porifera

Skills to Develop

- Describe the organizational features of the simplest multicellular organisms
- Explain the various body forms and bodily functions of sponges

The invertebrates, or invertebrata, are animals that do not contain bony structures, such as the cranium and vertebrae. The simplest of all the invertebrates are the Parazoans, which include only the phylum Porifera: the sponges (Figure 5.7.2.1). Parazoans ("beside animals") do not display tissue-level organization, although they do have specialized cells that perform specific functions. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum. Since water is vital to sponges for excretion, feeding, and gas exchange, their body structure facilitates the movement of water through the sponge. Structures such as canals, chambers, and cavities enable water to move through the sponge to nearly all body cells.

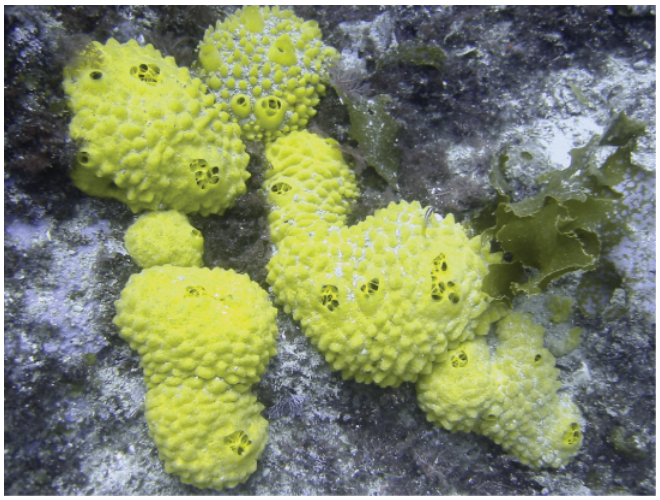
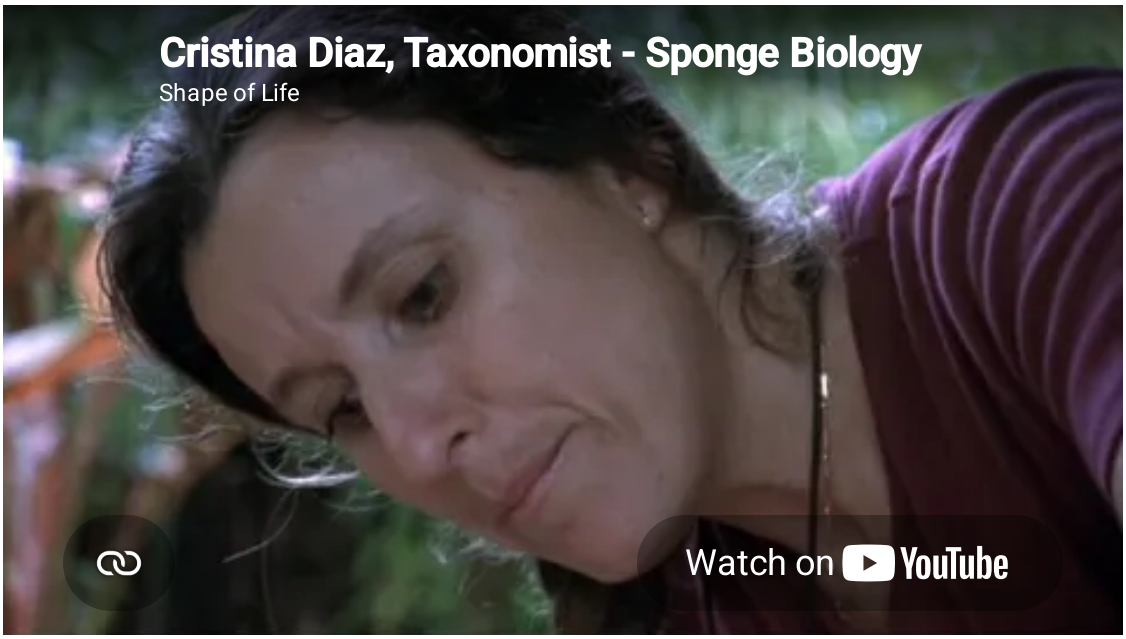


Figure 5.7.2.1: Sponges are members of the Phylum Porifera, which contains the simplest invertebrates. (credit: Andrew Turner)





Morphology of Sponges

The morphology of the simplest sponges takes the shape of a cylinder with a large central cavity, the spongocoel, occupying the inside of the cylinder. Water can enter into the spongocoel from numerous pores in the body wall. Water entering the spongocoel is extruded via a large common opening called the osculum. However, sponges exhibit a range of diversity in body forms, including variations in the size of the spongocoel, the number of osculi, and where the cells that filter food from the water are located.

While sponges (excluding the hexactinellids) do not exhibit tissue-layer organization, they do have different cell types that perform distinct functions. Pinacocytes, which are epithelial-like cells, form the outermost layer of sponges and enclose a jelly-like substance called mesohyl. Mesohyl is an extracellular matrix consisting of a collagen-like gel with suspended cells that perform various functions. The gel-like consistency of mesohyl acts like an endoskeleton and maintains the tubular morphology of sponges. In addition to the osculum, sponges have multiple pores called ostia on their bodies that allow water to enter the sponge. In some sponges, ostia are formed by porocytes, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. In other sponges, ostia are formed by folds in the body wall of the sponge.

Choanocytes (“collar cells”) are present at various locations, depending on the type of sponge, but they always line the inner portions of some space through which water flows (the spongocoel in simple sponges, canals within the body wall in more complex sponges, and chambers scattered throughout the body in the most complex sponges). Whereas pinacocytes line the outside of the sponge, choanocytes tend to line certain inner portions of the sponge body that surround the mesohyl. The structure of a choanocyte is critical to its function, which is to generate a water current through the sponge and to trap and ingest food particles by phagocytosis. Note the similarity in appearance between the sponge choanocyte and choanoflagellates (Protista). This similarity suggests that sponges and choanoflagellates are closely related and likely share a recent common ancestry. The cell body is embedded in mesohyl and contains all organelles required for normal cell function, but protruding into the “open space” inside of the sponge is a mesh-like collar composed of microvilli with a single flagellum in the center of the column. The cumulative effect of the flagella from all choanocytes aids the movement of water through the sponge: drawing water into the sponge through the numerous ostia, into the spaces lined by choanocytes, and eventually out through the osculum (or osculi). In the meantime, food particles, including waterborne bacteria and algae, are trapped by the sieve-like collar of the choanocytes, slide down into the body of the cell, are ingested by phagocytosis, and become encased in a food vacuole. Lastly, choanocytes will differentiate into sperm for sexual reproduction, where they will become dislodged from the mesohyl and leave the sponge with expelled water through the osculum.

The second crucial cells in sponges are called amoebocytes (or archaeocytes), named for the fact that they move throughout the mesohyl in an amoeba-like fashion. Amoebocytes have a variety of functions: delivering nutrients from choanocytes to other cells within the sponge, giving rise to eggs for sexual reproduction (which remain in the mesohyl), delivering phagocytized sperm from choanocytes to eggs, and differentiating into more-specific cell types. Some of these more-specific cell types include collencytes and lophocytes, which produce the collagen-like protein to maintain the mesohyl, sclerocytes, which produce spicules in some sponges, and spongocytes, which produce the protein spongin in the majority of sponges. These cells produce collagen to maintain the consistency of the mesohyl. The different cell types in sponges are shown in Figure 5.7.2.2.

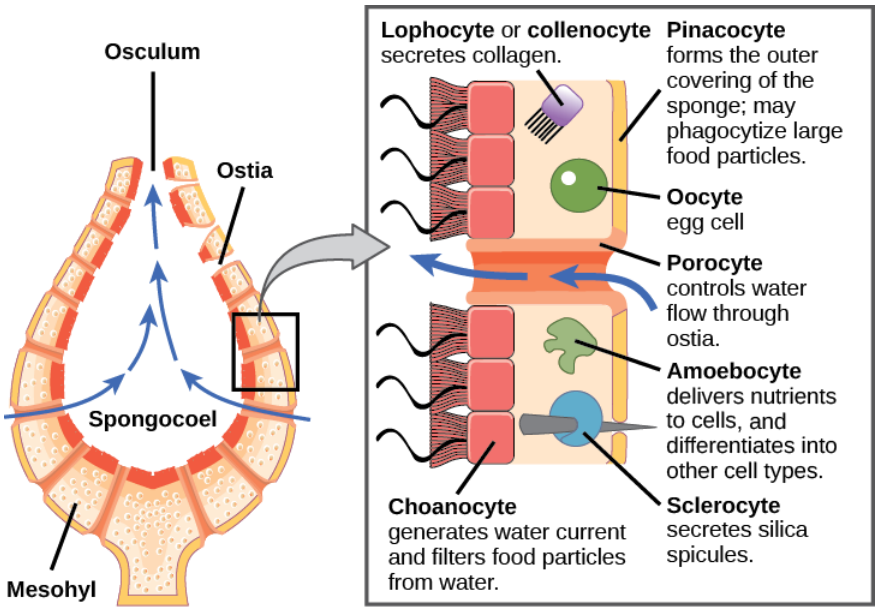


Figure 5.7.2.2: The sponge's (a) basic body plan and (b) some of the specialized cell types found in sponges are shown.

? Exercise 5.7.2.1

Which of the following statements is false?

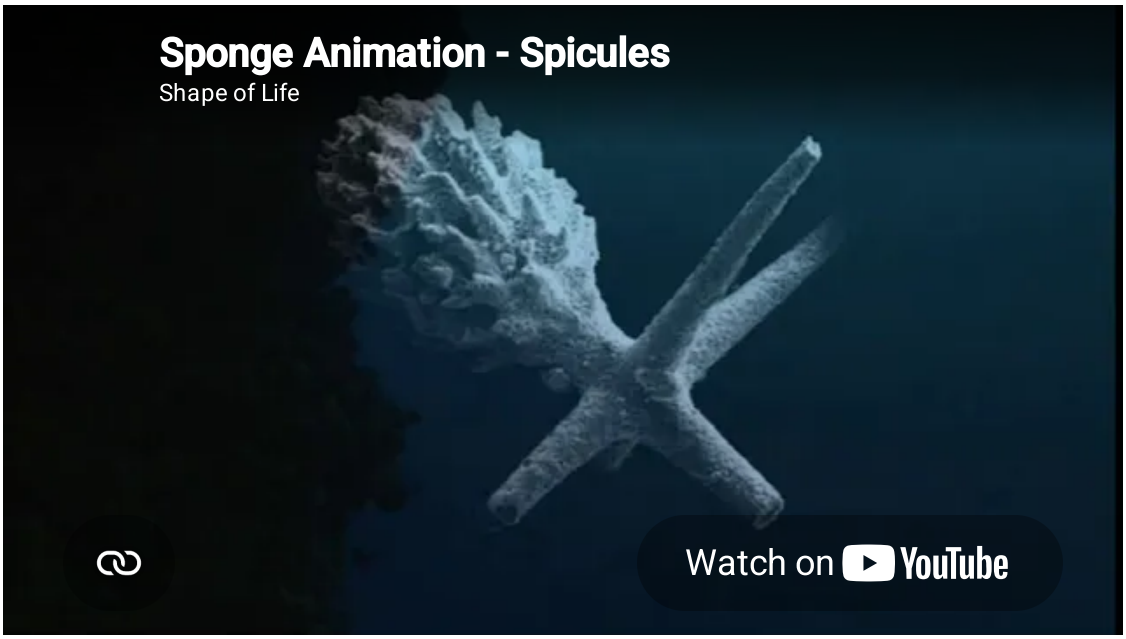
A. Choanocytes have flagella that propel water through the body.
B. Pinacocytes can transform into any cell type.
C. Lophocytes secrete collagen.
D. Porocytes control the flow of water through pores in the sponge body.

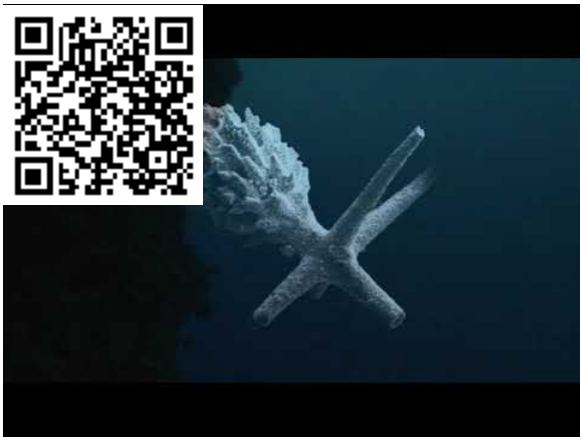
Answer

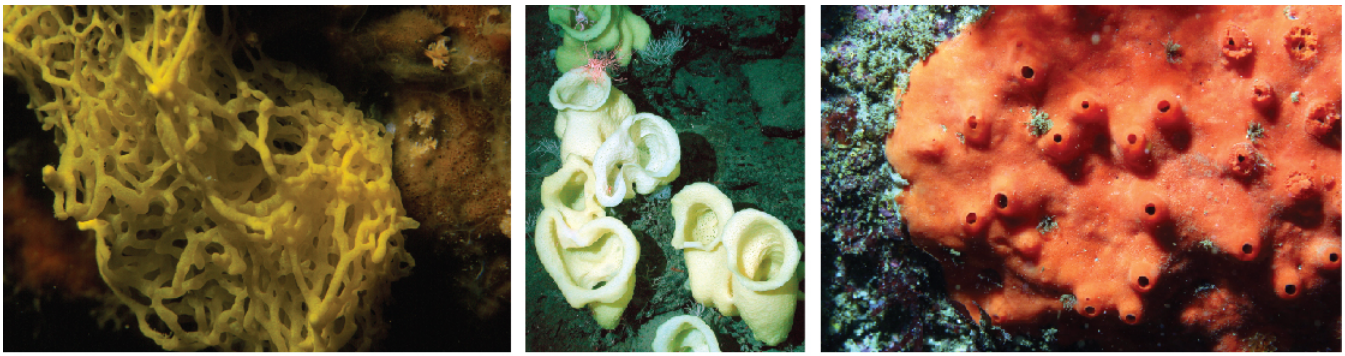
B

In some sponges, sclerocytes secrete small spicules into the mesohyl, which are composed of either calcium carbonate or silica, depending on the type of sponge. These spicules serve to provide additional stiffness to the body of the sponge. Additionally, spicules, when present externally, may ward off predators. Another type of protein, spongin, may also be present in the mesohyl of some sponges.

The presence and composition of spicules/spongin are the differentiating characteristics of the three classes of sponges (Figure 5.7.2.3): Class Calcarea contains calcium carbonate spicules and no spongin, class Hexactinellida contains six-rayed siliceous spicules and no spongin, and class Demospongia contains spongin and may or may not have spicules; if present, those spicules are siliceous. Spicules are most conspicuously present in class Hexactinellida, the order consisting of glass sponges. Some of the spicules may attain giant proportions (in relation to the typical size range of glass sponges of 3 to 10 mm) as seen in *Monorhaphis chuni*, which grows up to 3 m long.







(a) (b) (c)

Figure 5.7.2.3: (a) *Clathrina clathrus* belongs to class Calcarea, (b) *Staurocalyptus* spp. (common name: yellow Picasso sponge) belongs to class Hexactinellida, and (c) *Acarnus erithacus* belongs to class Demospongia. (credit a: modification of work by Parent Géry; credit b: modification of work by Monterey Bay Aquarium Research Institute, NOAA; credit c: modification of work by Sanctuary Integrated Monitoring Network, Monterey Bay National Marine Sanctuary, NOAA)

Physiological Processes in Sponges

Sponges, despite being simple organisms, regulate their different physiological processes through a variety of mechanisms. These processes regulate their metabolism, reproduction, and locomotion.

Digestion

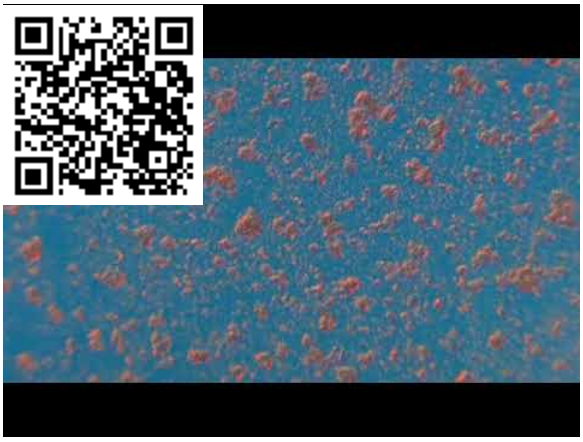
Sponges lack complex digestive, respiratory, circulatory, reproductive, and nervous systems. Their food is trapped when water passes through the ostia and out through the osculum. Bacteria smaller than 0.5 microns in size are trapped by choanocytes, which are the principal cells engaged in nutrition, and are ingested by phagocytosis. Particles that are larger than the ostia may be phagocytized by pinacocytes. In some sponges, amoebocytes transport food from cells that have ingested food particles to those that do not. For this type of digestion, in which food particles are digested within individual cells, the sponge draws water through diffusion. The limit of this type of digestion is that food particles must be smaller than individual cells.

All other major body functions in the sponge (gas exchange, circulation, excretion) are performed by diffusion between the cells that line the openings within the sponge and the water that is passing through those openings. All cell types within the sponge obtain oxygen from water through diffusion. Likewise, carbon dioxide is released into seawater by diffusion. In addition, nitrogenous waste produced as a byproduct of protein metabolism is excreted via diffusion by individual cells into the water as it passes through the sponge.

Reproduction

Sponges reproduce by sexual as well as asexual methods. The typical means of asexual reproduction is either fragmentation (where a piece of the sponge breaks off, settles on a new substrate, and develops into a new individual) or budding (a genetically identical outgrowth grows from the parent and eventually detaches or remains attached to form a colony). An atypical type of asexual reproduction is found only in freshwater sponges and occurs through the formation of gemmules. Gemmules are environmentally resistant structures produced by adult sponges wherein the typical sponge morphology is inverted. In gemmules, an inner layer of amoebocytes is surrounded by a layer of collagen (spongin) that may be reinforced by spicules. The collagen that is normally found in the mesohyl becomes the outer protective layer. In freshwater sponges, gemmules may survive hostile environmental conditions like changes in temperature and serve to recolonize the habitat once environmental conditions stabilize. Gemmules are capable of attaching to a substratum and generating a new sponge. Since gemmules can withstand harsh environments, are resistant to desiccation, and remain dormant for long periods, they are an excellent means of colonization for a sessile organism.





Sexual reproduction in sponges occurs when gametes are generated. Sponges are monoecious (hermaphroditic), which means that one individual can produce both gametes (eggs and sperm) simultaneously. In some sponges, production of gametes may occur throughout the year, whereas other sponges may show sexual cycles depending upon water temperature. Sponges may also become sequentially hermaphroditic, producing oocytes first and spermatozoa later. Oocytes arise by the differentiation of amoebocytes and are retained within the spongocoel, whereas spermatozoa result from the differentiation of choanocytes and are ejected via the osculum. Ejection of spermatozoa may be a timed and coordinated event, as seen in certain species. Spermatozoa carried along by water currents can fertilize the oocytes borne in the mesohyl of other sponges. Early larval development occurs within the sponge, and free-swimming larvae are then released via the osculum.

Locomotion

Sponges are generally sessile as adults and spend their lives attached to a fixed substratum. They do not show movement over large distances like other free-swimming marine invertebrates. However, sponge cells are capable of creeping along substrata via organizational plasticity. Under experimental conditions, researchers have shown that sponge cells spread on a physical support demonstrate a leading edge for directed movement. It has been speculated that this localized creeping movement may help sponges adjust to microenvironments near the point of attachment. It must be noted, however, that this pattern of movement has been documented in laboratories, but it remains to be observed in natural sponge habitats.

Summary

Animals included in phylum Porifera are Parazoans because they do not show the formation of true tissues (except in class Hexactinellida). These organisms show very simple organization, with a rudimentary endoskeleton. Sponges have multiple cell types that are geared toward executing various metabolic functions. Although these animals are very simple, they perform several complex physiological functions.

Glossary

amoebocyte

sponge cell with multiple functions, including nutrient delivery, egg formation, sperm delivery, and cell differentiation

choanocyte

(also, collar cell) sponge cell that functions to generate a water current and to trap and ingest food particles via phagocytosis

gemmule

structure produced by asexual reproduction in freshwater sponges where the morphology is inverted

invertebrata

(also, invertebrates) category of animals that do not possess a cranium or vertebral column

mesohyl

collagen-like gel containing suspended cells that perform various functions in the sponge

osculum

large opening in the sponge’s body through which water leaves

ostium

pore present on the sponge’s body through which water enters

pinacocyte

epithelial-like cell that forms the outermost layer of sponges and encloses a jelly-like substance called mesohyl

Porifera

phylum of animals with no true tissues, but a porous body with rudimentary endoskeleton

sclerocyte

cell that secretes silica spicules into the mesohyl

spicule

structure made of silica or calcium carbonate that provides structural support for sponges

spongocoel

central cavity within the body of some sponges

This page titled 5.7.2: Phylum Porifera is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.1: Phylum Porifera** by OpenStax is licensed CC BY 4.0.

5.7.3: Phylum Cnidaria

Skills to Develop

- Compare structural and organization characteristics of Porifera and Cnidaria
- Describe the progressive development of tissues and their relevance to animal complexity

Phylum Cnidaria includes animals that show radial or biradial symmetry and are diploblastic, that is, they develop from two embryonic layers. Nearly all (about 99 percent) cnidarians are marine species.

Cnidarians contain specialized cells known as cnidocytes ("stinging cells") containing organelles called nematocysts (stingers). These cells are present around the mouth and tentacles, and serve to immobilize prey with toxins contained within the cells. Nematocysts contain coiled threads that may bear barbs. The outer wall of the cell has hairlike projections called cnidocils, which are sensitive to touch. When touched, the cells are known to fire coiled threads that can either penetrate the flesh of the prey or predators of cnidarians (see Figure 5.7.3.1) or ensnare it. These coiled threads release toxins into the target and can often immobilize prey or scare away predators.





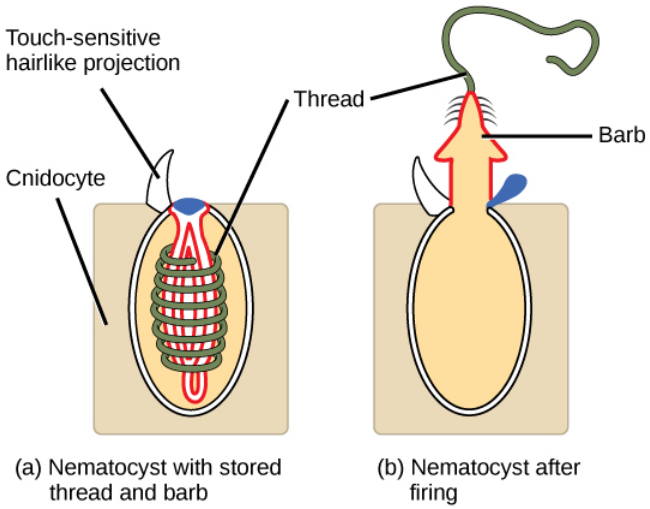


Figure 5.7.3.1: Animals from the phylum Cnidaria have stinging cells called cnidocytes. Cnidocytes contain large organelles called (a) nematocysts that store a coiled thread and barb. When hairlike projections on the cell surface are touched, (b) the thread, barb, and a toxin are fired from the organelle.

Animals in this phylum display two distinct morphological body plans: polyp or "stalk" and medusa or "bell" (Figure 5.7.3.2). An example of the polyp form is *Hydra* spp.; perhaps the most well-known medusoid animals are the jellies (jellyfish). Polyp forms are sessile as adults, with a single opening to the digestive system (the mouth) facing up with tentacles surrounding it. Medusa forms are motile, with the mouth and tentacles hanging down from an umbrella-shaped bell.





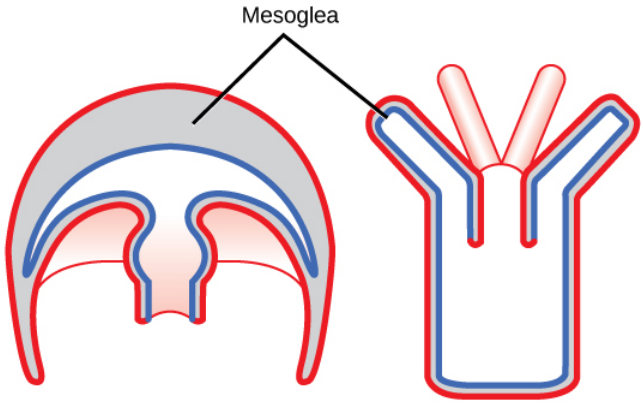


Figure 5.7.3.2: Cnidarians have two distinct body plans, the medusa (a) and the polyp (b). All cnidarians have two membrane layers, with a jelly-like mesoglea between them.

Some cnidarians are polymorphic, that is, they have two body plans during their life cycle. An example is the colonial hydroid called an *Obelia*. The sessile polyp form has, in fact, two types of polyps, shown in Figure 5.7.3.3. The first is the gastrozooid, which is adapted for capturing prey and feeding; the other type of polyp is the gonozooid, adapted for the asexual budding of medusa. When the reproductive buds mature, they break off and become free-swimming medusa, which are either male or female (dioecious). The male medusa makes sperm, whereas the female medusa makes eggs. After fertilization, the zygote develops into a blastula, which develops into a planula larva. The larva is free swimming for a while, but eventually attaches and a new colonial reproductive polyp is formed.

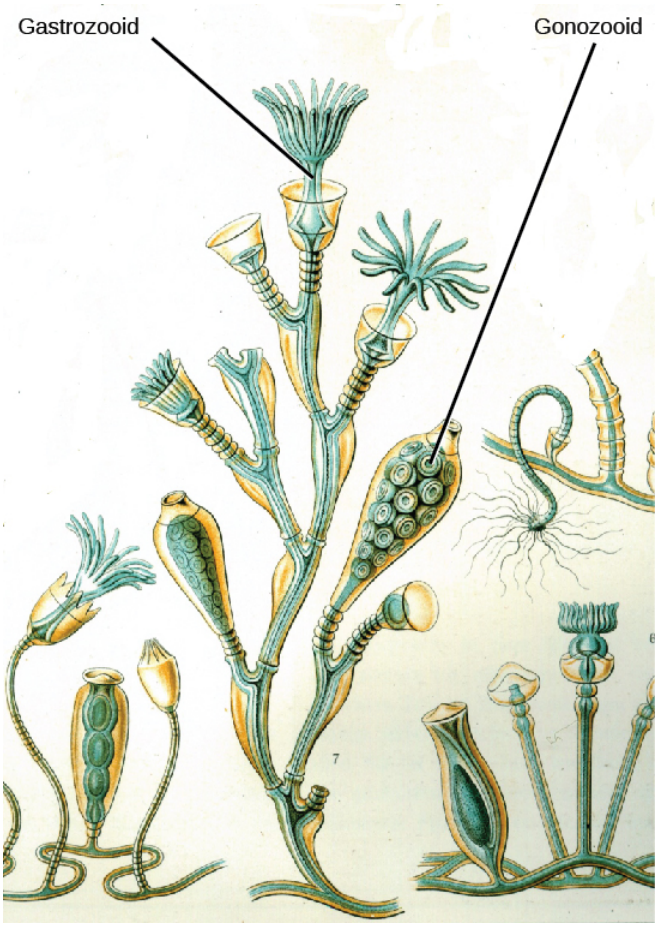
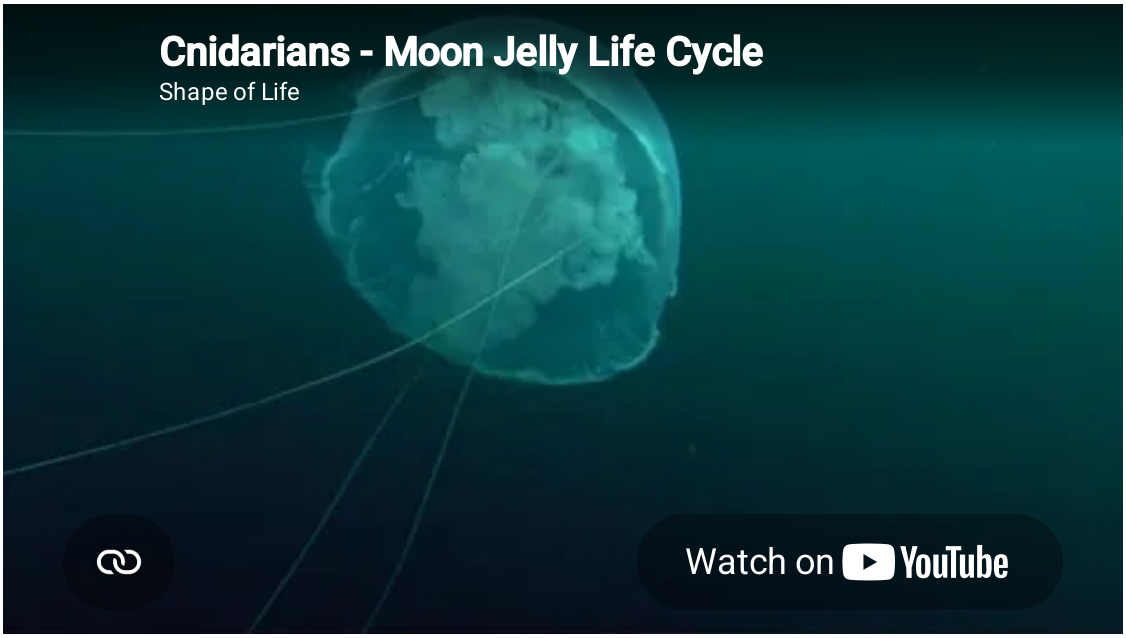
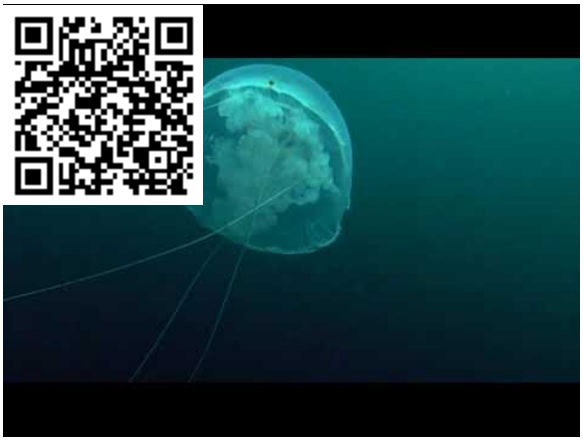


Figure 5.7.3.3: The sessile form of *Obelia geniculate* has two types of polyps: gastrozooids, which are adapted for capturing prey, and gonozooids, which bud to produce medusae asexually.





All cnidarians show the presence of two membrane layers in the body that are derived from the endoderm and ectoderm of the embryo. The outer layer (from ectoderm) is called the epidermis and lines the outside of the animal, whereas the inner layer (from endoderm) is called the gastrodermis and lines the digestive cavity. Between these two membrane layers is a non-living, jelly-like mesoglea connective layer. In terms of cellular complexity, cnidarians show the presence of differentiated cell types in each tissue layer, such as nerve cells, contractile epithelial cells, enzyme-secreting cells, and nutrient-absorbing cells, as well as the presence of intercellular connections. However, the development of organs or organ systems is not advanced in this phylum.

The nervous system is primitive, with nerve cells scattered across the body. This nerve net may show the presence of groups of cells in the form of nerve plexi (singular plexus) or nerve cords. The nerve cells show mixed characteristics of motor as well as sensory neurons. The predominant signaling molecules in these primitive nervous systems are chemical peptides, which perform both excitatory and inhibitory functions. Despite the simplicity of the nervous system, it coordinates the movement of tentacles, the drawing of captured prey to the mouth, the digestion of food, and the expulsion of waste.

The cnidarians perform extracellular digestion in which the food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients. The gastrovascular cavity has only one opening that serves as both a mouth and an anus, which is termed an incomplete digestive system. Cnidarian cells exchange oxygen and carbon dioxide by diffusion between cells in the epidermis with water in the environment, and between cells in the gastrodermis with water in the gastrovascular cavity. The lack of a circulatory system to move dissolved gases limits the thickness of the body wall and necessitates a non-living mesoglea between the layers. There is no excretory system or organs, and nitrogenous wastes simply diffuse from the cells into the water outside the animal or in the gastrovascular cavity. There is also no circulatory system, so nutrients must move from the cells that absorb them in the lining of the gastrovascular cavity through the mesoglea to other cells.

The phylum Cnidaria contains about 10,000 described species divided into four classes: Anthozoa, Scyphozoa, Cubozoa, and Hydrozoa. The anthozoans, the sea anemones and corals, are all sessile species, whereas the scyphozoans (jellyfish) and cubozoans (box jellies) are swimming forms. The hydrozoans contain sessile forms and swimming colonial forms like the Portuguese Man O' War.

Class Anthozoa

The class Anthozoa includes all cnidarians that exhibit a polyp body plan only; in other words, there is no medusa stage within their life cycle. Examples include sea anemones (Figure 5.7.3.4), sea pens, and corals, with an estimated number of 6,100 described species. Sea anemones are usually brightly colored and can attain a size of 1.8 to 10 cm in diameter. These animals are usually cylindrical in shape and are attached to a substrate. A mouth opening is surrounded by tentacles bearing cnidocytes.


Cnidarian Animation - Anemone Body Plan
Shape of Life
Watch on YouTube



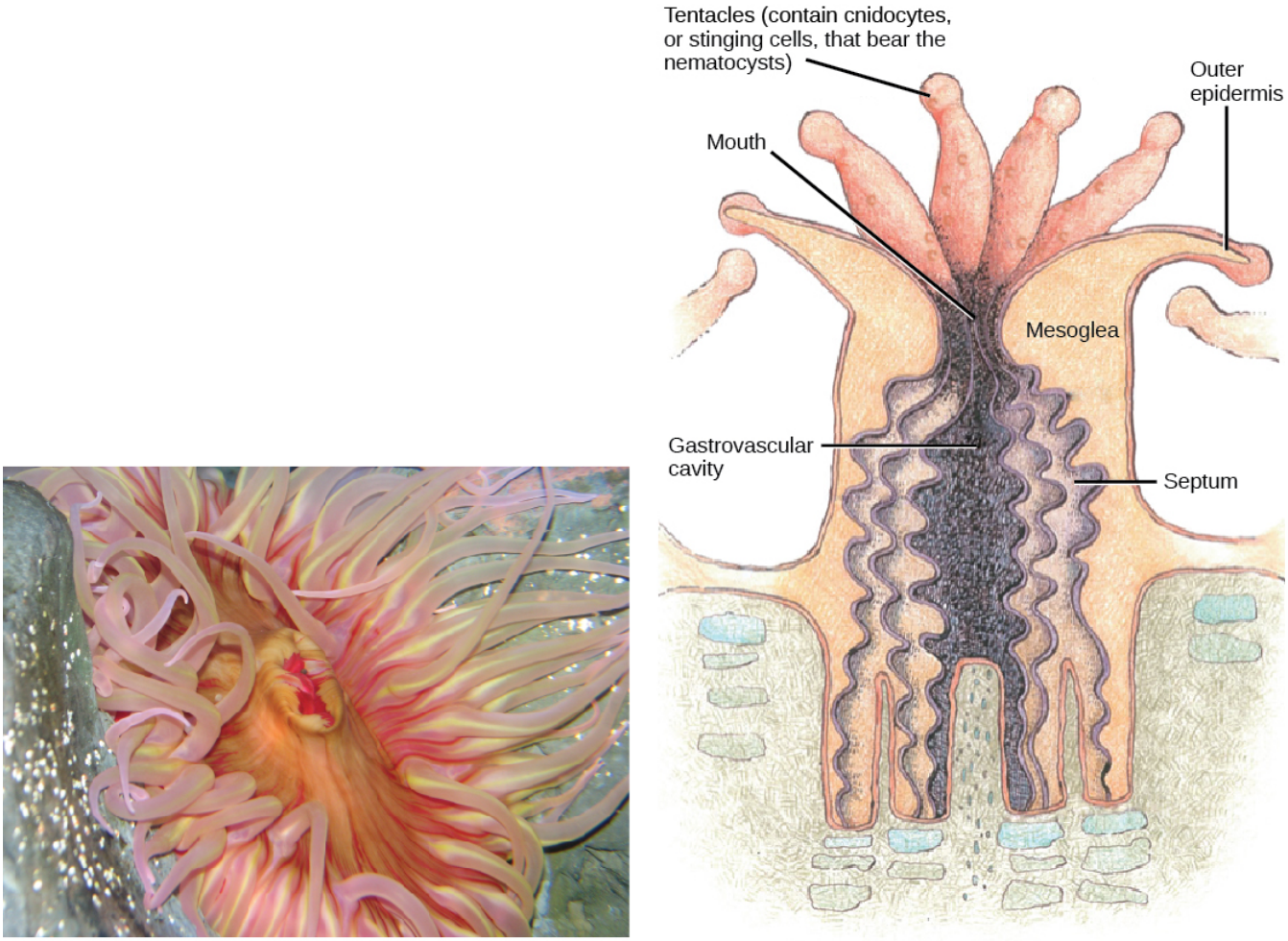


Figure 5.7.3.4: The sea anemone is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Dancing With Ghosts"/Flickr; credit b: modification of work by NOAA)

The mouth of a sea anemone is surrounded by tentacles that bear cnidocytes. The slit-like mouth opening and pharynx are lined by a groove called a siphonophore. The pharynx is the muscular part of the digestive system that serves to ingest as well as egest food, and may extend for up to two-thirds the length of the body before opening into the gastrovascular cavity. This cavity is divided into several chambers by longitudinal septa called mesenteries. Each mesentery consists of one ectodermal and one endodermal cell layer with the mesoglea sandwiched in between. Mesenteries do not divide the gastrovascular cavity completely, and the smaller cavities coalesce at the pharyngeal opening. The adaptive benefit of the mesenteries appears to be an increase in surface area for absorption of nutrients and gas exchange.

Sea anemones feed on small fish and shrimp, usually by immobilizing their prey using the cnidocytes. Some sea anemones establish a mutualistic relationship with hermit crabs by attaching to the crab's shell. In this relationship, the anemone gets food particles from prey caught by the crab, and the crab is protected from the predators by the stinging cells of the anemone. Anemone fish, or clownfish, are able to live in the anemone since they are immune to the toxins contained within the nematocysts.

Anthozoans remain polypoid throughout their lives and can reproduce asexually by budding or fragmentation, or sexually by producing gametes. Both gametes are produced by the polyp, which can fuse to give rise to a free-swimming planula larva. The larva settles on a suitable substratum and develops into a sessile polyp.

Class Scyphozoa

Class Scyphozoa includes all the jellies and is exclusively a marine class of animals with about 200 known species. The defining characteristic of this class is that the medusa is the prominent stage in the life cycle, although there is a polyp stage present.

Members of this species range from 2 to 40 cm in length but the largest scyphozoan species, *Cyanea capillata*, can reach a size of 2 m across. Scyphozoans display a characteristic bell-like morphology (Figure 5.7.3.5).

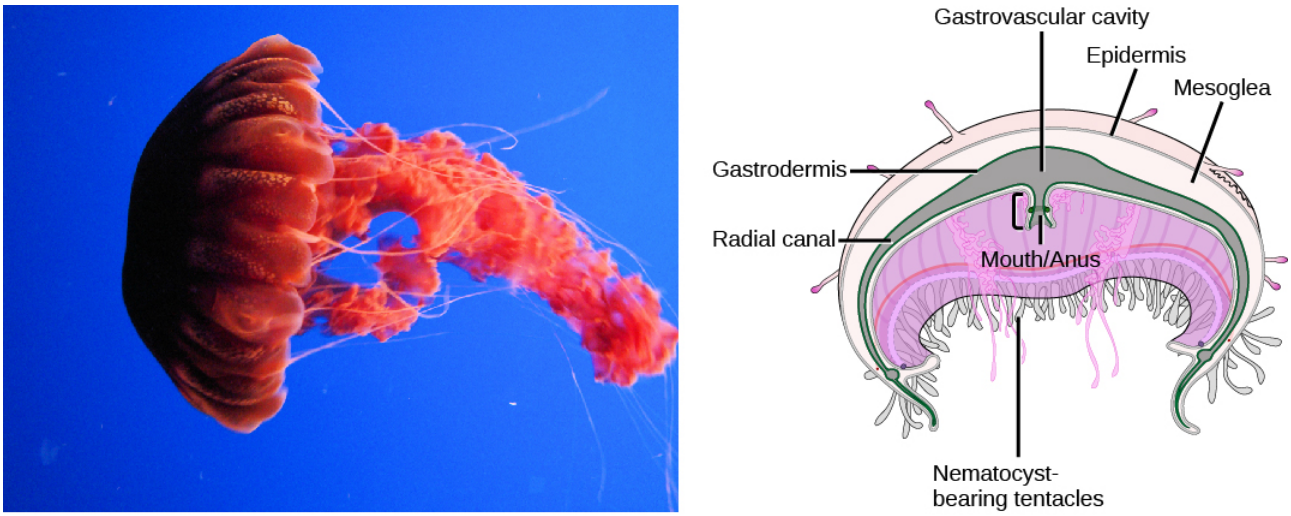


Figure 5.7.3.5: A jelly is shown (a) photographed and (b) in a diagram illustrating its morphology. (credit a: modification of work by "Jimg944"/Flickr; credit b: modification of work by Mariana Ruiz Villareal)

In the jellyfish, a mouth opening is present on the underside of the animal, surrounded by tentacles bearing nematocysts. Scyphozoans live most of their life cycle as free-swimming, solitary carnivores. The mouth leads to the gastrovascular cavity, which may be sectioned into four interconnected sacs, called diverticuli. In some species, the digestive system may be further branched into radial canals. Like the septa in anthozoans, the branched gastrovascular cells serve two functions: to increase the surface area for nutrient absorption and diffusion; thus, more cells are in direct contact with the nutrients in the gastrovascular cavity.

In scyphozoans, nerve cells are scattered all over the body. Neurons may even be present in clusters called rhopalia. These animals possess a ring of muscles lining the dome of the body, which provides the contractile force required to swim through water. Scyphozoans are dioecious animals, that is, the sexes are separate. The gonads are formed from the gastrodermis and gametes are expelled through the mouth. Planula larvae are formed by external fertilization; they settle on a substratum in a polypoid form known as scyphistoma. These forms may produce additional polyps by budding or may transform into the medusoid form. The life cycle (Figure 5.7.3.6) of these animals can be described as polymorphic, because they exhibit both a medusal and polypoid body plan at some point in their life cycle.

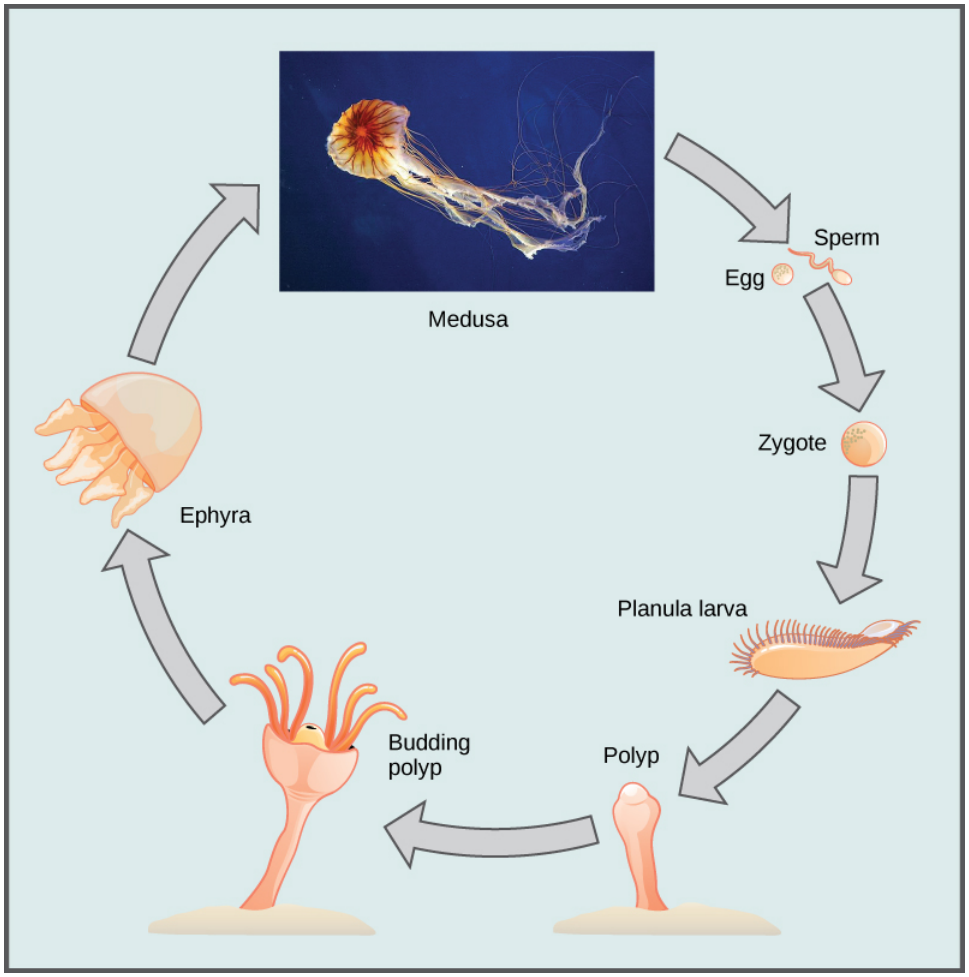


Figure 5.7.3.6: The lifecycle of a jellyfish includes two stages: the medusa stage and the polyp stage. The polyp reproduces asexually by budding, and the medusa reproduces sexually. (credit "medusa": modification of work by Francesco Crippa).

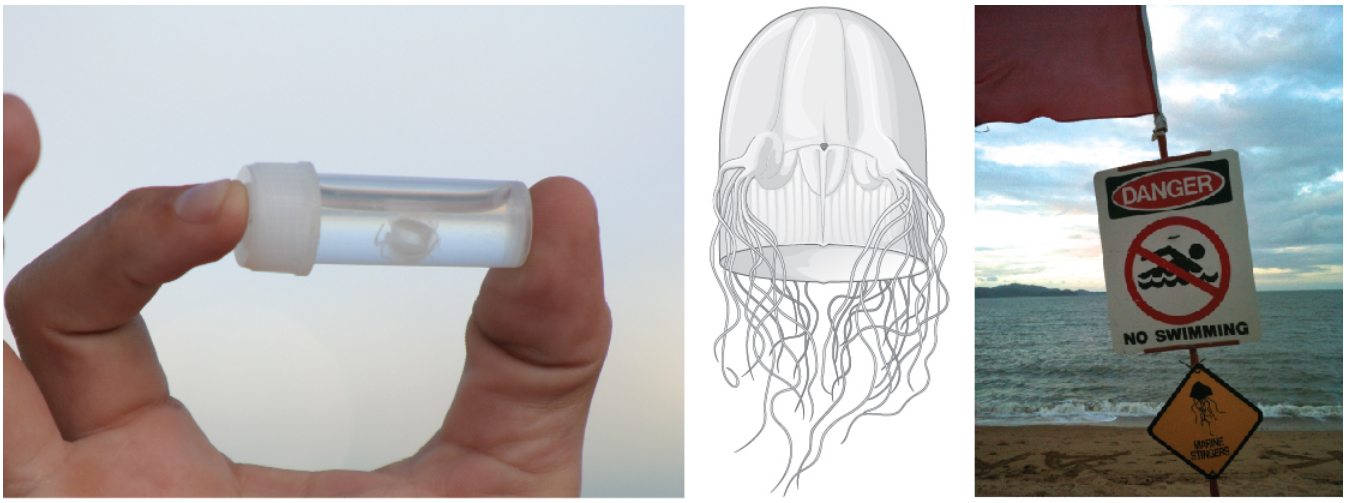




Class Cubozoa

This class includes jellies that have a box-shaped medusa, or a bell that is square in cross-section; hence, are colloquially known as “box jellyfish.” These species may achieve sizes of 15–25 cm. Cubozoans display overall morphological and anatomical characteristics that are similar to those of the scyphozoans. A prominent difference between the two classes is the arrangement of tentacles. This is the most venomous group of all the cnidarians (Figure 5.7.3.7).

The cubozoans contain muscular pads called pedalia at the corners of the square bell canopy, with one or more tentacles attached to each pedalium. These animals are further classified into orders based on the presence of single or multiple tentacles per pedalium. In some cases, the digestive system may extend into the pedalia. Nematocysts may be arranged in a spiral configuration along the tentacles; this arrangement helps to effectively subdue and capture prey. Cubozoans exist in a polypoid form that develops from a planula larva. These polyps show limited mobility along the substratum and, like scyphozoans, may bud to form more polyps to colonize a habitat. Polyp forms then transform into the medusoid forms.



(a) (b) (c)

Figure 5.7.3.7: The (a) tiny cubazoan jelly *Malo kingi* is thimble shaped and, like all cubozoan jellies, (b) has four muscular pedalia to which the tentacles attach. *M. kingi* is one of two species of jellies known to cause Irukandji syndrome, a condition characterized by excruciating muscle pain, vomiting, increased heart rate, and psychological symptoms. Two people in Australia, where Irukandji jellies are most commonly found, are believed to have died from Irukandji stings. (c) A sign on a beach in northern Australia warns swimmers of the danger. (credit c: modification of work by Peter Shanks)

Class Hydrozoa

Hydrozoa includes nearly 3,200 species; most are marine, although some freshwater species are known (Figure 5.7.3.8). Animals in this class are polymorphs, and most exhibit both polypoid and medusoid forms in their lifecycle, although this is variable.

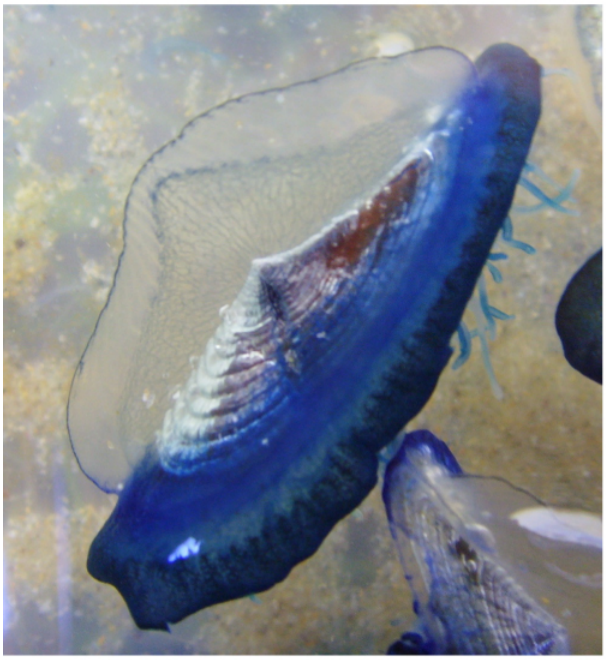
The polyp form in these animals often shows a cylindrical morphology with a central gastrovascular cavity lined by the gastrodermis. The gastrodermis and epidermis have a simple layer of mesoglea sandwiched between them. A mouth opening, surrounded by tentacles, is present at the oral end of the animal. Many hydrozoans form colonies that are composed of a branched colony of specialized polyps that share a gastrovascular cavity, such as in the colonial hydroid *Obelia*. Colonies may also be free-floating and contain medusoid and polypoid individuals in the colony as in *Physalia* (the Portuguese Man O' War) or *Velella* (By-the-wind sailor). Even other species are solitary polyps (*Hydra*) or solitary medusae (*Gonionemus*). The true characteristic shared by all of these diverse species is that their gonads for sexual reproduction are derived from epidermal tissue, whereas in all other cnidarians they are derived from gastrodermal tissue.



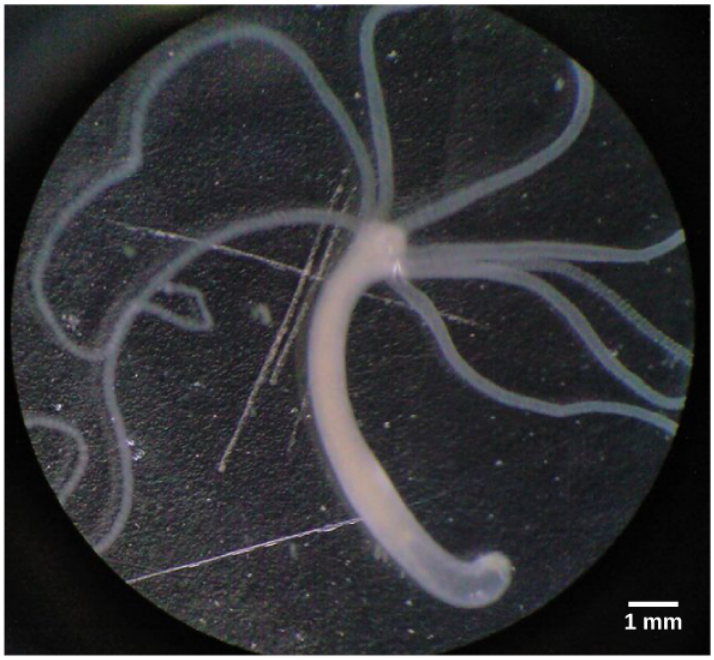
(a) *Obelia*



(b) *Physalia physalis* (Portuguese Man O' War)



(c) *Velella bae*



(d) *Hydra*

Figure 5.7.3.8: (a) *Obelia*, (b) *Physalia physalis*, known as the Portuguese Man O‘ War, (c) *Velella bae*, and (d) *Hydra* have different body shapes but all belong to the family Hydrozoa. (credit b: modification of work by NOAA; scale-bar data from Matt Russell)

Summary

Cnidarians represent a more complex level of organization than Porifera. They possess outer and inner tissue layers that sandwich a noncellular mesoglea. Cnidarians possess a well-formed digestive system and carry out extracellular digestion. The cnidocyte is a specialized cell for delivering toxins to prey as well as warning off predators. Cnidarians have separate sexes and have a lifecycle that involves morphologically distinct forms. These animals also show two distinct morphological forms—medusoid and polypoid—at various stages in their lifecycle.

Cnidaria
phylum of animals that are diploblastic and have radial symmetry

cnidocyte
specialized stinging cell found in Cnidaria

epidermis
outer layer (from ectoderm) that lines the outside of the animal

extracellular digestion
food is taken into the gastrovascular cavity, enzymes are secreted into the cavity, and the cells lining the cavity absorb nutrients

gastrodermis
inner layer (from endoderm) that lines the digestive cavity

gastrovascular cavity
opening that serves as both a mouth and an anus, which is termed an incomplete digestive system

medusa
free-floating cnidarian body plan with mouth on underside and tentacles hanging down from a bell

mesoglea
non-living, gel-like matrix present between ectoderm and endoderm in cnidarians

nematocyst
harpoon-like organelle within cnidocyte with pointed projectile and poison to stun and entangle prey

polyp
stalk-like sessile life form of a cnidarians with mouth and tentacles facing upward, usually sessile but may be able to glide along surface

polymorphic
possessing multiple body plans within the lifecycle of a group of organisms

siphonophore
tubular structure that serves as an inlet for water into the mantle cavity

---

This page titled 5.7.3: Phylum Cnidaria is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.2: Phylum Cnidaria** by OpenStax is licensed CC BY 4.0.

5.7.4: Superphylum Lophotrochozoa

Skills to Develop

- Describe the unique anatomical and morphological features of flatworms, rotifers, Nemertea, mollusks, and annelids
- Describe the development of an extracoelomic cavity
- Discuss the advantages of true body segmentation
- Explain the key features of Platyhelminthes and their importance as parasites
- Describe the features of animals classified in phylum Annelida

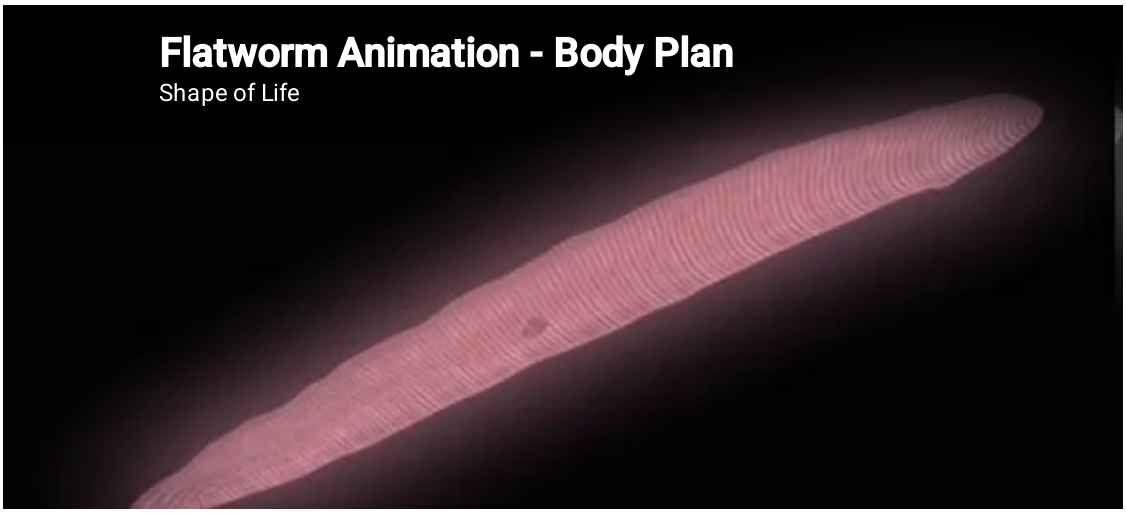
Animals belonging to superphylum Lophotrochozoa are protostomes, in which the blastopore, or the point of involution of the ectoderm or outer germ layer, becomes the mouth opening to the alimentary canal. This is called protostomy or “first mouth.” In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band and then splits internally to form the coelom; this protostomic coelom is hence termed schizocoelom.

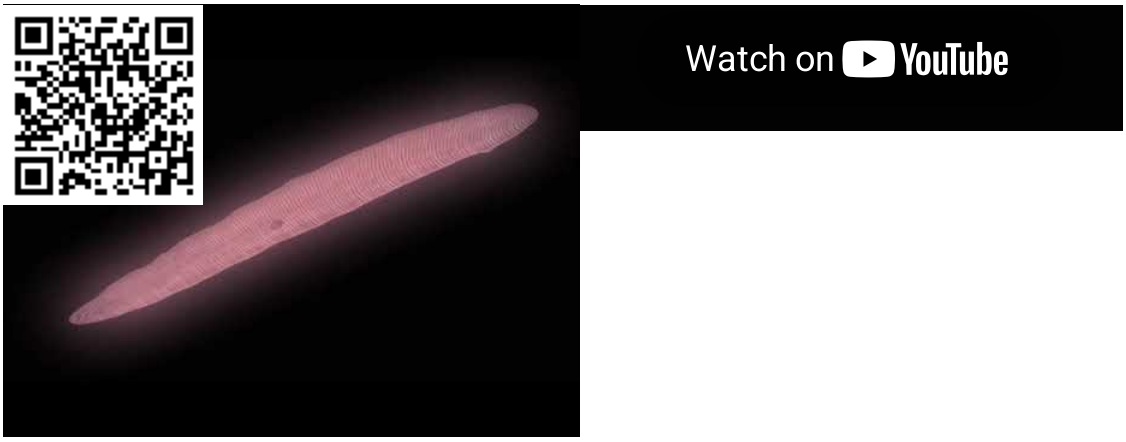
As lophotrochozoans, the organisms in this superphylum possess either a lophophore or trochophore larvae. The lophophores include groups that are united by the presence of the lophophore, a set of ciliated tentacles surrounding the mouth. Lophophorata include the flatworms and several other phyla. These clades are upheld when RNA sequences are compared. Trochophore larvae are characterized by two bands of cilia around the body.

The lophotrochozoans are triploblastic and possess an embryonic mesoderm sandwiched between the ectoderm and endoderm found in the diploblastic cnidarians. These phyla are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. It also means the beginning of cephalization, the evolution of a concentration of nervous tissues and sensory organs in the head of the organism, which is where it first encounters its environment.

Phylum Platyhelminthes

The flatworms are acoelomate organisms that include many free-living and parasitic forms. Most of the flatworms are classified in the superphylum Lophotrochozoa, which also includes the mollusks and annelids. The Platyhelminthes consist of two lineages: the Catenulida and the Rhabditophora. The Catenulida, or "chain worms" is a small clade of just over 100 species. These worms typically reproduce asexually by budding. However, the offspring do not fully attach from the parents and, resemble a chain in appearance. All of the remaining flatworms discussed here are part of the Rhabditophora. Many flatworms are parasitic, including important parasites of humans. Flatworms have three embryonic tissue layers that give rise to surfaces that cover tissues (from ectoderm), internal tissues (from mesoderm), and line the digestive system (from endoderm). The epidermal tissue is a single layer cells or a layer of fused cells (syncytium) that covers a layer of circular muscle above a layer of longitudinal muscle. The mesodermal tissues include mesenchymal cells that contain collagen and support secretory cells that secrete mucus and other materials at the surface. The flatworms are acoelomates, so their bodies are solid between the outer surface and the cavity of the digestive system.





Physiological Processes of Flatworms

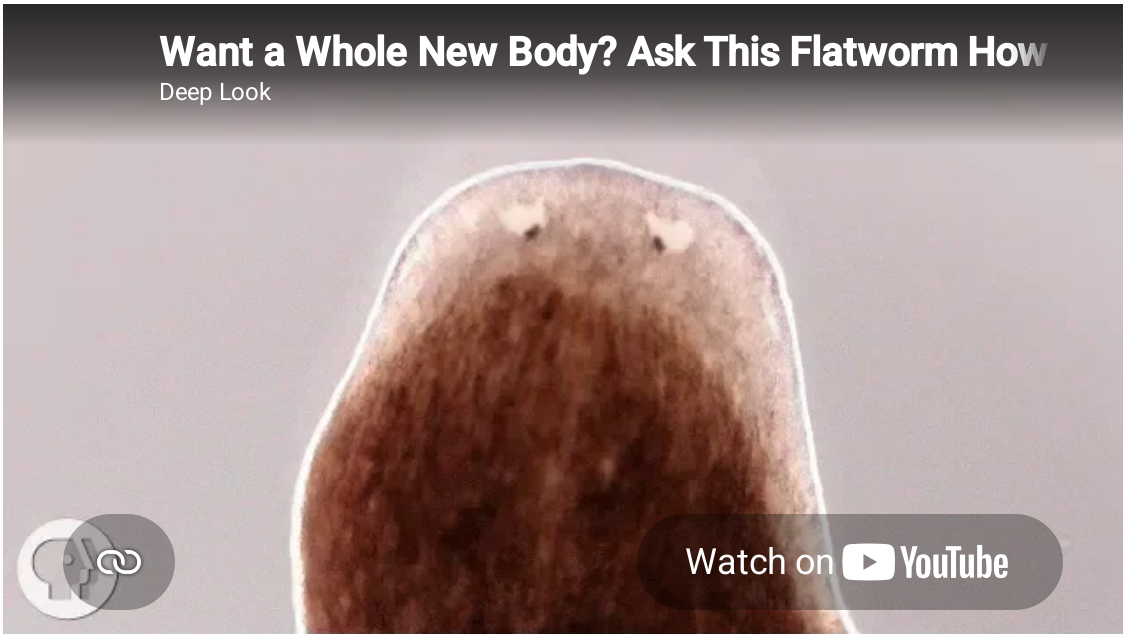
The free-living species of flatworms are predators or scavengers. Parasitic forms feed on the tissues of their hosts. Most flatworms, such as the planarian shown in Figure 5.7.4.1, have a gastrovascular cavity rather than a complete digestive system. In such animals, the “mouth” is also used to expel waste materials from the digestive system. Some species also have an anal opening. The gut may be a simple sac or highly branched. Digestion is extracellular, with digested materials taken in to the cells of the gut lining by phagocytosis. One group, the cestodes, lacks a digestive system. Flatworms have an excretory system with a network of tubules throughout the body with openings to the environment and nearby flame cells, whose cilia beat to direct waste fluids concentrated in the tubules out of the body. The system is responsible for the regulation of dissolved salts and the excretion of nitrogenous wastes. The nervous system consists of a pair of nerve cords running the length of the body with connections between them and a large ganglion or concentration of nerves at the anterior end of the worm, where there may also be a concentration of photosensory and chemosensory cells.

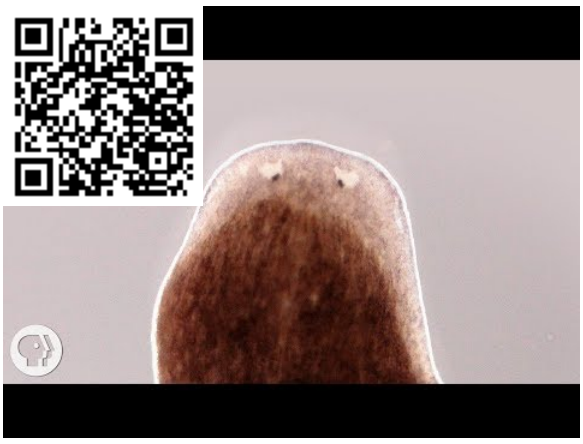
There is neither a circulatory nor respiratory system, with gas and nutrient exchange dependent on diffusion and cell-cell junctions. This necessarily limits the thickness of the body in these organisms, constraining them to be “flat” worms.

Most flatworm species are monoecious, and fertilization is typically internal. Asexual reproduction is common in some groups.









img alt="Illustration shows the digestive, nervous and excretory systems in a flat, worm-like planaria. The digestive system starts at the ventral mouth opening in the middle of the animal, and then extends to the head through the middle of the body, and toward the along the sides of the body. Many lateral branches occur along the digestive system. The nervous system has 2 cerebral ganglia at the eyes in the head, and 2 ventral nerve cords with transverse connections along the length of the body to the tail. The excretory system is arranged in 2 long mesh-like structures down each side of the body." src="/@api/deki/files/1598/Figure_28_03_01.jpg" />

Figure 5.7.4.1: The planarian is a flatworm that has a gastrovascular cavity with one opening that serves as both mouth and anus. The excretory system is made up of tubules connected to excretory pores on both sides of the body. The nervous system is composed of two interconnected nerve cords running the length of the body, with cerebral ganglia and eyespots at the anterior end.

Diversity of Flatworms

Platyhelminthes are traditionally divided into four classes: Turbellaria, Monogenea, Trematoda, and Cestoda (Figure 5.7.4.2). As discussed above, the relationships among members of these classes is being reassessed, with the turbellarians in particular now viewed as a paraphyletic group, a group that does not have a single common ancestor.

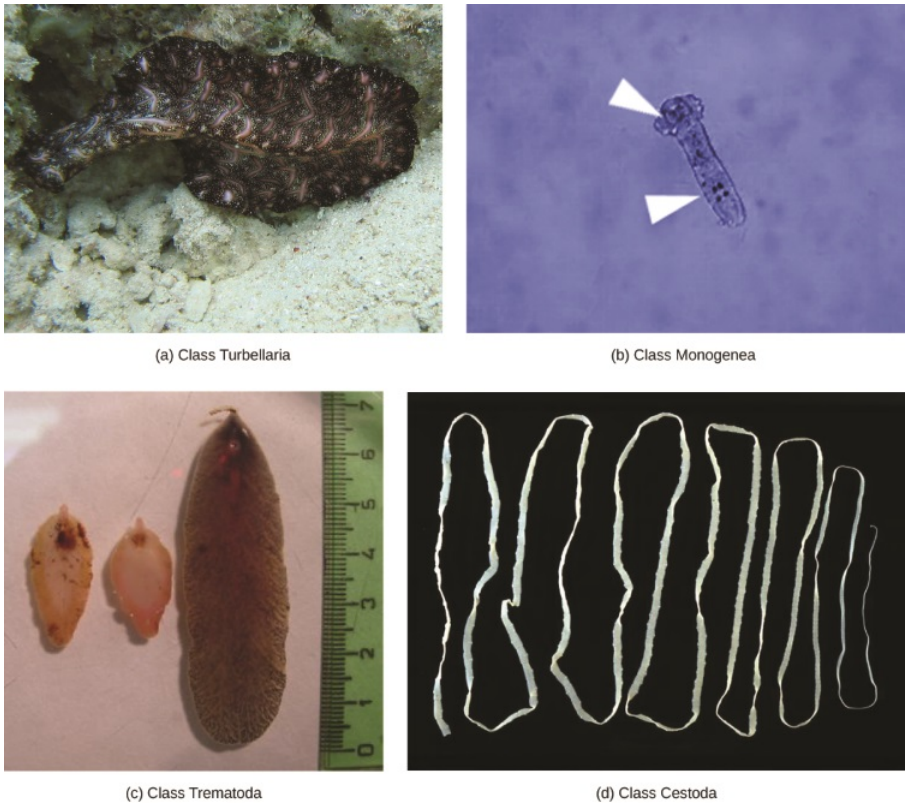


Figure 5.7.4.2: Phylum Platyhelminthes is divided into four classes. (a) Class Turbellaria includes the Bedford's flatworm (*Pseudobiceros bedfordi*), which is about 8–10 cm in length. (b) The parasitic class Monogenea includes *Dactylogyrus* spp. *Dactylogyrus*, commonly called a gill fluke, is about 0.2 mm in length and has two anchors, indicated by arrows, that it uses to latch onto the gills of host fish. (c) The Trematoda class includes *Fascioloides magna* (right) and *Fasciaola hepatica* (two specimens of left, also known as the common liver fluke). (d) Class Cestoda includes tapeworms such as this *Taenia saginata*. *T. saginata*, which infects both cattle and humans, can reach 4–10 meters in length; the specimen shown here is about 4 meters. (credit a: modification of work by Jan Derk; credit d: modification of work by CDC)

The class Turbellaria includes mainly free-living, marine species, although some species live in freshwater or moist terrestrial environments. The ventral epidermis of turbellarians is ciliated and facilitates their locomotion. Some turbellarians are capable of remarkable feats of regeneration in which they may regrow the body, even from a small fragment.

The monogeneans are ectoparasites, mostly of fish, with simple lifecycles that consist of a free-swimming larva that attaches to a fish to begin transformation to the parasitic adult form. The parasite has only one host and that host is usually only one species. The worms may produce enzymes that digest the host tissues or simply graze on surface mucus and skin particles. Most monogeneans are hermaphroditic, but the male gametes develop first and so cross-fertilization is quite common.

The trematodes, or flukes, are internal parasites of mollusks and many other groups, including humans. Trematodes have complex lifecycles that involve a primary host in which sexual reproduction occurs, and one or more secondary hosts in which asexual reproduction occurs. The primary host is almost always a mollusk. Trematodes are responsible for serious human diseases including schistosomiasis, a blood fluke. The disease infects an estimated 200 million people in the tropics, leading to organ damage and chronic symptoms like fatigue. Infection occurs when the human enters the water and a larva, released from the primary snail host, locates and penetrates the skin. The parasite infects various organs in the body and feeds on red blood cells

before reproducing. Many of the eggs are released in feces and find their way into a waterway, where they are able to reinfect the primary snail host.

The cestodes, or tapeworms, are also internal parasites, mainly of vertebrates (Figure 5.7.4.3). Tapeworms live in the intestinal tract of the primary host and remain fixed using a sucker on the anterior end, or scolex, of the tapeworm body. The remaining body of the tapeworm is made up of a long series of units called proglottids, each of which may contain an excretory system with flame cells, but contain reproductive structures, both male and female. Tapeworms do not possess a digestive system; instead, they absorb nutrients from the food matter passing them in the host's intestine.

Proglottids are produced at the scolex and gradually migrate to the end of the tapeworm; at this point, they are "mature" and all structures except fertilized eggs have degenerated. Most reproduction occurs by cross-fertilization. The proglottid detaches from the body of the worm and is released into the feces of the organism. The eggs are eaten by an intermediate host. The juvenile worm infects the intermediate host and takes up residence, usually in muscle tissue. When the muscle tissue is eaten by the primary host, the cycle is completed. There are several tapeworm parasites of humans that are transmitted by eating uncooked or poorly cooked pork, beef, and fish.





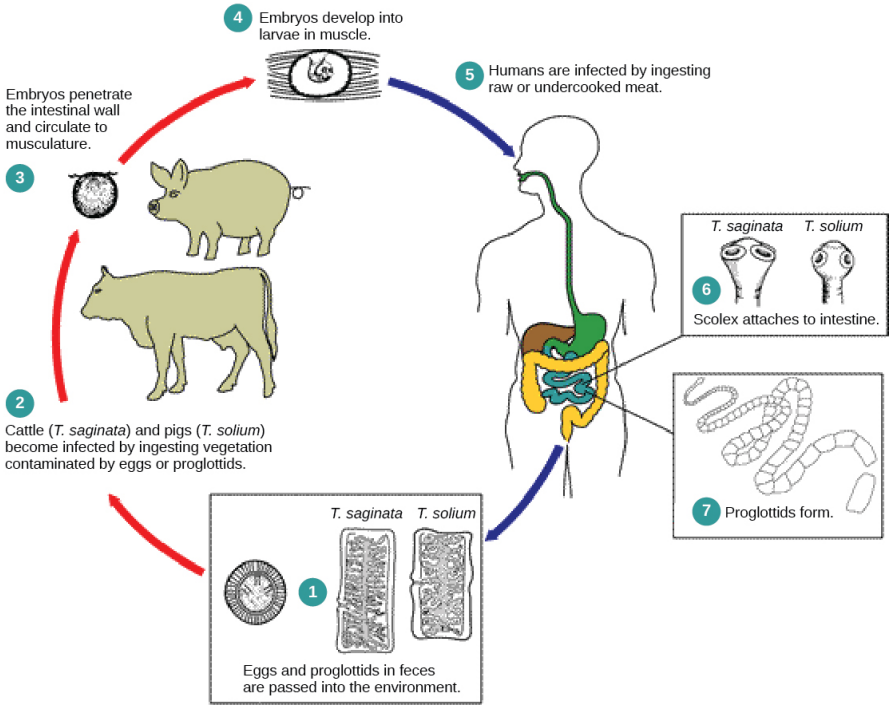


Figure 5.7.4.3: Tapeworm (*Taenia* spp.) infections occur when humans consume raw or undercooked infected meat. (credit: modification of work by CDC)

Phylum Rotifera

The rotifers are a microscopic (about 100 µm to 30 mm) group of mostly aquatic organisms that get their name from the corona, a rotating, wheel-like structure that is covered with cilia at their anterior end (Figure 5.7.4.4). Although their taxonomy is currently in flux, one treatment places the rotifers in three classes: Bdelloidea, Monogononta, and Seisonidea. The classification of the group is currently under revision, however, as more phylogenetic evidence becomes available. It is possible that the "spiny headed worms" currently in phylum Acanthocephala will be incorporated into this group in the future.

The body form of rotifers consists of a head (which contains the corona), a trunk (which contains the organs), and the foot. Rotifers are typically free-swimming and truly planktonic organisms, but the toes or extensions of the foot can secrete a sticky material forming a holdfast to help them adhere to surfaces. The head contains sensory organs in the form of a bi-lobed brain and small eyespots near the corona.



(a) Bdelloidea (a) Monogonota

Figure 5.7.4.4: Shown are examples from two of the three classes of rotifer. (a) Species from the class Bdelloidea are characterized by a large corona, shown separately from the whole animals in the center of this scanning electron micrograph. (b) *Polyarthra*, from the class Monogononta, has a smaller corona than Bdelloid rotifers, and a single gonad, which give the class its name. (credit a: modification of work by Diego Fontaneto; credit b: modification of work by U.S. EPA; scale-bar data from Cory Zanker)

The rotifers are filter feeders that will eat dead material, algae, and other microscopic living organisms, and are therefore very important components of aquatic food webs. Rotifers obtain food that is directed toward the mouth by the current created from the movement of the corona. The food particles enter the mouth and travel to the mastax (pharynx with jaw-like structures). Food then passes by digestive and salivary glands, and into the stomach, then onto the intestines. Digestive and excretory wastes are collected in a cloacal bladder before being released out the anus.





Rotifers are pseudocoelomates commonly found in fresh water and some salt water environments throughout the world. Figure 5.7.4.5 shows the anatomy of a rotifer belonging to class Bdelloidea. About 2,200 species of rotifers have been identified. Rotifers are dioecious organisms (having either male or female genitalia) and exhibit sexual dimorphism (males and females have different forms). Many species are parthenogenic and exhibit haplodiploidy, a method of gender determination in which a fertilized egg develops into a female and an unfertilized egg develops into a male. In many dioecious species, males are short-lived and smaller with no digestive system and a single testis. Females can produce eggs that are capable of dormancy for protection during harsh environmental conditions.

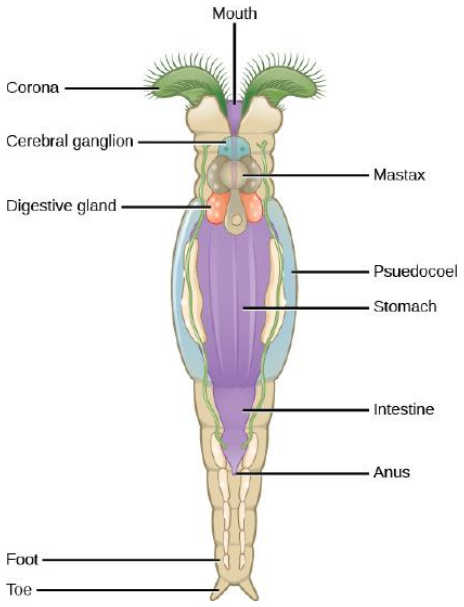


Figure 5.7.4.5: This illustration shows the anatomy of a bdelloid rotifer.

Phylum Nemertea

The Nemertea are colloquially known as ribbon worms. Most species of phylum Nemertea are marine, predominantly benthic or bottom dwellers, with an estimated 900 species known. However, nemertini have been recorded in freshwater and terrestrial habitats as well. Most nemerteans are carnivores, feeding on worms, clams, and crustaceans. Some species are scavengers, and some nemertini species, like *Malacobdella grossa*, have also evolved commensalistic relationships with some mollusks. Some species have devastated commercial fishing of clams and crabs. Nemerteans have almost no predators and two species are sold as fish bait.

Morphology

Ribbon worms vary in size from 1 cm to several meters. They show bilateral symmetry and remarkable contractile properties. Because of their contractility, they can change their morphological presentation in response to environmental cues. Animals in phylum Nemertea show a flattened morphology, that is, they are flat from front to back, like a flattened tube. Nemertea are soft and unsegmented animals (Figure 5.7.4.6).

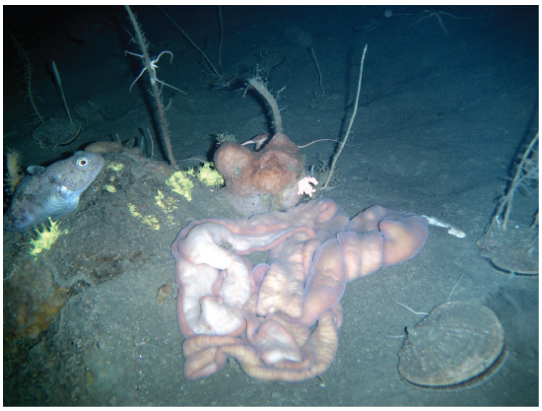


Figure 5.7.4.6: The proboscis worm (*Parborlasia corrugatus*) is a scavenger that combs the sea floor for food. The species is a member of the phylum Nemertea. The specimen shown here was photographed in the Ross Sea, Antarctica. (credit: Henry Kaiser, National Science Foundation)

A unique characteristic of this phylum is the presence of a proboscis enclosed in a rhynchocoel. The proboscis serves to capture food and may be ornamented with barbs in some species. The rhynchocoel is a fluid-filled cavity that extends from the head to nearly two-thirds of the length of the gut in these animals (Figure 5.7.4.7). The proboscis may be extended or retracted by the retractor muscle attached to the wall of the rhynchocoel.





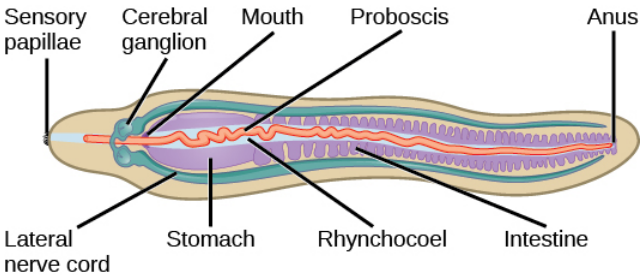


Figure 5.7.4.7: The anatomy of a Nemertean is shown.

Digestive System

The nemertini show a very well-developed digestive system. A mouth opening that is ventral to the rhynchocoel leads into the foregut, followed by the intestine. The intestine is present in the form of diverticular pouches and ends in a rectum that opens via an anus. Gonads are interspersed with the intestinal diverticular pouches and open outwards via genital pores. A circulatory system consists of a closed loop of a pair of lateral blood vessels. The circulatory system is derived from the coelomic cavity of the embryo. Some animals may also have cross-connecting vessels in addition to lateral ones. Although these are called blood vessels, since they are of coelomic origin, the circulatory fluid is colorless. Some species bear hemoglobin as well as other yellow or green pigments. The blood vessels are connected to the rhynchocoel. The flow of fluid in these vessels is facilitated by the contraction of

muscles in the body wall. A pair of protonephridia, or primitive kidneys, is present in these animals to facilitate osmoregulation. Gaseous exchange occurs through the skin in the nemertini.

Nervous System

Nemertini have a ganglion or “brain” situated at the anterior end between the mouth and the foregut, surrounding the digestive system as well as the rhynchocoel. A ring of four nerve masses called “ganglia” composes the brain in these animals. Paired longitudinal nerve cords emerge from the brain ganglia and extend to the posterior end. Ocelli or eyespots are present in pairs, in multiples of two in the anterior portion of the body. It is speculated that the eyespots originate from neural tissue and not from the epidermis.

Reproduction

Animals in phylum Nemertea show sexual dimorphism, although freshwater species may be hermaphroditic. Eggs and sperm are released into the water, and fertilization occurs externally. The zygote then develops into a planuliform larva. In some nemertine species, a pilidium larva may develop inside the young worm, from a series of imaginal discs. This larval form, characteristically shaped like a deerstalker cap, devours tissues from the young worm for survival before metamorphosing into the adult-like morphology.

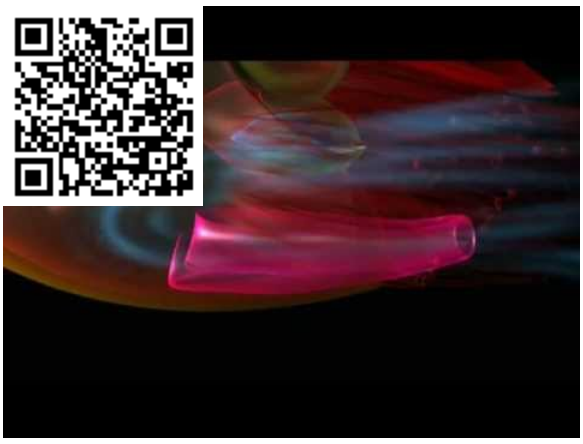
Phylum Mollusca

Phylum Mollusca is the predominant phylum in marine environments. It is estimated that 23 percent of all known marine species are mollusks; there are over 75,000 described species, making them the second most diverse phylum of animals. The name “mollusca” signifies a soft body, since the earliest descriptions of mollusks came from observations of unshelled cuttlefish. Mollusks are predominantly a marine group of animals; however, they are known to inhabit freshwater as well as terrestrial habitats. Mollusks display a wide range of morphologies in each class and subclass, but share a few key characteristics, including a muscular foot, a visceral mass containing internal organs, and a mantle that may or may not secrete a shell of calcium carbonate (Figure 5.7.4.8).




MOLLUSCS!


Shape of Life: Molluscs - The Survival Game
HS Science Videos
Watch on YouTube



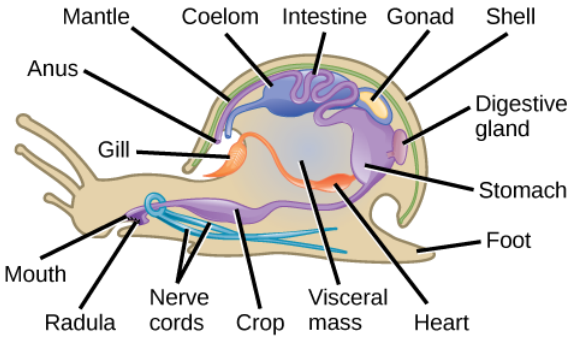


Figure 5.7.4.8: There are many species and variations of mollusks; this illustration shows the anatomy of an aquatic gastropod.

? Exercise 5.7.4.1

Which of the following statements about the anatomy of a mollusk is false?

a. Mollusks have a radula for grinding food.
b. A digestive gland is connected to the stomach.
c. The tissue beneath the shell is called the mantle.
d. The digestive system includes a gizzard, a stomach, a digestive gland, and the intestine.

Answer

d

Mollusks have a muscular foot, which is used for locomotion and anchorage, and varies in shape and function, depending on the type of mollusk under study. In shelled mollusks, this foot is usually the same size as the opening of the shell. The foot is a retractable as well as an extendable organ. The foot is the ventral-most organ, whereas the mantle is the limiting dorsal organ. Mollusks are eucoelomate, but the coelomic cavity is restricted to a cavity around the heart in adult animals. The mantle cavity develops independently of the coelomic cavity.

The visceral mass is present above the foot, in the visceral hump. This includes digestive, nervous, excretory, reproductive, and respiratory systems. Mollusk species that are exclusively aquatic have gills for respiration, whereas some terrestrial species have lungs for respiration. Additionally, a tongue-like organ called a radula, which bears chitinous tooth-like ornamentation, is present in many species, and serves to shred or scrape food. The mantle (also known as the pallium) is the dorsal epidermis in mollusks; shelled mollusks are specialized to secrete a chitinous and hard calcareous shell.

Most mollusks are dioecious animals and fertilization occurs externally, although this is not the case in terrestrial mollusks, such as snails and slugs, or in cephalopods. In some mollusks, the zygote hatches and undergoes two larval stages—trochophore and veliger—before becoming a young adult; bivalves may exhibit a third larval stage, glochidia.

Classification of Phylum Mollusca

Phylum Mollusca is a very diverse (85,000 species) group of mostly marine species. Mollusks have a dramatic variety of form, ranging from large predatory squids and octopus, some of which show a high degree of intelligence, to grazing forms with elaborately sculpted and colored shells. This phylum can be segregated into seven classes: Aplacophora, Monoplacophora, Polyplacophora, Bivalvia, Gastropoda, Cephalopoda, and Scaphopoda.

Class Aplacophora (“bearing no plates”) includes worm-like animals primarily found in benthic marine habitats. These animals lack a calcareous shell but possess aragonite spicules on their epidermis. They have a rudimentary mantle cavity and lack eyes, tentacles, and nephridia (excretory organs). Members of class Monoplacophora (“bearing one plate”) posses a single, cap-like shell that encloses the body. The morphology of the shell and the underlying animal can vary from circular to ovate. A looped digestive system, multiple pairs of excretory organs, many gills, and a pair of gonads are present in these animals. The monoplacophorans were believed extinct and only known via fossil records until the discovery of *Neopilina galathaea* in 1952. Today, scientists have identified nearly two dozen extant species.

Animals in the class Polyplacophora (“bearing many plates”) are commonly known as “chitons” and bear an armor-like eight-plated shell (Figure 5.7.4.9). These animals have a broad, ventral foot that is adapted for suction to rocks and other substrates, and a mantle that extends beyond the shell in the form of a girdle. Calcareous spines may be present on the girdle to offer protection from predators. Respiration is facilitated by ctenidia (gills) that are present ventrally. These animals possess a radula that is modified for scraping. The nervous system is rudimentary with only buccal or “cheek” ganglia present at the anterior end. Eyespots are absent in these animals. A single pair of nephridia for excretion is present.



Figure 5.7.4.9: This chiton from the class Polyplacaphora has the eight-plated shell that is indicative of its class. (credit: Jerry Kirkhart)

Class Bivalvia (“two shells”) includes clams, oysters, mussels, scallops, and geoducks. Members of this class are found in marine as well as freshwater habitats. As the name suggests, bivalves are enclosed in a pair of shells (valves are commonly called “shells”) that are hinged at the dorsal end by shell ligaments as well as shell teeth (Figure 5.7.4.10). The overall morphology is laterally flattened, and the head region is poorly developed. Eyespots and statocysts may be absent in some species. Since these animals are suspension feeders, a radula is absent in this class of mollusks. Respiration is facilitated by a pair of ctenidia, whereas excretion and osmoregulation are brought about by a pair of nephridia. Bivalves often possess a large mantle cavity. In some species, the posterior edges of the mantle may fuse to form two siphons that serve to take in and exude water.



Figure 5.7.4.10: These mussels, found in the intertidal zone in Cornwall, England, are bivalves. (credit: Mark A. Wilson)

One of the functions of the mantle is to secrete the shell. Some bivalves like oysters and mussels possess the unique ability to secrete and deposit a calcareous nacre or “mother of pearl” around foreign particles that may enter the mantle cavity. This property has been commercially exploited to produce pearls.

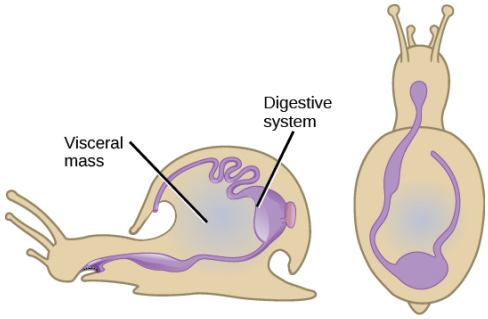
Animals in class Gastropoda (“stomach foot”) include well-known mollusks like snails, slugs, conchs, sea hares, and sea butterflies. Gastropoda includes shell-bearing species as well as species with a reduced shell. These animals are asymmetrical and usually present a coiled shell (Figure 5.7.4.11). Shells may be planospiral (like a garden hose wound up), commonly seen in garden snails, or conispiral, (like a spiral staircase), commonly seen in marine conches.



(a) (b)

Figure 5.7.4.11: (a) Snails and (b) slugs are both gastropods, but slugs lack a shell. (credit a: modification of work by Murray Stevenson; credit b: modification of work by Rosendahl)

The visceral mass in the shelled species displays torsion around the perpendicular axis on the center of the foot, which is the key characteristic of this group, along with a foot that is modified for crawling (Figure 5.7.4.12). Most gastropods bear a head with tentacles, eyes, and a style. A complex radula is used by the digestive system and aids in the ingestion of food. Eyes may be absent in some gastropods species. The mantle cavity encloses the ctenidia as well as a pair of nephridia.



(a) (b)

Figure 5.7.4.12: During embryonic development of gastropods, the visceral mass undergoes torsion, or counterclockwise rotation of anatomical features. As a result, the anus of the adult animal is located over the head. Torsion is an independent process from coiling of the shell.

Everyday Connection: Can Snail Venom Be Used as a Pharmacological Painkiller?

Marine snails of the genus *Conus* (Figure 5.7.4.13) attack prey with a venomous sting. The toxin released, known as conotoxin, is a peptide with internal disulfide linkages. Conotoxins can bring about paralysis in humans, indicating that this toxin attacks neurological targets. Some conotoxins have been shown to block neuronal ion channels. These findings have led researchers to study conotoxins for possible medical applications.

Conotoxins are an exciting area of potential pharmacological development, since these peptides may be possibly modified and used in specific medical conditions to inhibit the activity of specific neurons. For example, these toxins may be used to induce paralysis in muscles in specific health applications, similar to the use of botulinum toxin. Since the entire spectrum of conotoxins, as well as their mechanisms of action, are not completely known, the study of their potential applications is still in its infancy. Most research to date has focused on their use to treat neurological diseases. They have also shown some efficacy in relieving chronic pain, and the pain associated with conditions like sciatica and shingles. The study and use of biotoxins—toxins derived from living organisms—are an excellent example of the application of biological science to modern medicine.



Figure 5.7.4.13: Members of the genus *Conus* produce neurotoxins that may one day have medical uses. (credit: David Burdick, NOAA)

Class Cephalopoda (“head foot” animals), include octopuses, squids, cuttlefish, and nautilus. Cephalopods are a class of shell-bearing animals as well as mollusks with a reduced shell. They display vivid coloration, typically seen in squids and octopuses, which is used for camouflage. All animals in this class are carnivorous predators and have beak-like jaws at the anterior end. All cephalopods show the presence of a very well-developed nervous system along with eyes, as well as a closed circulatory system. The foot is lobed and developed into tentacles, and a funnel, which is used as their mode of locomotion. Suckers are present on the tentacles in octopuses and squid. Ctenidia are enclosed in a large mantle cavity and are serviced by large blood vessels, each with its own heart associated with it; the mantle has siphonophores that facilitate exchange of water.

Locomotion in cephalopods is facilitated by ejecting a stream of water for propulsion. This is called “jet” propulsion. A pair of nephridia is present within the mantle cavity. Sexual dimorphism is seen in this class of animals. Members of a species mate, and the female then lays the eggs in a secluded and protected niche. Females of some species care for the eggs for an extended period of time and may end up dying during that time period. Cephalopods such as squids and octopuses also produce sepia or a dark ink, which is squirted upon a predator to assist in a quick getaway.

Reproduction in cephalopods is different from other mollusks in that the egg hatches to produce a juvenile adult without undergoing the trochophore and veliger larval stages.

In the shell-bearing *Nautilus* spp., the spiral shell is multi-chambered. These chambers are filled with gas or water to regulate buoyancy. The shell structure in squids and cuttlefish is reduced and is present internally in the form of a squid pen and cuttlefish bone, respectively. Examples are shown in Figure 5.7.4.14.

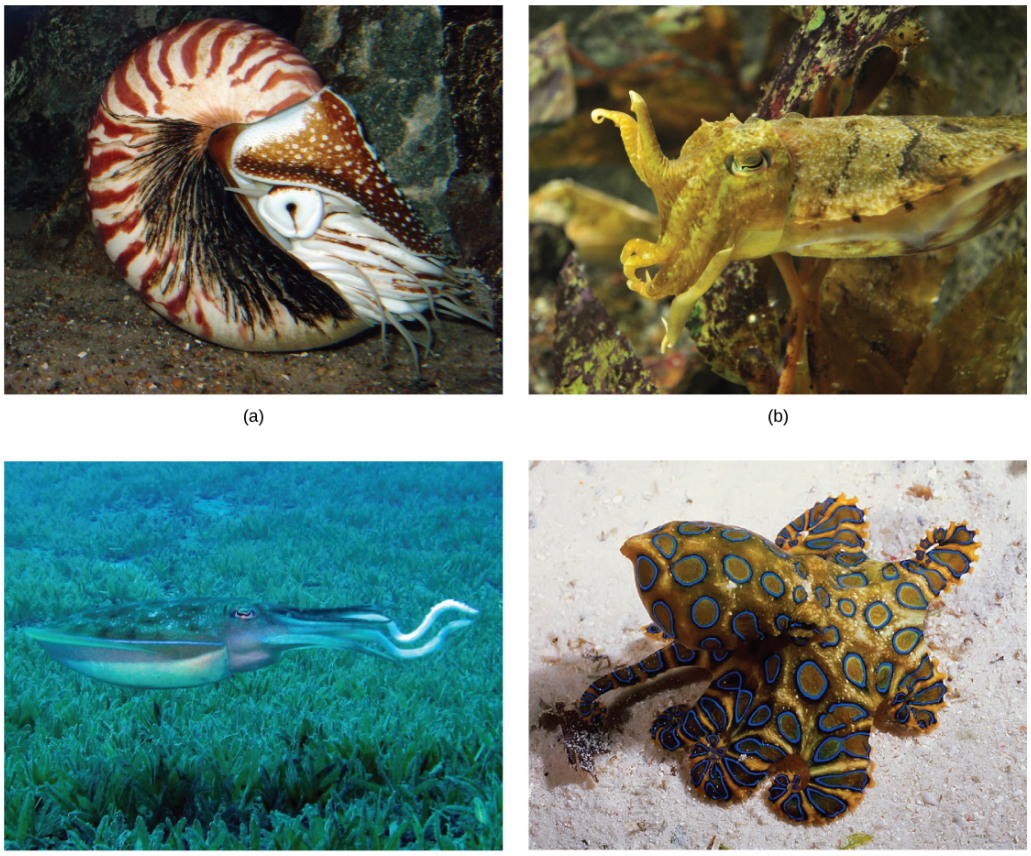


Figure 5.7.4.14: The (a) nautilus, (b) giant cuttlefish, (c) reef squid, and (d) blue-ring octopus are all members of the class Cephalopoda. (credit a: modification of work by J. Baecker; credit b: modification of work by Adrian Mohedano; credit c: modification of work by Silke Baron; credit d: modification of work by Angell Williams)

Members of class Scaphopoda (“boat feet”) are known colloquially as “tusk shells” or “tooth shells,” as evident when examining *Dentalium*, one of the few remaining scaphopod genera (Figure 5.7.4.15). Scaphopods are usually buried in sand with the anterior opening exposed to water. These animals bear a single conical shell, which has both ends open. The head is rudimentary and protrudes out of the posterior end of the shell. These animals do not possess eyes, but they have a radula, as well as a foot modified into tentacles with a bulbous end, known as captaculae. Captaculae serve to catch and manipulate prey. Ctenidia are absent in these animals.

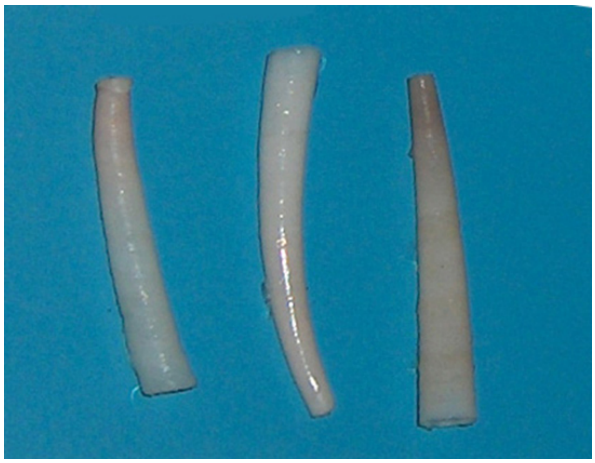
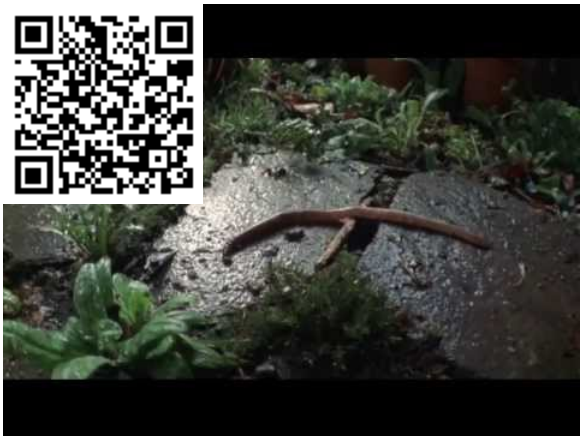


Figure 5.7.4.15: Antalis vulgaris shows the classic Dentaliidae shape that gives these animals their common name of "tusk shell." (credit: Georges Jansoone)

Phylum Annelida

Phylum Annelida includes segmented worms. These animals are found in marine, terrestrial, and freshwater habitats, but a presence of water or humidity is a critical factor for their survival, especially in terrestrial habitats. The name of the phylum is derived from the Latin word *annellus*, which means a small ring. Animals in this phylum show parasitic and commensal symbioses with other species in their habitat. Approximately 16,500 species have been described in phylum Annelida. The phylum includes earthworms, polychaete worms, and leeches. Annelids show protostomic development in embryonic stages and are often called “segmented worms” due to their key characteristic of metamerism, or true segmentation.





Morphology

Annelids display bilateral symmetry and are worm-like in overall morphology. Annelids have a segmented body plan wherein the internal and external morphological features are repeated in each body segment. Metamerism allows animals to become bigger by adding “compartments” while making their movement more efficient. This metamerism is thought to arise from identical teloblast cells in the embryonic stage, which give rise to identical mesodermal structures. The overall body can be divided into head, body, and pygidium (or tail). The clitellum is a reproductive structure that generates mucus that aids in sperm transfer and gives rise to a cocoon within which fertilization occurs; it appears as a fused band in the anterior third of the animal (Figure 5.7.4.16).



Figure 5.7.4.16: The clitellum, seen here as a protruding segment with different coloration than the rest of the body, is a structure that aids in annelid reproduction. (credit: Rob Hille)

Anatomy

The epidermis is protected by an acellular, external cuticle, but this is much thinner than the cuticle found in the ecdysozoans and does not require periodic shedding for growth. Circular as well as longitudinal muscles are located interior to the epidermis. Chitinous hairlike extensions, anchored in the epidermis and projecting from the cuticle, called setae/chaetae are present in every segment. Annelids show the presence of a true coelom, derived from embryonic mesoderm and protostomy. Hence, they are the most advanced worms. A well-developed and complete digestive system is present in earthworms (oligochaetes) with a mouth, muscular pharynx, esophagus, crop, and gizzard being present. The gizzard leads to the intestine and ends in an anal opening. A cross-sectional view of a body segment of an earthworm (a terrestrial type of annelid) is shown in Figure 5.7.4.17; each segment is limited by a membranous septum that divides the coelomic cavity into a series of compartments.

Annelids possess a closed circulatory system of dorsal and ventral blood vessels that run parallel to the alimentary canal as well as capillaries that service individual tissues. In addition, these vessels are connected by transverse loops in every segment. These animals lack a well-developed respiratory system, and gas exchange occurs across the moist body surface. Excretion is facilitated by a pair of metanephridia (a type of primitive “kidney” that consists of a convoluted tubule and an open, ciliated funnel) that is present in every segment towards the ventral side. Annelids show well-developed nervous systems with a nerve ring of fused ganglia present around the pharynx. The nerve cord is ventral in position and bears enlarged nodes or ganglia in each segment.

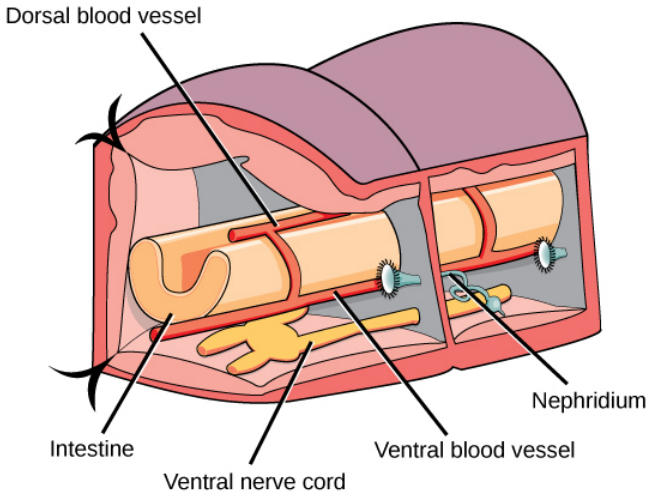


Figure 5.7.4.17: This schematic drawing shows the basic anatomy of annelids in a cross-sectional view.

Annelids may be either monoecious with permanent gonads (as in earthworms and leeches) or dioecious with temporary or seasonal gonads that develop (as in polychaetes). However, cross-fertilization is preferred in hermaphroditic animals. These

animals may also show simultaneous hermaphroditism and participate in simultaneous sperm exchange when they are aligned for copulation.

Classification of Phylum Annelida

Phylum Annelida contains the class Polychaeta (the polychaetes) and the class Oligochaeta (the earthworms, leeches and their relatives).

Earthworms are the most abundant members of the class Oligochaeta, distinguished by the presence of the clitellum as well as few, reduced chaetae ("oligo- = "few"; -chaetae = "hairs"). The number and size of chaetae are greatly diminished in Oligochaeta compared to the polychaetes (*poly*=many, *chaetae* = hairs). The many chetae of polychaetes are also arranged within fleshy, flat, paired appendages that protrude from each segment called parapodia, which may be specialized for different functions in the polychates. The subclass Hirudinea includes leeches such as *Hirudo medicinalis* and *Hemiclepsis marginata*. The class Oligochaeta includes the subclass Hirudinia and the subclass Brachiobdella. A significant difference between leeches and other annelids is the development of suckers at the anterior and posterior ends and a lack of chaetae. Additionally, the segmentation of the body wall may not correspond to the internal segmentation of the coelomic cavity. This adaptation possibly helps the leeches to elongate when they ingest copious quantities of blood from host vertebrates. The subclass Brachiobdella includes species like *Branchiobdella balcanica sketi* and *Branchiobdella astaci*, worms that show similarity with leeches as well as oligochaetes.



(a) (b) (c)

Figure 5.7.4.18: The (a) earthworm, (b) leech, and (c) featherduster are all annelids. (credit a: modification of work by S. Shepherd; credit b: modification of work by "Sarah G..."/Flickr; credit c: modification of work by Chris Gotschalk, NOAA)

Summary

Phylum Annelida includes vermiform, segmented animals. Segmentation is seen in internal anatomy as well, which is called metamerism. Annelids are protostomes. These animals have well-developed neuronal and digestive systems. Some species bear a specialized band of segments known as a clitellum. Annelids show the presence numerous chitinous projections termed chaetae, and polychaetes possess parapodia. Suckers are seen in order Hirudinea. Reproductive strategies include sexual dimorphism, hermaphroditism, and serial hermaphroditism. Internal segmentation is absent in class Hirudinea.

Flatworms are acoelomate, triploblastic animals. They lack circulatory and respiratory systems, and have a rudimentary excretory system. This digestive system is incomplete in most species. There are four traditional classes of flatworms, the largely free-living turbellarians, the ectoparasitic monogeneans, and the endoparasitic trematodes and cestodes. Trematodes have complex lifecycles involving a molluscan secondary host and a primary host in which sexual reproduction takes place. Cestodes, or tapeworms, infect the digestive systems of primary vertebrate hosts.

The rotifers are microscopic, multicellular, mostly aquatic organisms that are currently under taxonomic revision. The group is characterized by the rotating, ciliated, wheel-like structure, the corona, on their head. The mastax or jawed pharynx is another structure unique to this group of organisms.

The nemertini are the simplest eucoelomates. These ribbon-shaped animals bear a specialized proboscis enclosed within a rhynchocoel. The development of a closed circulatory system derived from the coelom is a significant difference seen in this species compared to other pseudocoelomate phyla. Alimentary, nervous, and excretory systems are more developed in the nemertini than in less advanced phyla. Embryonic development of nemertine worms proceeds via a planuliform larval stage.

Phylum Mollusca is a large, marine group of invertebrates. Mollusks show a variety of morphological variations within the phylum. This phylum is also distinct in that some members exhibit a calcareous shell as an external means of protection. Some mollusks have evolved a reduced shell. Mollusks are protostomes. The dorsal epidermis in mollusks is modified to form the mantle, which encloses the mantle cavity and visceral organs. This cavity is quite distinct from the coelomic cavity, which in the adult animal surrounds the heart. Respiration is facilitated by gills known as ctenidia. A chitinous-toothed tongue called the radula is present in most mollusks. Early development in some species occurs via two larval stages: trochophore and veliger. Sexual dimorphism is the predominant sexual strategy in this phylum. Mollusks can be divided into seven classes, each with distinct morphological characteristics.

Glossary

Annelida
phylum of vermiform animals with metamerism

captacula
tentacle-like projection that is present in tusks shells to catch prey

clitellum
specialized band of fused segments, which aids in reproduction

conispiral
shell shape coiled around a horizontal axis

corona
wheel-like structure on the anterior portion of the rotifer that contains cilia and moves food and water toward the mouth

ctenidium
specialized gill structure in mollusks

mantle
(also, pallium) specialized epidermis that encloses all visceral organs and secretes shells

mastax
jawed pharynx unique to the rotifers

metamerism
series of body structures that are similar internally and externally, such as segments

Mollusca
phylum of protostomes with soft bodies and no segmentation

nacre
calcareous secretion produced by bivalves to line the inner side of shells as well as to coat intruding particulate matter

Nemertea
phylum of dorsoventrally flattened protostomes known as ribbon worms

parapodium
fleshy, flat, appendage that protrudes in pairs from each segment of polychaetes

pilidium
larval form found in some nemertine species

planospiral

shell shape coiled around a vertical axis

planuliform
larval form found in phylum Nemertea

radula
tongue-like organ with chitinous ornamentation

rhynchocoel
cavity present above the mouth that houses the proboscis

schizocoelom
coelom formed by groups of cells that split from the endodermal layer

seta/chaeta
chitinous projection from the cuticle

trochophore
first of the two larval stages in mollusks

veliger
second of the two larval stages in mollusks

This page titled 5.7.4: Superphylum Lophotrochozoa is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.3: Superphylum Lophotrochozoa** by OpenStax is licensed CC BY 4.0.

5.7.5: Superphylum Ecdysozoa

Skills to Develop

- Describe the structural organization of nematodes
- Understand the importance of Caenorhabditis elegans in research
- Compare the internal systems and appendage specializations of phylum Arthropoda
- Discuss the environmental importance of arthropods
- Discuss the reasons for arthropod success and abundance

The superphylum Ecdysozoa contains an incredibly large number of species. This is because it contains two of the most diverse animal groups: phylum Nematoda (the roundworms) and Phylum Arthropoda (the arthropods). The most prominant distinguising feature of Ecdysozoans is their tough external covering called the cuticle. The cuticle provides a tough, but flexible exoskeleton tht protects these animals from water loss, predators and other aspects of the external environment. All members of this superphylum periodically molt, or shed their cuticle as they grow. After molting, they secrete a new cuticle that will last until their next growth phase. The process of molting and replacing the cuticle is called ecdysis, which is how the superphylum derived its name.

Phylum Nematoda

The Nematoda, like most other animal phyla, are triploblastic and possess an embryonic mesoderm that is sandwiched between the ectoderm and endoderm. They are also bilaterally symmetrical, meaning that a longitudinal section will divide them into right and left sides that are symmetrical. Furthermore, the nematodes, or roundworms, possess a pseudocoelom and consist of both free-living and parasitic forms.

It has been said that were all the non-nematode matter of the biosphere removed, there would remain a shadow of the former world in the form of **nematodes**.[1] The arthropods, one of the most successful taxonomic groups on the planet, are coelomate organisms characterized by a hard exoskeleton and jointed appendages. Both the nematodes and arthropods belong to the superphylum Ecdysozoa that is believed to be a clade consisting of all evolutionary descendants from one common ancestor. The name derives from the word ecdysis, which refers to the shedding, or molting, of the exoskeleton. The phyla in this group have a hard cuticle that covers their bodies, which must be periodically shed and replaced for them to increase in size.

Phylum Nematoda includes more than 28,000 species with an estimated 16,000 being parasitic in nature. The name Nematoda is derived from the Greek word “Nemos,” which means “thread” and includes roundworms. Nematodes are present in all habitats with a large number of individuals of each species present in each. The free-living nematode, *Caenorhabditis elegans* has been extensively used as a model system in laboratories all over the world.



Morphology

In contrast with cnidarians, nematodes show a tubular morphology and circular cross-section. These animals are pseudocoelomates and show the presence of a complete digestive system with a distinct mouth and anus. This is in contrast with the cnidarians, where

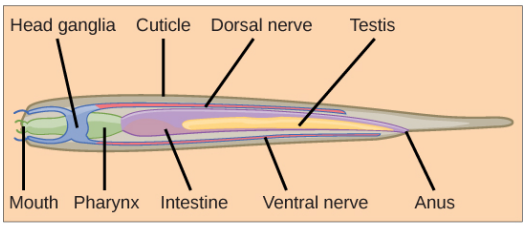
only one opening is present (an incomplete digestive system).

The cuticle of Nematodes is rich in collagen and a carbohydrate-protein polymer called chitin, and forms an external “skeleton” outside the epidermis. The cuticle also lines many of the organs internally, including the pharynx and rectum. The epidermis can be either a single layer of cells or a syncytium, which is a multinucleated cell formed from the fusion of uninucleated cells.

The overall morphology of these worms is cylindrical, as seen in Figure 5.7.5.1. The head is radially symmetrical. A mouth opening is present at the anterior end with three or six lips as well as teeth in some species in the form of cuticle extensions. Some nematodes may present other external modifications like rings, head shields, or warts. Rings, however, do not reflect true internal body segmentation. The mouth leads to a muscular pharynx and intestine, which leads to a rectum and anal opening at the posterior end. The muscles of nematodes differ from those of most animals: They have a longitudinal layer only, which accounts for the whip-like motion of their movement.



(a)



(b)

Figure 5.7.5.1: Scanning electron micrograph shows (a) the soybean cyst nematode (*Heterodera glycines*) and a nematode egg. (b) A schematic representation shows the anatomy of a typical nematode. (credit a: modification of work by USDA ARS; scale-bar data from Matt Russell)

Excretory System

In nematodes, specialized excretory systems are not well developed. Nitrogenous wastes may be lost by diffusion through the entire body or into the pseudocoelom (body cavity), where they are removed by specialized cells. Regulation of water and salt content of the body is achieved by renette glands, present under the pharynx in marine nematodes.

Nervous system

Most nematodes possess four longitudinal nerve cords that run along the length of the body in dorsal, ventral, and lateral positions. The ventral nerve cord is better developed than the dorsal or lateral cords. All nerve cords fuse at the anterior end, around the pharynx, to form head ganglia or the “brain” of the worm (which take the form of a ring around the pharynx) as well as at the posterior end to form the tail ganglia. In *C. elegans*, the nervous system accounts for nearly one-third of the total number of cells in the animal.

Reproduction

Nematodes employ a variety of reproductive strategies that range from monoecious to dioecious to parthenogenic, depending upon the species under consideration. *C. elegans* is a monoecious species and shows development of ova contained in a uterus as well as sperm contained in the spermatheca. The uterus has an external opening known as the vulva. The female genital pore is near the middle of the body, whereas the male's is at the tip. Specialized structures at the tail of the male keep him in place while he deposits sperm with copulatory spicules. Fertilization is internal, and embryonic development starts very soon after fertilization. The embryo is released from the vulva during the gastrulation stage. The embryonic development stage lasts for 14 hours; development then continues through four successive larval stages with ecdysis between each stage—L1, L2, L3, and L4—ultimately leading to the development of a young male or female adult worm. Adverse environmental conditions like overcrowding and lack of food can result in the formation of an intermediate larval stage known as the dauer larva.

Everyday Connection: *C. elegans*: The Model System for Linking Developmental Studies with Genetics

If biologists wanted to research how nicotine dependence develops in the body, how lipids are regulated, or observe the attractant or repellant properties of certain odors, they would clearly need to design three very different experiments. However, they might only need one object of study: *C. elegans*. The nematode *Caenorhabditis elegans* was brought into the focus of mainstream biological research by Dr. Sydney Brenner. Since 1963, Dr. Brenner and scientists worldwide have used this animal as a model system to study various physiological and developmental mechanisms.

C. elegans is a free-living organism found in soil. It is easy to culture this organism on agar plates (10,000 worms/plate), it feeds on *Escherichia coli* (another long-term resident of biological laboratories worldwide), and therefore, it can be readily grown and maintained in a laboratory. The biggest asset of this nematode is its transparency, which helps researchers to observe and monitor changes within the animal with ease. It is also a simple organism with fewer than 1,000 cells and a genome of 20,000 genes. It shows chromosomal organization of DNA into five pairs of autosomes plus a pair of sex chromosomes, making it an ideal candidate to study genetics. Since every cell can be visualized and identified, this organism is useful for studying cellular phenomena like cell-cell interactions, cell-fate determinations, cell division, apoptosis, and intracellular transport.

Another tremendous asset is the short life cycle of this worm (Figure 5.7.5.2). It takes only 3 days to achieve the "egg to adult to daughter egg;" therefore, tracking genetic changes is easier in this animal. The total life span of *C. elegans* is 2 to 3 weeks; hence, age-related phenomena are easy to observe. Another feature that makes *C. elegans* an excellent experimental model system is that the position and number of the 959 cells present in adult hermaphrodites of this organism is constant. This feature is extremely significant when studying cell differentiation, cell-cell communication, and apoptosis. Lastly, *C. elegans* is also amenable to genetic manipulations using molecular methods, rounding off its usefulness as a model system.

Biologists worldwide have created information banks and groups dedicated to research using *C. elegans*. Their findings have led, for example, to better understandings of cell communication during development, neuronal signaling and insight into lipid regulation (which is important in addressing health issues like the development of obesity and diabetes). In recent years, studies have enlightened the medical community with a better understanding of polycystic kidney disease. This simple organism has led biologists to complex and significant findings, growing the field of science in ways that touch the everyday world.

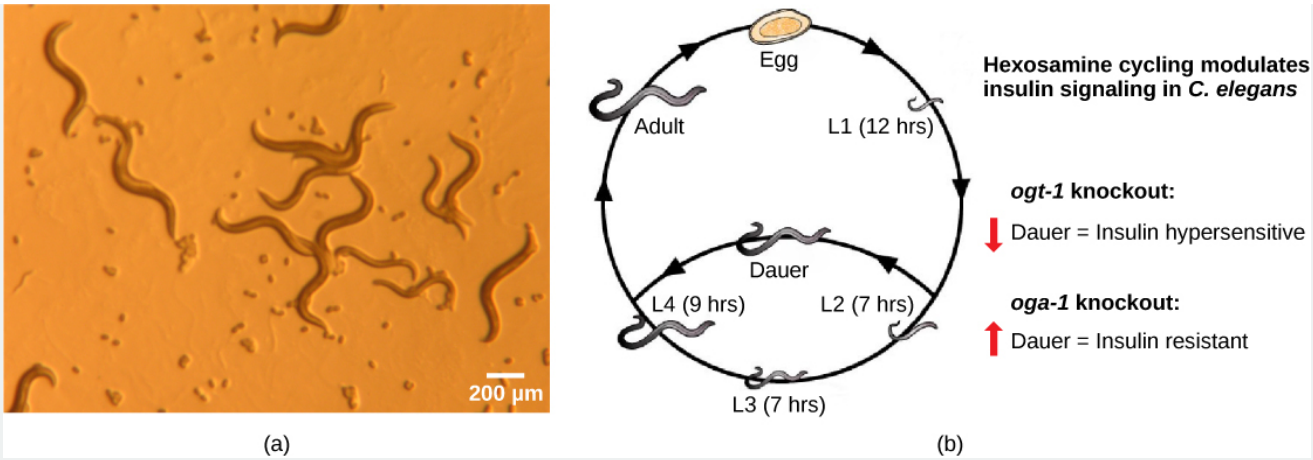
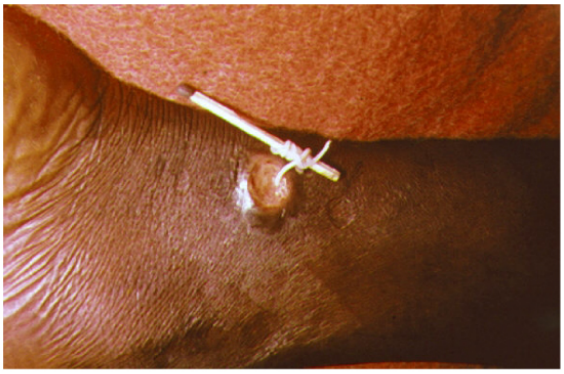


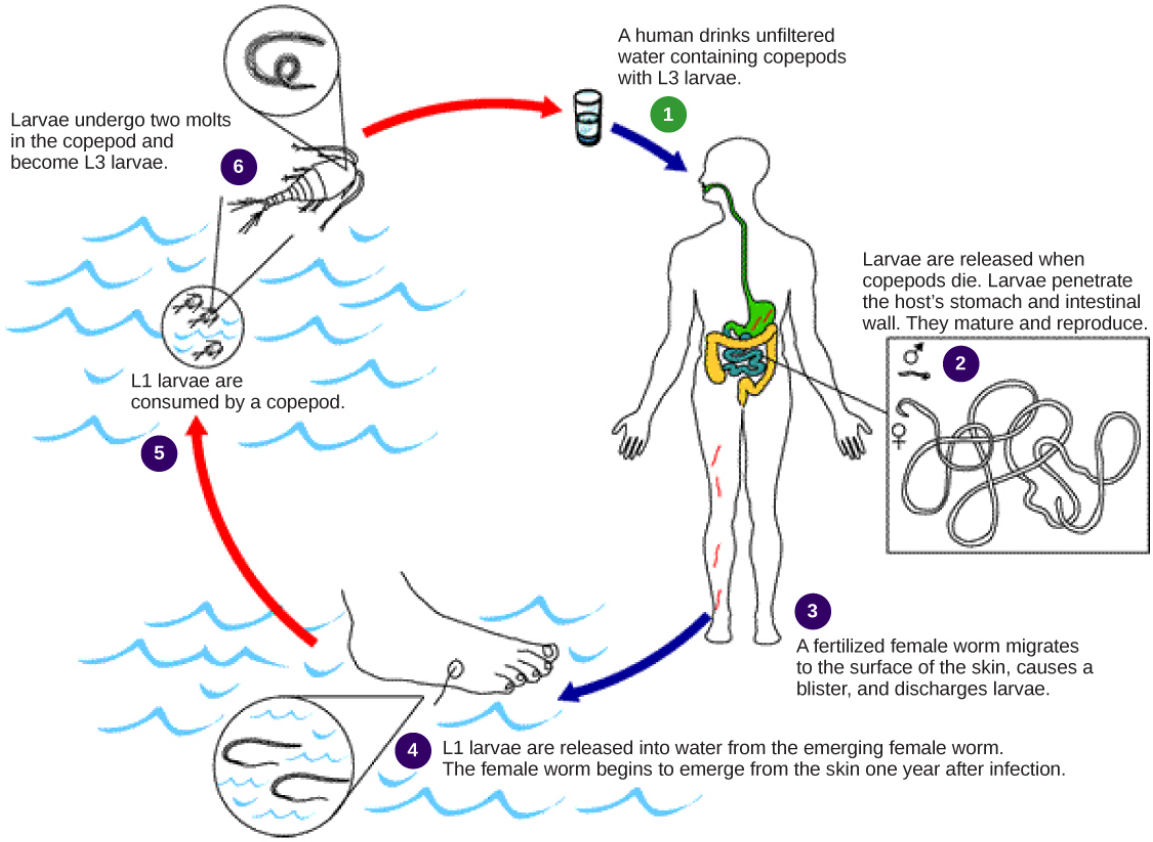
Figure 5.7.5.2: (a) This light micrograph shows *Caenorhabditis elegans*. Its transparent adult stage consists of exactly 959 cells. (b) The life cycle of *C. elegans* has four juvenile stages (L1 through L4) and an adult stage. Under ideal conditions, the nematode spends a set amount of time at each juvenile stage, but under stressful conditions, it may enter a dauer state that does not age. The worm is hermaphroditic in the adult state, and mating of two worms produces a fertilized egg. (credit a: modification of work by "snickclunk"/Flickr: credit b: modification of work by NIDDK, NIH; scale-bar data from Matt Russell)

A number of common parasitic nematodes serve as prime examples of parasitism. These animals exhibit complex lifecycles that involve multiple hosts, and they can have significant medical and veterinary impacts. Humans may become infected by *Dracunculus medinensis*, known as guinea worms, when they drink unfiltered water containing copepods (Figure 5.7.5.3). Hookworms, such as *Ancyclostoma* and *Necator*, infest the intestines and feed on the blood of mammals, especially in dogs, cats, and humans. Trichina worms (*Trichinella*) are the causal organism of trichinosis in humans, often resulting from the consumption of undercooked pork; *Trichinella* can infect other mammalian hosts as well. *Ascaris*, a large intestinal roundworm, steals nutrition from its human host and may create physical blockage of the intestines. The filarial worms, such as *Dirofilaria* and *Wuchereria*, are commonly vectored by mosquitoes, which pass the infective agents among mammals through their blood-sucking activity. *Dirofilaria immitis*, a blood-infective parasite, is the notorious dog heartworm species. *Wuchereria bancrofti* infects the lymph nodes of humans, resulting in the non-lethal but deforming condition called elephantiasis, in which parts of the body become swelled to gigantic proportions due to obstruction of lymphatic drainage and inflammation of lymphatic tissues.





(a)



(b)

Figure 5.7.5.3: The guinea worm *Dracunculus medinensis* infects about 3.5 million people annually, mostly in Africa. (a) Here, the worm is wrapped around a stick so it can be extracted. (b) Infection occurs when people consume water contaminated by infected copepods, but this can easily be prevented by simple filtration systems. (credit: modification of work by CDC)

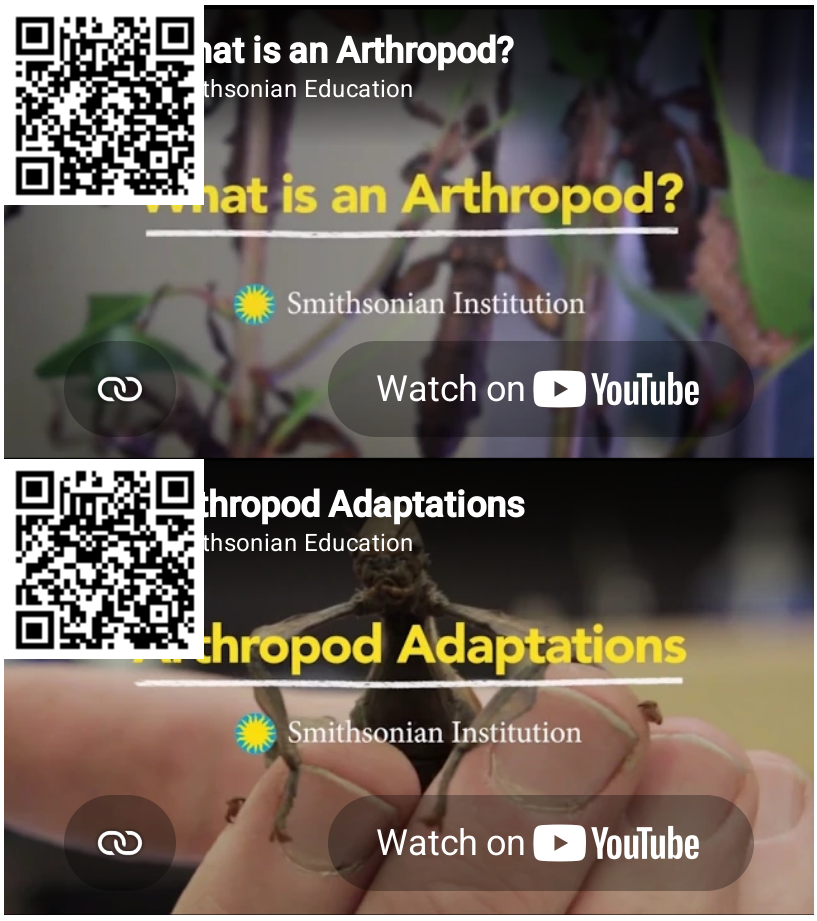
Phylum Arthropoda

The name "arthropoda" means "jointed legs" (in the Greek, "arthros" means "joint" and "podos" means "leg"); it aptly describes the enormous number of invertebrates included in this phylum. Arthropoda dominate the animal kingdom with an estimated 85 percent of known species included in this phylum and many arthropods yet undocumented. The principal characteristics of all the animals in this phylum are functional segmentation of the body and presence of jointed appendages. Arthropods also show the presence of an exoskeleton made principally of chitin, which is a waterproof, tough polysaccharide. Phylum Arthropoda is the largest phylum in the animal world, and insects form the single largest class within this phylum. Arthropods are eucoelomate, protostomic organisms.

Phylum Arthropoda includes animals that have been successful in colonizing terrestrial, aquatic, and aerial habitats. This phylum is further classified into five subphyla: Trilobitomorpha (trilobites, all extinct), Hexapoda (insects and relatives), Myriapoda (millipedes, centipedes, and relatives), Crustaceans (crabs, lobsters, crayfish, isopods, barnacles, and some zooplankton), and Chelicerata (horseshoe crabs, arachnids, scorpions, and daddy longlegs). Trilobites are an extinct group of arthropods found chiefly in the pre-Cambrian Era that are probably most closely related to the Chelicerata. These are identified based on fossil records (Figure 5.7.5.4).



Figure 5.7.5.4: Trilobites, like the one in this fossil, are an extinct group of arthropods. (credit: Kevin Walsh)



Morphology

A unique feature of animals in the arthropod phylum is the presence of a segmented body and fusion of sets of segments that give rise to functional body regions called tagma. Tagma may be in the form of a head, thorax, and abdomen, or a cephalothorax and abdomen, or a head and trunk. A central cavity, called the hemocoel (or blood cavity), is present, and the open circulatory system is regulated by a tubular or single-chambered heart. Respiratory systems vary depending on the group of arthropod: insects and

myriapods use a series of tubes (tracheae) that branch through the body, open to the outside through openings called spiracles, and perform gas exchange directly between the cells and air in the tracheae, whereas aquatic crustaceans utilize gills, terrestrial chelicerates employ book lungs, and aquatic chelicerates use book gills (Figure 5.7.5.5). The book lungs of arachnids (scorpions, spiders, ticks and mites) contain a vertical stack of hemocoel wall tissue that somewhat resembles the pages of a book. Between each of the "pages" of tissue is an air space. This allows both sides of the tissue to be in contact with the air at all times, greatly increasing the efficiency of gas exchange. The gills of crustaceans are filamentous structures that exchange gases with the surrounding water. Groups of arthropods also differ in the organs used for excretion, with crustaceans possessing green glands and insects using Malpighian tubules, which work in conjunction with the hindgut to reabsorb water while ridding the body of nitrogenous waste. The cuticle is the covering of an arthropod. It is made up of two layers: the epicuticle, which is a thin, waxy water-resistant outer layer containing no chitin, and the layer beneath it, the chitinous procuticle. Chitin is a tough, flexible polysaccharide. In order to grow, the arthropod must shed the exoskeleton during a process called ecdysis (“to strip off”); this is a cumbersome method of growth, and during this time, the animal is vulnerable to predation. The characteristic morphology of representative animals from each subphylum is described below.

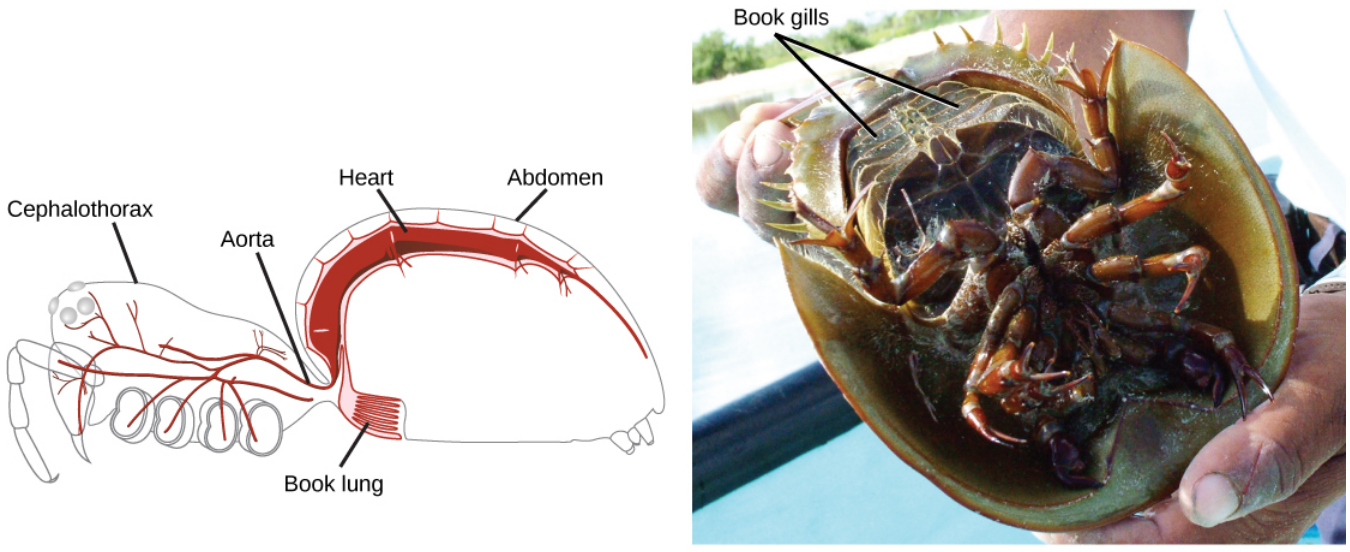


Figure 5.7.5.5: The book lungs of (a) arachnids are made up of alternating air pockets and hemocoel tissue shaped like a stack of books. The book gills of (b) crustaceans are similar to book lungs but are external so that gas exchange can occur with the surrounding water. (credit a: modification of work by Ryan Wilson based on original work by John Henry Comstock; credit b: modification of work by Angel Schatz)

Subphylum Hexapoda

The name Hexapoda denotes the presence of six legs (three pairs) in these animals as differentiated from the number of pairs present in other arthropods. Hexapods are characterized by the presence of a head, thorax, and abdomen, constituting three tagma. The thorax bears the wings as well as six legs in three pairs. Many of the common insects we encounter on a daily basis—including ants, cockroaches, butterflies, and flies—are examples of Hexapoda.

Amongst the hexapods, the insects (Figure 5.7.5.6) are the largest class in terms of species diversity as well as biomass in terrestrial habitats. Typically, the head bears one pair of sensory antennae, mandibles as mouthparts, a pair of compound eyes, and some ocelli (simple eyes) along with numerous sensory hairs. The thorax bears three pairs of legs (one pair per segment) and two pairs of wings, with one pair each on the second and third thoracic segments. The abdomen usually has eleven segments and bears reproductive apertures. Hexapoda includes insects that are winged (like fruit flies) and wingless (like fleas).



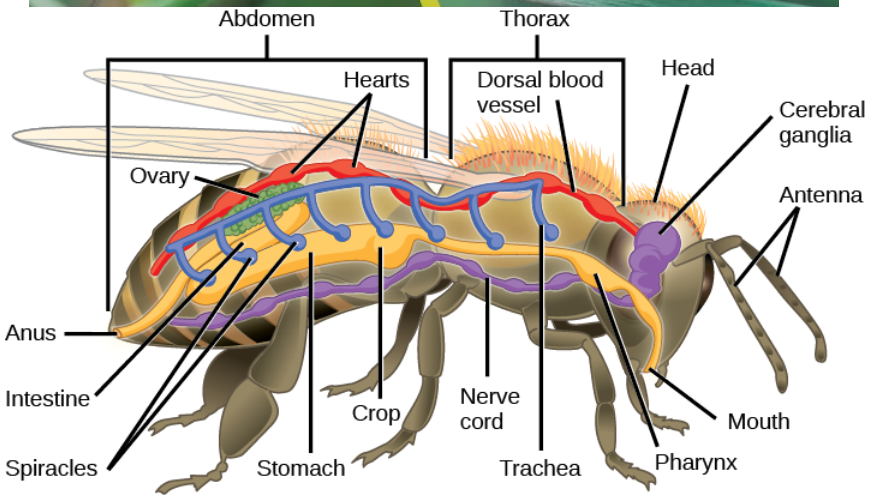


Figure 5.7.5.6: In this basic anatomy of a hexapod insect, note that insects have a developed digestive system (yellow), a respiratory system (blue), a circulatory system (red), and a nervous system (red).

? Exercise 5.7.5.1

Which of the following statements about insects is false?

a. Insects have both dorsal and ventral blood vessels.
b. Insects have spiracles, openings that allow air to enter.
c. The trachea is part of the digestive system.
d. Insects have a developed digestive system with a mouth, crop, and intestine.

Answer

c

Subphylum Myriapoda

Subphylum Myriapoda includes arthropods with numerous legs. Although the name is hyperbolic in suggesting that myriad legs are present in these invertebrates, the number of legs may vary from 10 to 750. This subphylum includes 13,000 species; the most commonly found examples are millipedes and centipedes. All myriapods are terrestrial animals and prefer a humid environment.

Myriapods are typically found in moist soils, decaying biological material, and leaf litter. Subphylum Myriapoda is divided into four classes: Chilopoda, Symphyla, Diplopoda, and Pauropoda. Centipedes like *Scutigera coleoptrata* (Figure 28.4.7) are classified as chilopods. These animals bear one pair of legs per segment, mandibles as mouthparts, and are somewhat dorsoventrally flattened. The legs in the first segment are modified to form forcipules (poison claws) that deliver poison to prey like spiders and cockroaches, as these animals are all predatory. Millipedes bear two pairs of legs per diplosegment, a feature that results from

embryonic fusion of adjacent pairs of body segments, are usually rounder in cross-section, and are herbivores or detritivores. Millipedes have visibly more numbers of legs as compared to centipedes, although they do not bear a thousand legs (Figure 5.7.5.7).

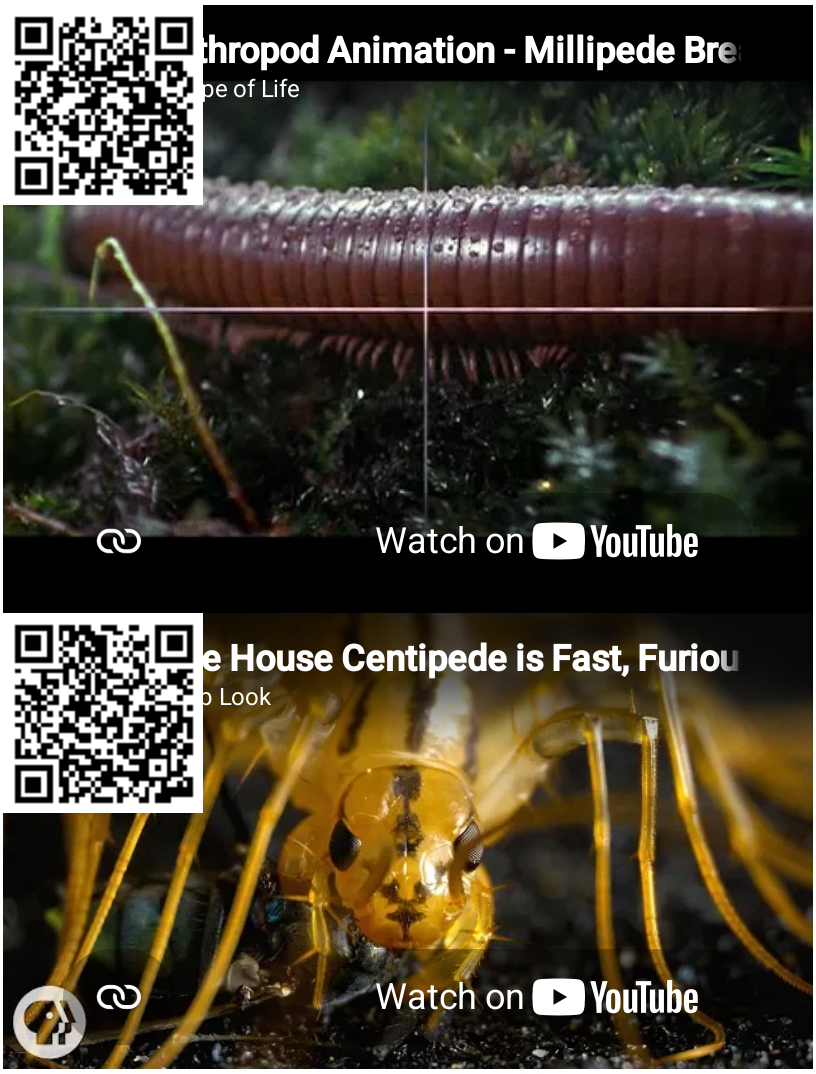
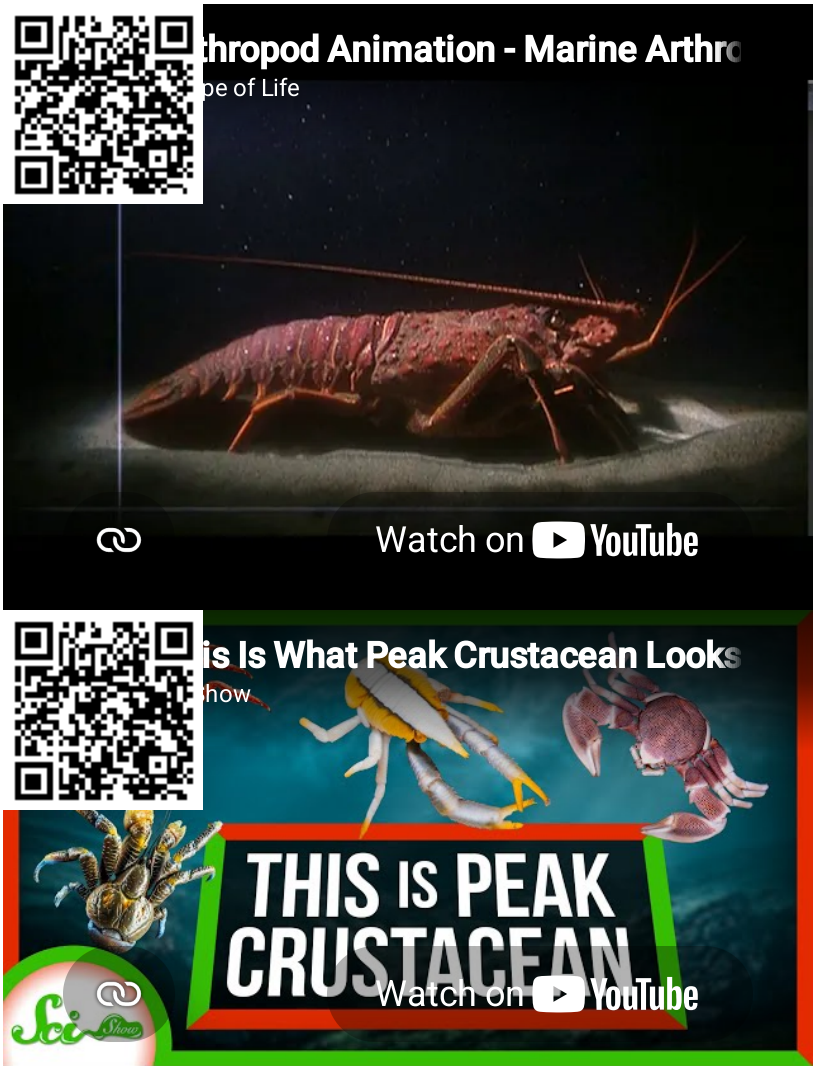




Figure 5.7.5.7: (a) The *Scutigera coleoptrata* centipede has up to 15 pairs of legs. (b) This North American millipede (*Narceus americanus*) bears many legs, although not a thousand, as its name might suggest. (credit a: modification of work by Bruce Marlin; credit b: modification of work by Cory Zanker)

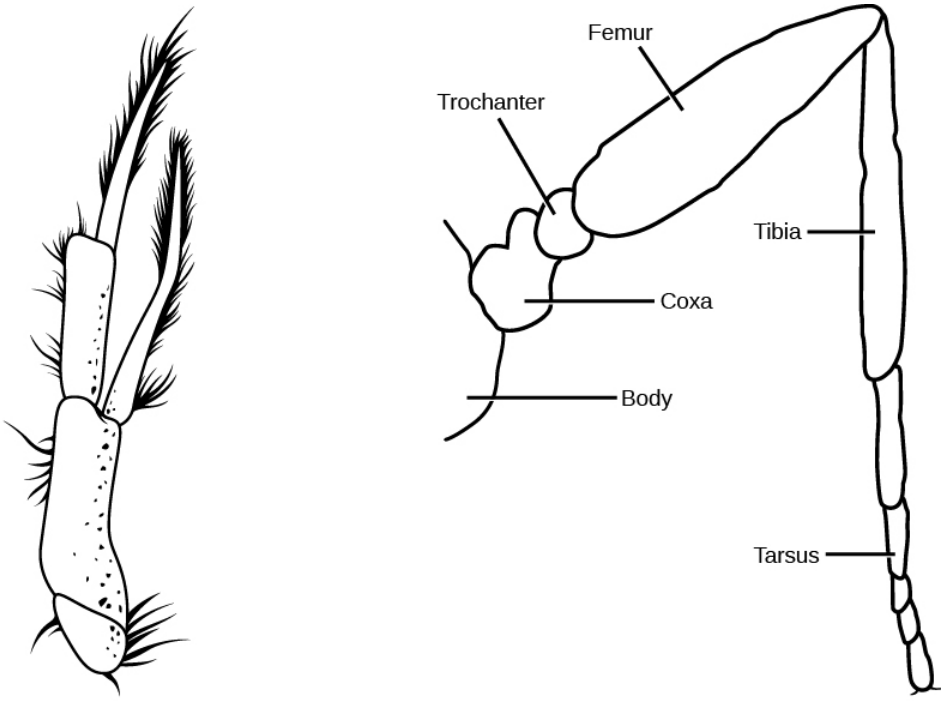


Crustaceans are the most dominant aquatic arthropods, since the total number of marine crustacean species stands at 67,000, but there are also freshwater and terrestrial crustacean species. Krill, shrimp, lobsters, crabs, and crayfish are examples of crustaceans (Figure 5.7.5.8). Terrestrial species like the wood lice (*Armadillidium* spp.) (also called pill bugs, rolly pollies, potato bugs, or isopods) are also crustaceans, although the number of non-aquatic species in this subphylum is relatively low.



Figure 5.7.5.8: The (a) crab and (b) shrimp krill are both crustaceans. (credit a: modification of work by William Warby; credit b: modification of work by Jon Sullivan)

Crustaceans possess two pairs of antennae, mandibles as mouthparts, and biramous ("two branched") appendages, which means that their legs are formed in two parts, as distinct from the uniramous ("one branched") myriapods and hexapods (Figure 5.7.5.9).



(a) Biramous appendage (crayfish leg) (b) Uniramous appendage (insect leg)

Figure 5.7.5.9: Arthropods may have (a) biramous (two-branched) appendages or (b) uniramous (one-branched) appendages. (credit b: modification of work by Nicholas W. Beeson)

Unlike that of the Hexapoda, the head and thorax of most crustaceans is fused to form a cephalothorax (Figure 5.7.5.10), which is covered by a plate called the carapace, thus producing a body structure of two tagma. Crustaceans have a chitinous exoskeleton that is shed by molting whenever the animal increases in size. The exoskeletons of many species are also infused with calcium carbonate, which makes them even stronger than in other arthropods. Crustaceans have an open circulatory system where blood is pumped into the hemocoel by the dorsally located heart. Hemocyanin and hemoglobin are the respiratory pigments present in these animals.

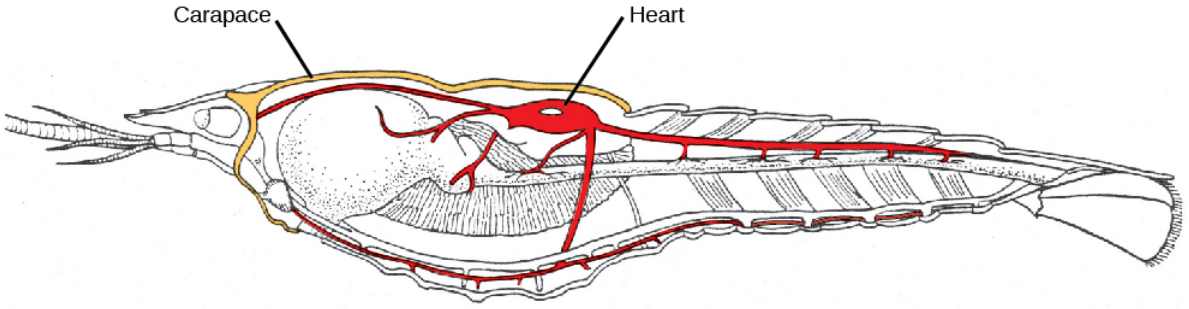
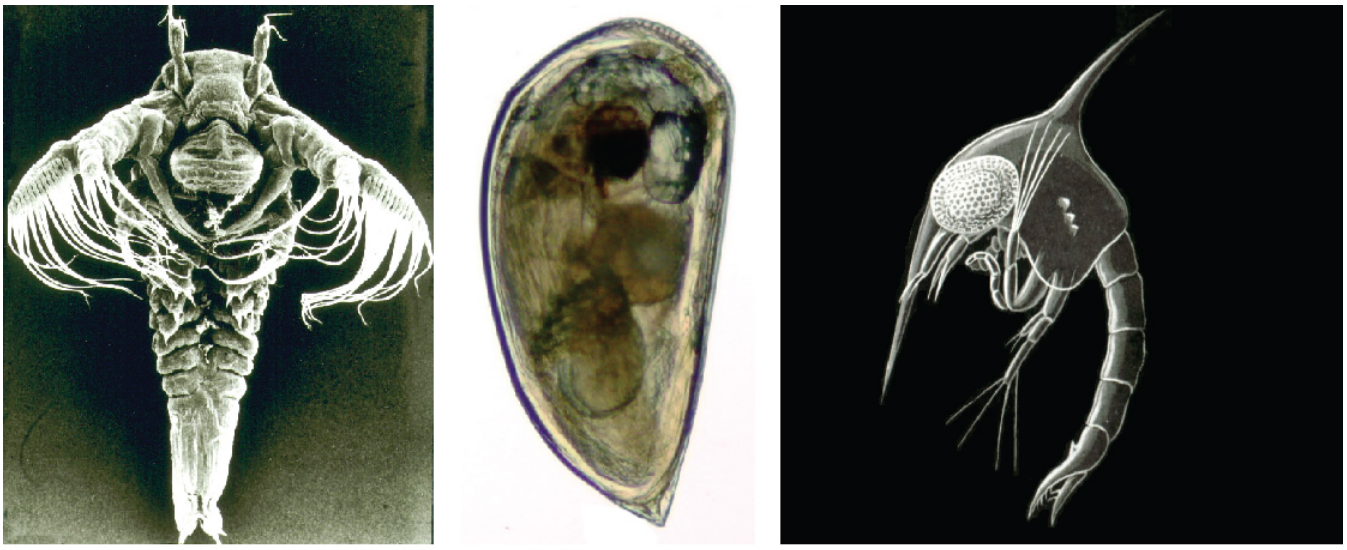


Figure 5.7.5.10: The crayfish is an example of a crustacean. It has a carapace around the cephalothorax and the heart in the dorsal thorax area. (credit: Jane Whitney)

Most crustaceans are dioecious, which means that the sexes are separate. Some species like barnacles may be hermaphrodites. Serial hermaphroditism, where the gonad can switch from producing sperm to ova, may also be seen in some species. Fertilized eggs may be held within the female of the species or may be released in the water. Terrestrial crustaceans seek out damp spaces in their habitats to lay eggs.

Larval stages—nauplius and zoea—are seen in the early development of crustaceans. A cypris larva is also seen in the early development of barnacles (Figure 5.7.5.11).



(a) Nauplius larva of a tadpole shrimp (b) Cypris larva of a barnacle (c) Zoea larva of a green crab

Figure 5.7.5.11: All crustaceans go through different larval stages. Shown are (a) the nauplius larval stage of a tadpole shrimp, (b) the cypris larval stage of a barnacle, and (c) the zoea larval stage of a green crab. (credit a: modification of work by USGS; credit b: modification of work by Mª. C. Mingorance Rodríguez; credit c: modification of work by B. Kimmel based on original work by Ernst Haeckel)

Crustaceans possess a tripartite brain and two compound eyes. Most crustaceans are carnivorous, but herbivorous and detritivorous species are also known. Crustaceans may also be cannibalistic when extremely high populations of these organisms are present.

Subphylum Chelicerata

This subphylum includes animals such as spiders, scorpions, horseshoe crabs, and sea spiders. This subphylum is predominantly terrestrial, although some marine species also exist. An estimated 77,000 species are included in subphylum Chelicerata. Chelicerates are found in almost all habitats.



The body of chelicerates may be divided into two parts: prosoma and opisthosoma, which are basically the equivalents of cephalothorax (usually smaller) and abdomen (usually larger). A “head” tagmum is not usually discernible. The phylum derives its name from the first pair of appendages: the chelicerae (Figure 5.7.5.12), which are specialized, claw-like or fang-like mouthparts. These animals do not possess antennae. The second pair of appendages is known as pedipalps. In some species, like sea spiders, an additional pair of appendages, called ovigers, is present between the chelicerae and pedipalps.



Figure 5.7.5.12: The chelicerae (first set of appendages) are well developed in the scorpion. (credit: Kevin Walsh)

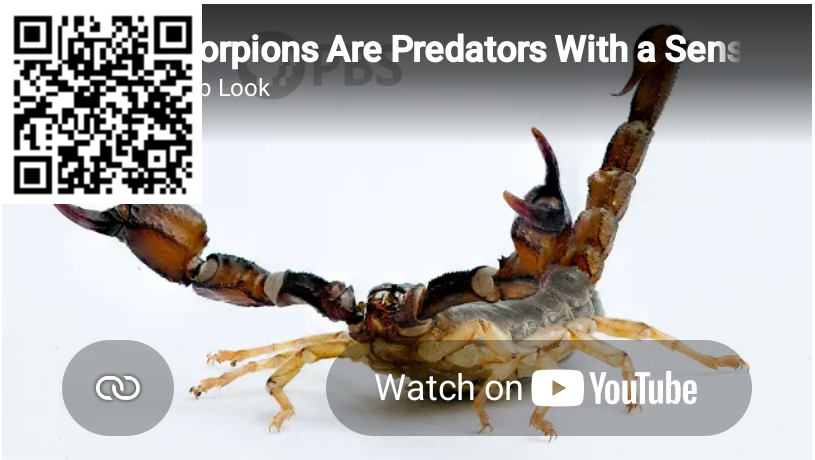
Chelicerae are mostly used for feeding, but in spiders, these are often modified into fangs that inject venom into their prey before feeding (Figure 5.7.5.13). Members of this subphylum have an open circulatory system with a heart that pumps blood into the hemocoel. Aquatic species have gills, whereas terrestrial species have either trachea or book lungs for gaseous exchange.



Figure 5.7.5.13: The trapdoor spider, like all spiders, is a member of the subphylum Chelicerata. (credit: Marshal Hedin)

Most chelicerates ingest food using a preoral cavity formed by the chelicerae and pedipalps. Some chelicerates may secrete digestive enzymes to pre-digest food before ingesting it. Parasitic chelicerates like ticks and mites have evolved blood-sucking apparatuses.

The nervous system in chelicerates consists of a brain and two ventral nerve cords. These animals use external fertilization as well as internal fertilization strategies for reproduction, depending upon the species and its habitat. Parental care for the young ranges from absolutely none to relatively prolonged care.



Summary

Nematodes are pseudocoelomate animals akin to flatworms, yet display more advanced neuronal development, a complete digestive system, and a body cavity. This phylum includes free-living as well as parasitic organisms like *Caenorhabditis elegans* and *Ascaris* spp., respectively. They include dioeceous as well as hermaphroditic species. Nematodes also possess an excretory system that is not quite well developed. Embryonic development is external and proceeds via three larval stages. A peculiar feature of nematodes is the secretion of a collagenous/chitinous cuticle outside the body.

Arthropods represent the most successful phylum of animal on Earth, in terms of the number of species as well as the number of individuals. These animals are characterized by a segmented body as well as the presence of jointed appendages. In the basic body plan, a pair of appendages is present per body segment. Within the phylum, traditional classification is based on mouthparts, number of appendages, and modifications of appendages present. Arthropods bear a chitinous exoskeleton. Gills, trachea, and book lungs facilitate respiration. Sexual dimorphism is seen in this phylum, and embryonic development includes multiple larval stages.

Footnotes

1. 1 Stoll, N. R., “This wormy world. 1947,” *Journal of Parasitology* 85(3) (1999): 392-396.

Glossary

Arthropoda
phylum of animals with jointed appendages

biramous
referring to two branches per appendage

cephalothorax
fused head and thorax in some species

chelicera
modified first pair of appendages in subphylum Chelicerata

cuticle (animal)
the tough, external layer possessed by members of the invertebrate class Ecdysozoa that is periodically molted and replaced

cypris
larval stage in the early development of crustaceans

hemocoel
internal body cavity seen in arthropods

hermaphrodite
referring to an animal where both male and female gonads are present in the same individual

nauplius
larval stage in the early development of crustaceans

Nematoda
phylum of worm-like animals that are triploblastic, pseudocoelomates that can be free-living or parasitic

oviger
additional pair of appendages present on some arthropods between the chelicerae and pedipalps

pedipalp
second pair of appendages in Chelicerata

uniramous

referring to one branch per appendage

zoea

larval stage in the early development of crustaceans

This page titled 5.7.5: Superphylum Ecdysozoa is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.4: Superphylum Ecdysozoa** by OpenStax is licensed CC BY 4.0.

5.7.6: Superphylum Deuterostomia

Skills to Develop

- Describe the distinguishing characteristics of echinoderms
- Describe the distinguishing characteristics of chordates

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning “mouth second,” indicating that the anus is the first to develop. There are a series of other developmental characteristics that differ between protostomes and deuterostomes, including the mode of formation of the coelom and the early cell division of the embryo. In deuterostomes, internal pockets of the endodermal lining called the archenteron fuse to form the coelom. The endodermal lining of the archenteron (or the primitive gut) forms membrane protrusions that bud off and become the mesodermal layer. These buds, known as coelomic pouches, fuse to form the coelomic cavity, as they eventually separate from the endodermal layer. The resultant coelom is termed an enterocoelom. The archenteron develops into the alimentary canal, and a mouth opening is formed by invagination of ectoderm at the pole opposite the blastopore of the gastrula. The blastopore forms the anus of the alimentary system in the juvenile and adult forms. The fates of embryonic cells in deuterostomes can be altered if they are experimentally moved to a different location in the embryo due to indeterminant cleavage in early embryogenesis.

Phylum Echinodermata

Echinodermata are so named owing to their spiny skin (from the Greek “echinos” meaning “spiny” and “dermos” meaning “skin”), and this phylum is a collection of about 7,000 described living species. Echinodermata are exclusively marine organisms. Sea stars (Figure 5.7.6.1), sea cucumbers, sea urchins, sand dollars, and brittle stars are all examples of echinoderms. To date, no freshwater or terrestrial echinoderms are known.

Morphology and Anatomy

Adult echinoderms exhibit pentaradial symmetry and have a calcareous endoskeleton made of ossicles, although the early larval stages of all echinoderms have bilateral symmetry. The endoskeleton is developed by epidermal cells and may possess pigment cells, giving vivid colors to these animals, as well as cells laden with toxins. Gonads are present in each arm. In echinoderms like sea stars, every arm bears two rows of tube feet on the oral side. These tube feet help in attachment to the substratum. These animals possess a true coelom that is modified into a unique circulatory system called a water vascular system. An interesting feature of these animals is their power to regenerate, even when over 75 percent of their body mass is lost.

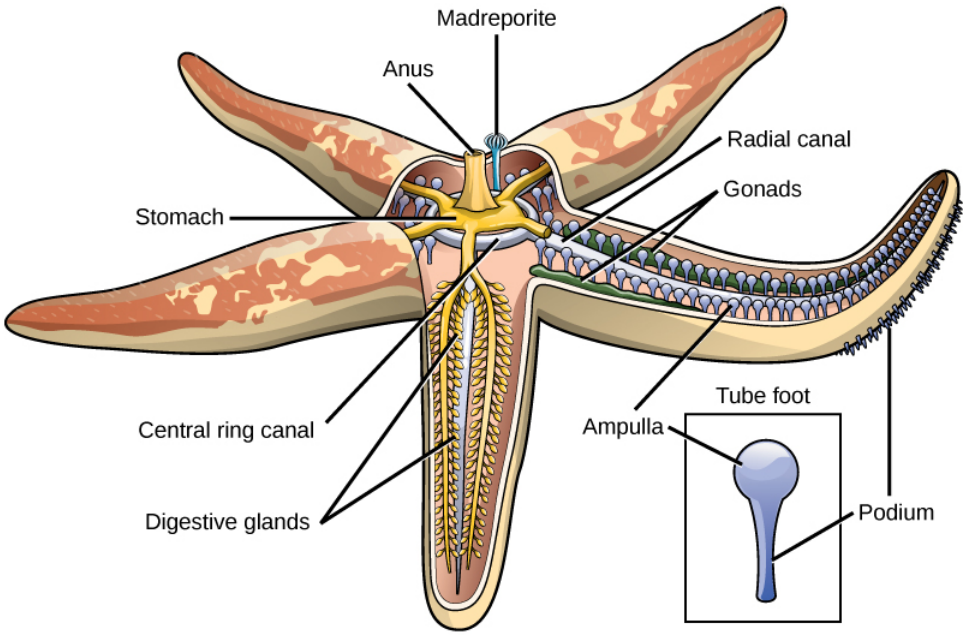


Figure 5.7.6.1: This diagram shows the anatomy of a sea star.

Water Vascular System

Echinoderms possess a unique ambulacral or water vascular system, consisting of a central ring canal and radial canals that extend along each arm. Water circulates through these structures and facilitates gaseous exchange as well as nutrition, predation, and locomotion. The water vascular system also projects from holes in the skeleton in the form of tube feet. These tube feet can expand or contract based on the volume of water present in the system of that arm. By using hydrostatic pressure, the animal can either protrude or retract the tube feet. Water enters the madreporite on the aboral side of the echinoderm. From there, it passes into the stone canal, which moves water into the ring canal. The ring canal connects the radial canals (there are five in a pentaradial animal), and the radial canals move water into the ampullae, which have tube feet through which the water moves. By moving water through the unique water vascular system, the echinoderm can move and force open mollusk shells during feeding.

Nervous System

The nervous system in these animals is a relatively simple structure with a nerve ring at the center and five radial nerves extending outward along the arms. Structures analogous to a brain or derived from fusion of ganglia are not present in these animals.

Excretory System

Podocytes, cells specialized for ultrafiltration of bodily fluids, are present near the center of echinoderms. These podocytes are connected by an internal system of canals to an opening called the madreporite.

Reproduction

Echinoderms are sexually dimorphic and release their eggs and sperm cells into water; fertilization is external. In some species, the larvae divide asexually and multiply before they reach sexual maturity. Echinoderms may also reproduce asexually, as well as regenerate body parts lost in trauma.


Sea Urchins Pull Themselves Inside Out to be Reb
Deep Look
Watch on YouTube




Echinoderm Animation - Sea Star Body Plan
Shape of Life
Watch on YouTube



Classes of Echinoderms

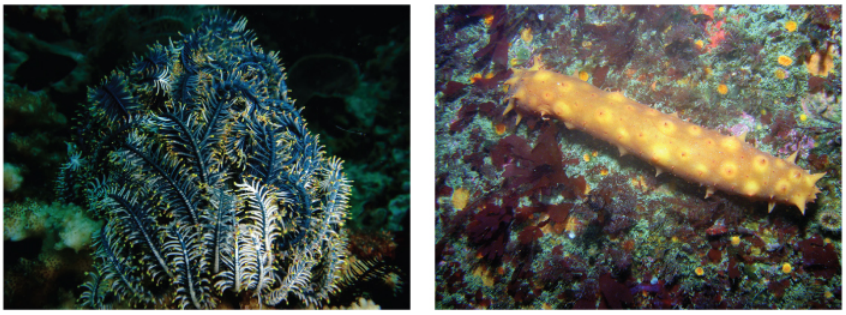
This phylum is divided into five extant classes: Asteroidea (sea stars), Ophiuroidea (brittle stars), Echinoidea (sea urchins and sand dollars), Crinoidea (sea lilies or feather stars), and Holothuroidea (sea cucumbers) (Figure 5.7.6.2).

The most well-known echinoderms are members of class Asteroidea, or sea stars. They come in a large variety of shapes, colors, and sizes, with more than 1,800 species known so far. The key characteristic of sea stars that distinguishes them from other echinoderm classes includes thick arms (ambulacra) that extend from a central disk where organs penetrate into the arms. Sea stars use their tube feet not only for gripping surfaces but also for grasping prey. Sea stars have two stomachs, one of which can protrude through their mouths and secrete digestive juices into or onto prey, even before ingestion. This process can essentially liquefy the prey and make digestion easier.

Brittle stars belong to the class Ophiuroidea. Unlike sea stars, which have plump arms, brittle stars have long, thin arms that are sharply demarcated from the central disk. Brittle stars move by lashing out their arms or wrapping them around objects and pulling themselves forward. Sea urchins and sand dollars are examples of Echinoidea. These echinoderms do not have arms, but are hemispherical or flattened with five rows of tube feet that help them in slow movement; tube feet are extruded through pores of a continuous internal shell called a test. Sea lilies and feather stars are examples of Crinoidea. Both of these species are suspension feeders. Sea cucumbers of class Holothuroidea are extended in the oral-aboral axis and have five rows of tube feet. These are the only echinoderms that demonstrate “functional” bilateral symmetry as adults, because the uniquely extended oral-aboral axis compels the animal to lie horizontally rather than stand vertically.



(a) (b) (c)



(d) (e)

Figure 5.7.6.2: Different members of Echinodermata include the (a) sea star of class Asteroidea, (b) the brittle star of class Ophiuroidea, (c) the sea urchins of class Echinoidea, (d) the sea lilies belonging to class Crinoidea, and (e) sea cucumbers, representing class Holothuroidea. (credit a: modification of work by Adrian Pingstone; credit b: modification of work by Joshua Ganderson; credit c: modification of work by Samuel Chow; credit d: modification of work by Sarah Depper; credit e: modification of work by Ed Bierman)



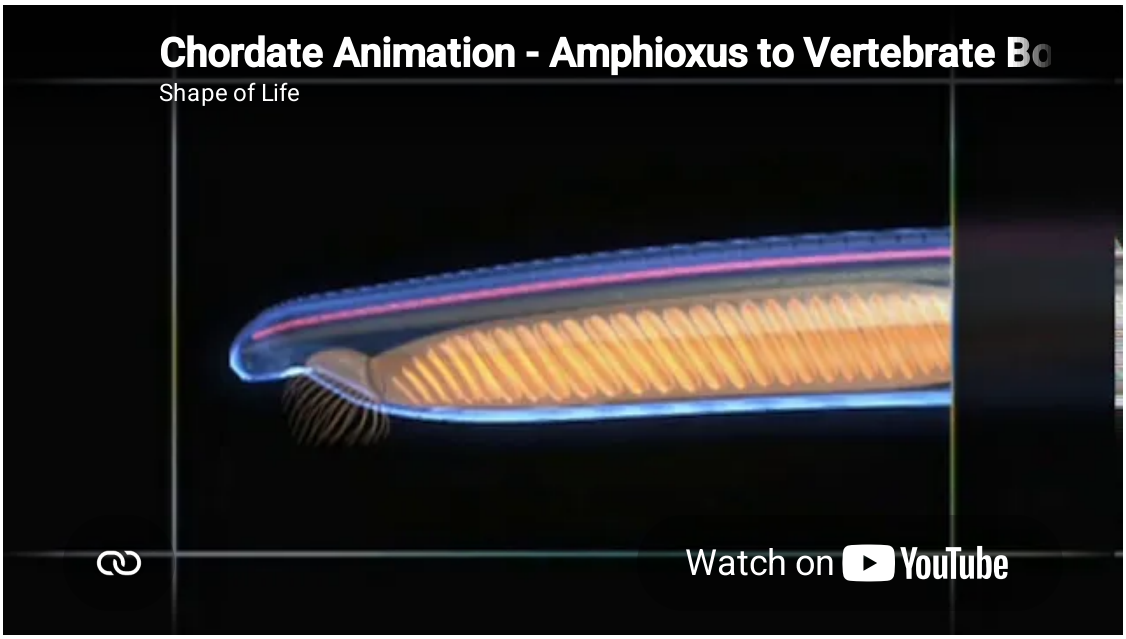


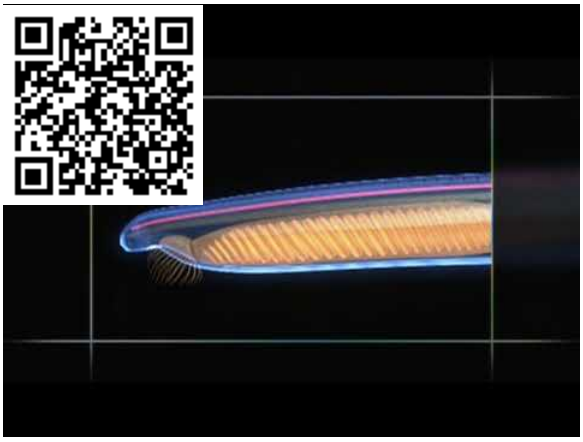


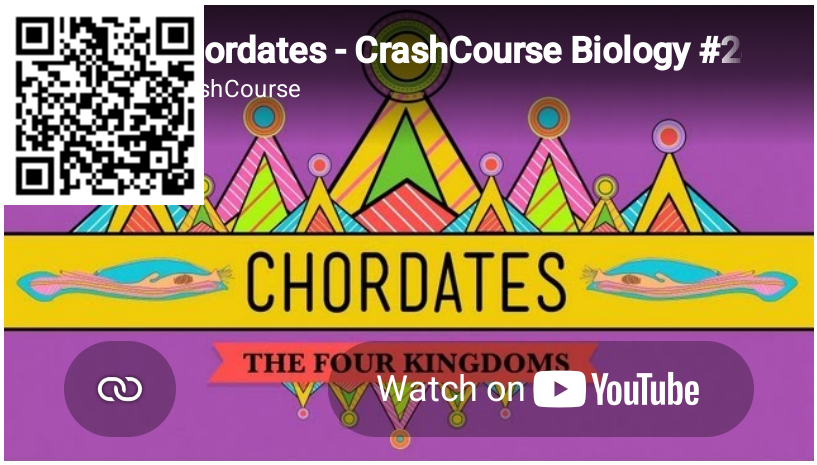


Phylum Chordata

Animals in the phylum Chordata share four key features that appear at some stage of their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. In some groups, some of these traits are present only during embryonic development. In addition to containing vertebrate classes, the phylum Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets). Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.







Summary

Echinoderms are deuterostomic marine organisms. This phylum of animals bears a calcareous endoskeleton composed of ossicles. These animals also have spiny skin. Echinoderms possess water-based circulatory systems. A pore termed the madreporite is the point of entry and exit for water into the water vascular system. Osmoregulation is carried out by specialized cells known as podocytes.

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms.

Glossary

archenteron
: primitive gut cavity within the gastrula that opens outwards via the blastopore

Chordata
: phylum of animals distinguished by their possession of a notochord, a dorsal, hollow nerve cord, pharyngeal slits, and a post-anal tail at some point in their development

Echinodermata
: phylum of deuterostomes with spiny skin; exclusively marine organisms

enterocoelom
: coelom formed by fusion of coelomic pouches budded from the endodermal lining of the archenteron

madreporite
: pore for regulating entry and exit of water into the water vascular system

water vascular system
: system in echinoderms where water is the circulatory fluid

This page titled 5.7.6: Superphylum Deuterostomia is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.5: Superphylum Deuterostomia** by OpenStax is licensed CC BY 4.0.

5.7.E: Invertebrates (Exercises)

28.1: Phylum Porifera

The simplest of all the invertebrates are the Parazoans, which include only the phylum Porifera: the sponges. Parazoans (“beside animals”) do not display tissue-level organization, although they do have specialized cells that perform specific functions. Sponge larvae are able to swim; however, adults are non-motile and spend their life attached to a substratum.

Review Questions

Mesohyl contains:

A. a polysaccharide gel and dead cells
B. a collagen-like gel and suspended cells for various functions
C. spicules composed of silica or calcium carbonate
D. multiple pores

Answer

B

The large central opening in the Parazoan body is called the:

A. gemmule
B. spicule
C. ostia
D. osculum

Answer

D

Cnidocytes are found in _____.

A. phylum Porifera
B. phylum Nemertea
C. phylum Nematoda
D. phylum Cnidaria

Answer

D

Cubozoans are _____.

A. polyps
B. medusoids
C. polymorphs
D. sponges

Answer

C

Free Response

Describe the different cell types and their functions in sponges.

Answer

Pinacocytes are epithelial-like cells, form the outermost layer of sponges, and enclose a jelly-like substance called mesohyl. In some sponges, porocytes form ostia, single tube-shaped cells that act as valves to regulate the flow of water into the spongocoel. Choanocytes ("collar cells") are present at various locations, depending on the type of sponge, but they always line some space through which water flows and are used in feeding.

Describe the feeding mechanism of sponges and identify how it is different from other animals.

Answer

The sponges draw water carrying food particles into the spongocoel using the beating of flagella on the choanocytes. The food particles are caught by the collar of the choanocyte and are brought into the cell by phagocytosis. Digestion of the food particle takes place inside the cell. The difference between this and the mechanisms of other animals is that digestion takes place within cells rather than outside of cells. It means that the organism can feed only on particles smaller than the cells themselves.

Explain the function of nematocysts in cnidarians.

Answer

Nematocysts are "stinging cells" designed to paralyze prey. The nematocysts contain a neurotoxin that renders prey immobile.

Compare the structural differences between Porifera and Cnidaria.

Answer

Poriferans do not possess true tissues, while cnidarians do have tissues. Because of this difference, poriferans do not have a nervous system or muscles for locomotion, which cnidarians have.

28.2: Phylum Cnidaria

Phylum Cnidaria includes animals that show radial or biradial symmetry and are diploblastic, that is, they develop from two embryonic layers. Nearly all (about 99 percent) cnidarians are marine species. Cnidarians contain specialized cells known as cnidocytes ("stinging cells") containing organelles called nematocysts (stingers). These cells are present around the mouth and tentacles, and serve to immobilize prey with toxins contained within the cells.

Review Questions

Annelids have a:

A. pseudocoelom
B. a true coelom
C. no coelom
D. none of the above

Answer

B

Which group of flatworms are primarily ectoparasites of fish?

A. monogeneans
B. trematodes
C. cestodes
D. turbellarians

Answer

A

A mantle and mantle cavity are present in:

A. phylum Echinodermata
B. phylum Adversoidea
C. phylum Mollusca
D. phylum Nemertea

Answer

C

The rhynchocoel is a _____.

A. circulatory system
B. fluid-filled cavity
C. primitive excretory system
D. proboscis

Answer

B

Free Response

Describe the morphology and anatomy of mollusks.

Answer

Mollusks have a large muscular foot that may be modified in various ways, such as into tentacles, but it functions in locomotion. They have a mantle, a structure of tissue that covers and encloses the dorsal portion of the animal, and secretes the shell when it is present. The mantle encloses the mantle cavity, which houses the gills (when present), excretory pores, anus, and gonadopores. The coelom of mollusks is restricted to the region around the systemic heart. The main body cavity is a hemocoel. Many mollusks have a radula near the mouth that is used for scraping food.

What are the anatomical differences between nemertines and mollusks?

Answer

Mollusks have a shell, even if it is a reduced shell. Nemertines do not have a shell. Nemertines have a proboscis; mollusks do not. Nemertines have a closed circulatory system, whereas Mollusks have an open circulatory system.

28.3: Superphylum Lophotrochozoa

Animals belonging to superphylum Lophotrochozoa are protostomes, in which the blastopore, or the point of involution of the ectoderm or outer germ layer, becomes the mouth opening to the alimentary canal. This is called protostomy or “first mouth.” In protostomy, solid groups of cells split from the endoderm or inner germ layer to form a central mesodermal layer of cells. This layer multiplies into a band and then splits internally to form the coelom.

28.4: Superphylum Ecdysozoa

The superphylum Ecdysozoa contains an incredibly large number of species. This is because it contains two of the most diverse animal groups: phylum Nematoda (the roundworms) and Phylum Arthropoda (the arthropods). The most prominant distinguising feature of Ecdysozoans is their tough external covering called the cuticle. The cuticle provides a tough, but flexible exoskeleton tht protects these animals from water loss, predators and other aspects of the external environment.

Review Questions

The embryonic development in nematodes can have up to _____ larval stages.

A. one
B. two
C. three
D. five

Answer

D

The nematode cuticle contains _____.

A. glucose
B. skin cells
C. chitin
D. nerve cells

Answer

C

Crustaceans are _____.

A. ecdysozoans
B. nematodes
C. arachnids
D. parazoans

Answer

A

Flies are_____.

A. chelicerates
B. hexapods
C. arachnids
D. crustaceans

Answer

B

Free Response

Enumerate features of *Caenorhabditis elegans* that make it a valuable model system for biologists.

Answer

It is a true animal with at least rudiments of the physiological systems—feeding, nervous, muscle, and reproductive—found in “higher animals” like mice and humans. It is so small that large numbers can be raised in Petri dishes. It reproduces rapidly. It is transparent so that every cell in the living animal can be seen under the microscope. Before it dies (after 2–3 weeks), it shows signs of aging and thus may provide general clues as to the aging process.

What are the different ways in which nematodes can reproduce?

Answer

There are nematodes with separate sexes and hermaphrodites in addition to species that reproduce parthenogentically. The nematode *Caenorhabditis elegans* has a self-fertilizing hermaphrodite sex and a pure male sex.

Describe the various superclasses that phylum Arthropoda can be divided into.

Answer

The Arthropoda include the Hexapoda, which are mandibulates with six legs, the Myriapoda, which are mandibulates with many legs and include the centipedes and millipedes, the Crustacea, which are mostly marine mandibulates, and the Chelicerata, which include the spiders and scorpions and their kin.

Compare and contrast the segmentation seen in phylum Annelida with that seen in phylum Arthropoda.

Answer

Arthropods have an exoskeleton, which is missing in annelids. Arthropod segmentation is more specialized with major organs concentrated in body tagma. Annelid segmentation is usually more uniform with the intestine extending through most segments.

28.5: Superphylum Deuterostomia

The phyla Echinodermata and Chordata (the phylum in which humans are placed) both belong to the superphylum Deuterostomia. Recall that protostome and deuterostomes differ in certain aspects of their embryonic development, and they are named based on which opening of the digestive cavity develops first. The word deuterostome comes from the Greek word meaning “mouth second,” indicating that the anus is the first to develop.

Review Questions

Echinoderms have _____.

A. triangular symmetry
B. radial symmetry
C. hexagonal symmetry
D. pentaradial symmetry

Answer

D

The circulatory fluid in echinoderms is _____.

A. blood
B. mesohyl
C. water
D. saline

Answer

C

Free Response

Describe the different classes of echinoderms using examples.

Answer

The Asteroidea are the sea stars, the Echinoidea are the sea urchins and sand dollars, the Ophiuroidea are the brittle stars, the Crinoidea are the sea lilies and feather stars, the Holothuroidea are the sea cucumbers.

This page titled 5.7.E: Invertebrates (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **28.E: Invertebrates (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

5.8: Vertebrates

Vertebrates are among the most recognizable organisms of the animal kingdom. More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, which reached sizes not seen before or after in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out in a mass extinction near the end of the Cretaceous period. Although it is not known with certainty what caused their extinction, a great deal is known about the anatomy of the dinosaurs, given the preservation of skeletal elements in the fossil record.

5.8.1: Prelude to Vertebrates
5.8.2: Chordates
5.8.3: Fishes
5.8.4: Amphibians
5.8.5: Reptiles
5.8.6: Birds
5.8.7: Mammals
5.8.8: The Evolution of Primates
5.8.E: Vertebrates (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 5.8: Vertebrates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

5.8.1: Prelude to Vertebrates

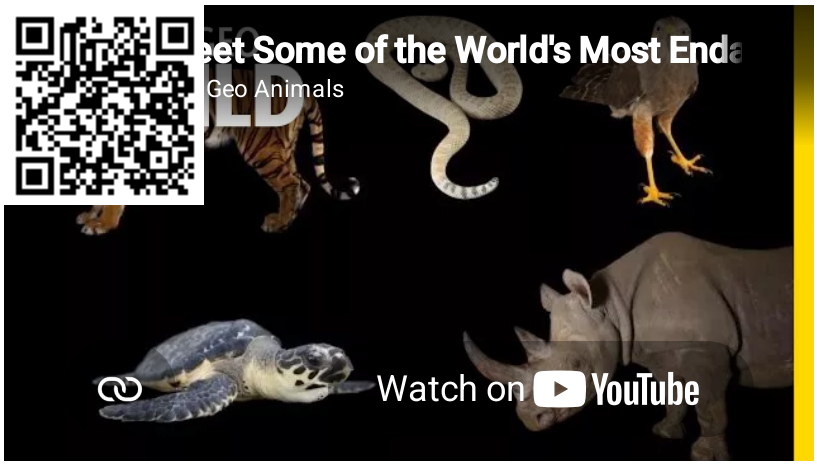


(a) (b) (c)

Figure 5.8.1.1: Examples of critically endangered vertebrate species include (a) the Siberian tiger (*Panthera tigris*), (b) the mountain gorilla (*Gorilla beringei*), and (c) the Philippine eagle (*Pithecophega jefferyi*). (credit a: modification of work by Dave Pape; credit b: modification of work by Dave Proffer; credit c: modification of work by "cuatrok77"/Flickr)

Vertebrates are among the most recognizable organisms of the animal kingdom. More than 62,000 vertebrate species have been identified. The vertebrate species now living represent only a small portion of the vertebrates that have existed. The best-known extinct vertebrates are the dinosaurs, a unique group of reptiles, which reached sizes not seen before or after in terrestrial animals. They were the dominant terrestrial animals for 150 million years, until they died out in a mass extinction near the end of the Cretaceous period. Although it is not known with certainty what caused their extinction, a great deal is known about the anatomy of the dinosaurs, given the preservation of skeletal elements in the fossil record.

Currently, a number of vertebrate species face extinction primarily due to habitat loss and pollution. According to the International Union for the Conservation of Nature, more than 6,000 vertebrate species are classified as threatened. Amphibians and mammals are the classes with the greatest percentage of threatened species, with 29 percent of all amphibians and 21 percent of all mammals classified as threatened. Attempts are being made around the world to prevent the extinction of threatened species. For example, the Biodiversity Action Plan is an international program, ratified by 188 countries, which is designed to protect species and habitats.



This page titled 5.8.1: Prelude to Vertebrates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.0: Prelude to Vertebrates** by OpenStax is licensed CC BY 4.0.

5.8.2: Chordates

Skills to Develop

- Describe the distinguishing characteristics of chordates
- Identify the derived character of craniates that sets them apart from other chordates
- Describe the developmental fate of the notochord in vertebrates

Vertebrates are members of the kingdom Animalia and the phylum Chordata (Figure 5.8.2.1). Recall that animals that possess bilateral symmetry can be divided into two groups—protostomes and deuterostomes—based on their patterns of embryonic development. The deuterostomes, whose name translates as "second mouth," consist of two phyla: Chordata and Echinodermata. Echinoderms are invertebrate marine animals that have pentaradial symmetry and a spiny body covering, a group that includes sea stars, sea urchins, and sea cucumbers. The most conspicuous and familiar members of Chordata are vertebrates, but this phylum also includes two groups of invertebrate chordates.

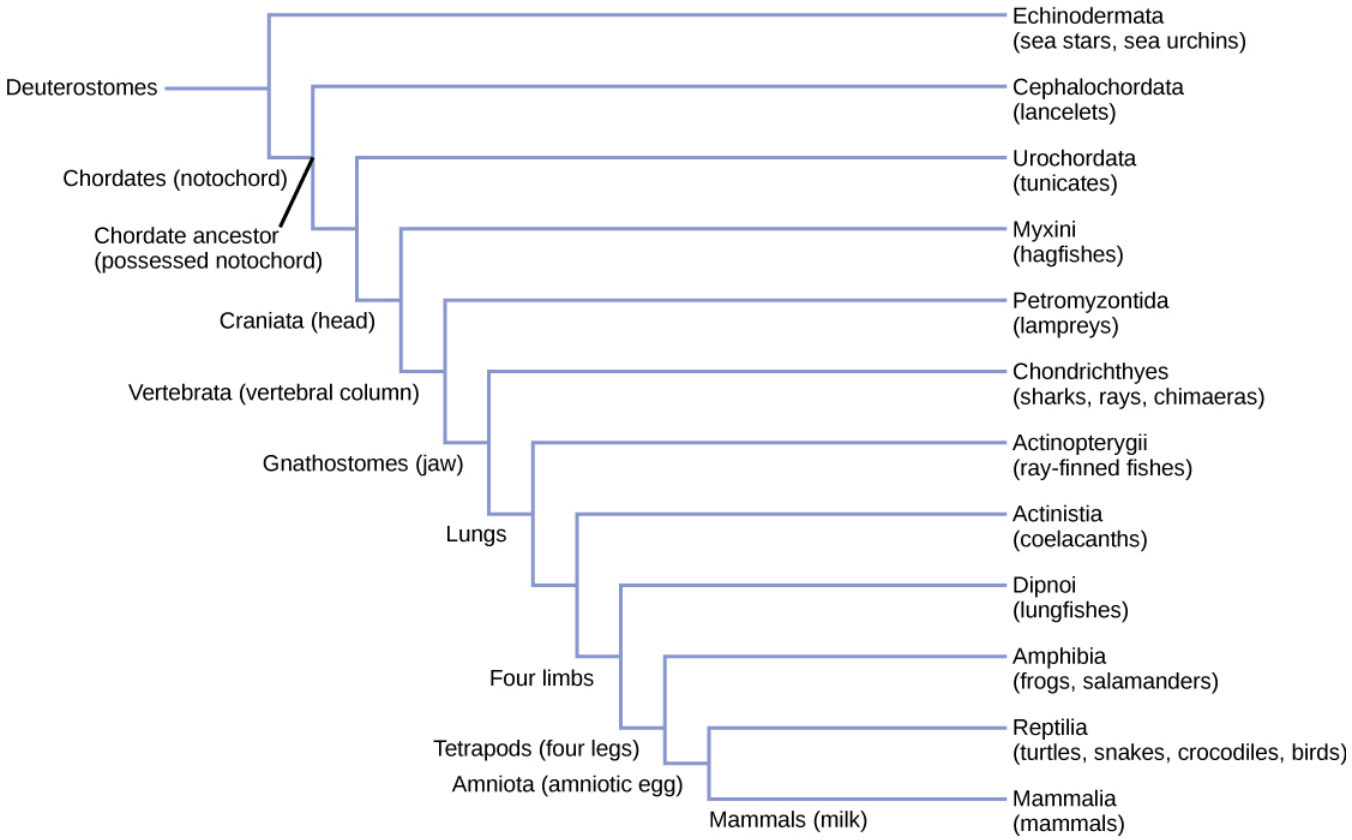


Figure 5.8.2.1: All chordates are deuterostomes possessing a notochord.

Characteristics of Chordata

Animals in the phylum Chordata share four key features that appear at some stage during their development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail (Figure 5.8.2.2). In some groups, some of these are present only during embryonic development.

The chordates are named for the notochord, which is a flexible, rod-shaped structure that is found in the embryonic stage of all chordates and in the adult stage of some chordate species. It is located between the digestive tube and the nerve cord, and provides skeletal support through the length of the body. In some chordates, the notochord acts as the primary axial support of the body throughout the animal's lifetime. In vertebrates, the notochord is present during embryonic development, at which time it induces

the development of the neural tube and serves as a support for the developing embryonic body. The notochord, however, is not found in the postnatal stage of vertebrates; at this point, it has been replaced by the vertebral column (that is, the spine).

Art Connection

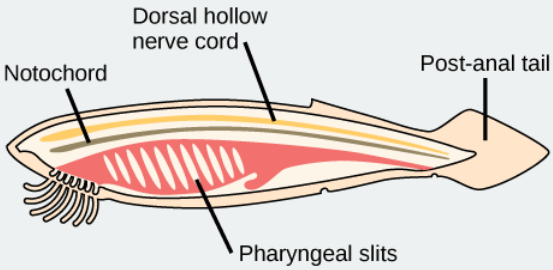


Figure 5.8.2.2: In chordates, four common features appear at some point during development: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

Which of the following statements about common features of chordates is true?

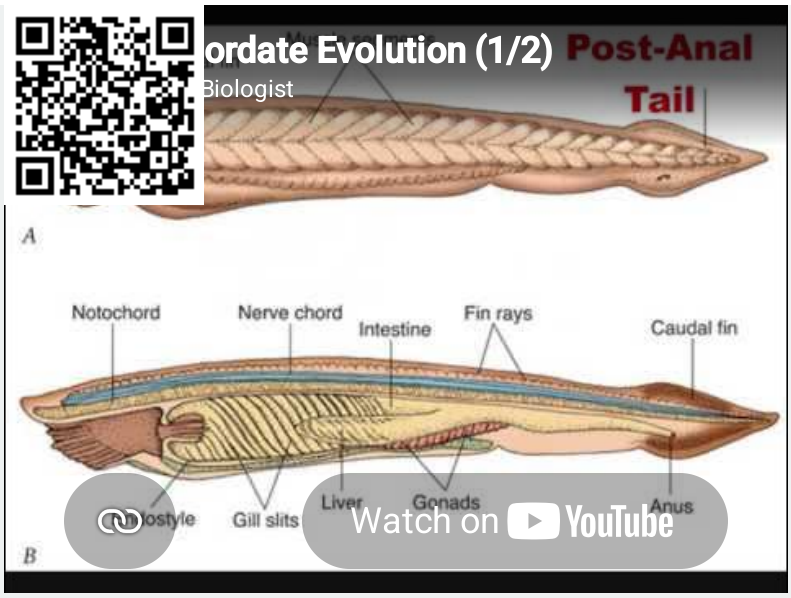
A. The dorsal hollow nerve cord is part of the chordate central nervous system.
B. In vertebrate fishes, the pharyngeal slits become the gills.
C. Humans are not chordates because humans do not have a tail.
D. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

The dorsal hollow nerve cord derives from ectoderm that rolls into a hollow tube during development. In chordates, it is located dorsal to the notochord. In contrast, other animal phyla are characterized by solid nerve cords that are located either ventrally or laterally. The nerve cord found in most chordate embryos develops into the brain and spinal cord, which compose the central nervous system.

Pharyngeal slits are openings in the pharynx (the region just posterior to the mouth) that extend to the outside environment. In organisms that live in aquatic environments, pharyngeal slits allow for the exit of water that enters the mouth during feeding. Some invertebrate chordates use the pharyngeal slits to filter food out of the water that enters the mouth. In vertebrate fishes, the pharyngeal slits are modified into gill supports, and in jawed fishes, into jaw supports. In tetrapods, the slits are modified into components of the ear and tonsils. Tetrapod literally means “four-footed,” which refers to the phylogenetic history of various groups that evolved accordingly, even though some now possess fewer than two pairs of walking appendages. Tetrapods include amphibians, reptiles, birds, and mammals.

The post-anal tail is a posterior elongation of the body, extending beyond the anus. The tail contains skeletal elements and muscles, which provide a source of locomotion in aquatic species, such as fishes. In some terrestrial vertebrates, the tail also helps with balance, courting, and signaling when danger is near. In humans, the post-anal tail is vestigial, that is, reduced in size and nonfunctional.

Link to Learning



Click for a video discussing the evolution of chordates and five characteristics that they share.

Chordates and the Evolution of Vertebrates

Chordata also contains two clades of invertebrates: Urochordata and Cephalochordata. Members of these groups also possess the four distinctive features of chordates at some point during their development.

Urochordata

Members of Urochordata are also known as tunicates (Figure 5.8.2.3). The name tunicate derives from the cellulose-like carbohydrate material, called the tunic, which covers the outer body of tunicates. Although adult tunicates are classified as chordates, they do not have a notochord, a dorsal hollow nerve cord, or a post-anal tail, although they do have pharyngeal slits. The larval form, however, possesses all four structures. Most tunicates are hermaphrodites. Tunicate larvae hatch from eggs inside the adult tunicate's body. After hatching, a tunicate larva swims for a few days until it finds a suitable surface on which it can attach, usually in a dark or shaded location. It then attaches via the head to the surface and undergoes metamorphosis into the adult form, at which point the notochord, nerve cord, and tail disappear.

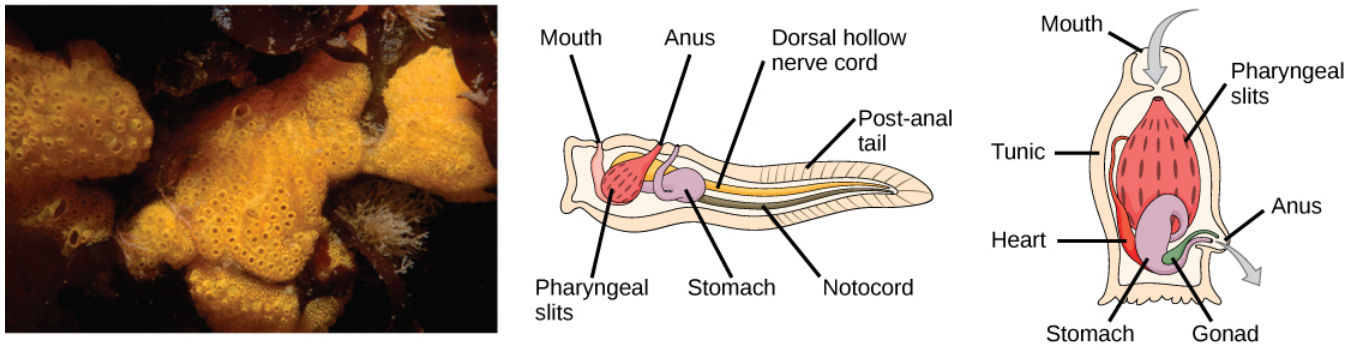


Figure 5.8.2.3: (a) This photograph shows a colony of the tunicate *Botrylloides violaceus*. (b) The larval stage of the tunicate possesses all of the features characteristic of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. (c) In the adult stage, the notochord, nerve cord, and tail disappear. (credit: modification of work by Dann Blackwood, USGS)

Most tunicates live a sessile existence on the ocean floor and are suspension feeders. The primary foods of tunicates are plankton and detritus. Seawater enters the tunicate's body through its incurrent siphon. Suspended material is filtered out of this water by a mucous net (pharyngeal slits) and is passed into the intestine via the action of cilia. The anus empties into the excurrent siphon, which expels wastes and water. Tunicates are found in shallow ocean waters around the world.

Cephalochordata

Members of Cephalochordata possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage (Figure 5.8.2.4). The notochord extends into the head, which gives the subphylum its name. Extinct members of this subphylum include *Pikaia*, which is the oldest known cephalochordate. *Pikaia* fossils were recovered from the Burgess shales of Canada and dated to the middle of the Cambrian age, making them more than 500 million years old.

Extant members of Cephalochordata are the lancelets, named for their blade-like shape. Lancelets are only a few centimeters long and are usually found buried in sand at the bottom of warm temperate and tropical seas. Like tunicates, they are suspension feeders.

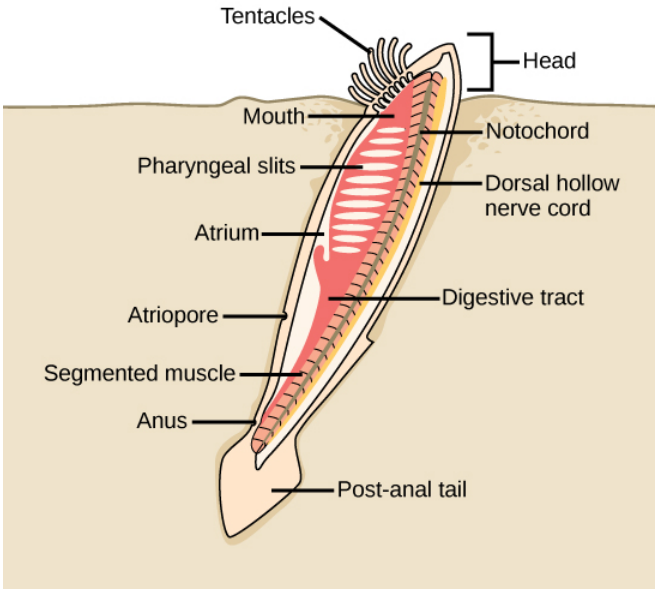


Figure 5.8.2.4: The lancelet, like all cephalochordates, has a head. Adult lancelets retain the four key features of chordates: a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Water from the mouth enters the pharyngeal slits, which filter out food particles. The filtered water then collects in the atrium and exits through the atriopore.

Craniata and Vertebrata

A cranium is a bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones (Figure 5.8.2.5). Most bilaterally symmetrical animals have a head; of these, those that have a cranium compose the clade Craniata. Craniata includes the hagfishes (Myxini), which have a cranium but lack a backbone, and all of the organisms called “vertebrates.”

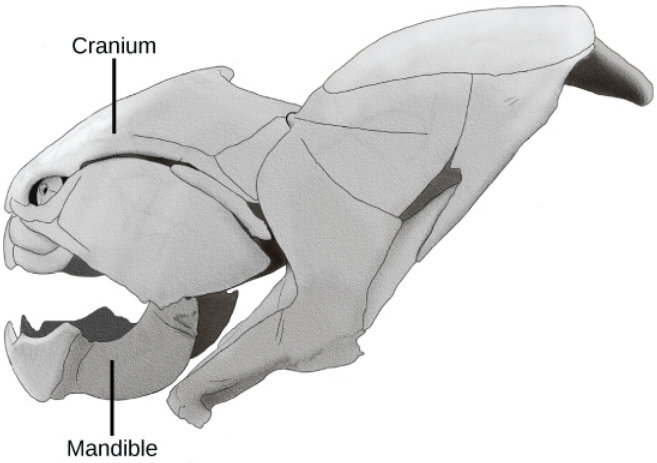


Figure 5.8.2.5: Craniata, including this fish (*Dunkleosteus* sp.), are characterized by the presence of a cranium, mandible, and other facial bones. (credit: “Steveoc 86”/Wikimedia Commons)

Vertebrates are members of the clade Vertebrata. Vertebrates display the four characteristic features of the chordates; however, members of this group also share derived characteristics that distinguish them from invertebrate chordates. Vertebrata is named for

the vertebral column, composed of vertebrae, a series of separate bones joined together as a backbone (Figure 5.8.2.6). In adult vertebrates, the vertebral column replaces the notochord, which is only seen in the embryonic stage.

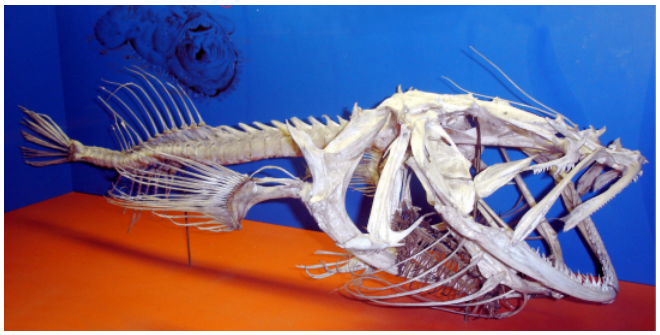
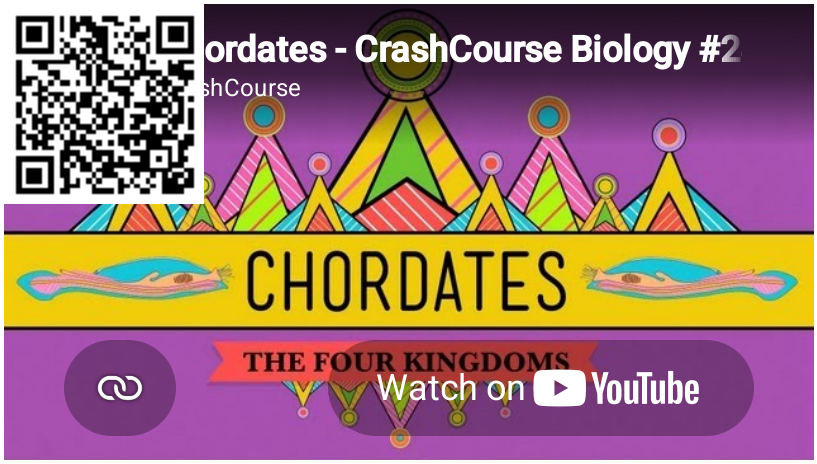


Figure 5.8.2.6: Vertebrata are characterized by the presence of a backbone, such as the one that runs through the middle of this fish. All vertebrates are in the Craniata clade and have a cranium. (credit: Ernest V. More; taken at Smithsonian Museum of Natural History, Washington, D.C.)

Based on molecular analysis, vertebrates appear to be more closely related to lancelets (cephalochordates) than to tunicates (urochordates) among the invertebrate chordates. This evidence suggests that the cephalochordates diverged from Urochordata and the vertebrates subsequently diverged from the cephalochordates. This hypothesis is further supported by the discovery of a fossil in China from the genus *Haikouella*. This organism seems to be an intermediate form between cephalochordates and vertebrates. The *Haikouella* fossils are about 530 million years old and appear similar to modern lancelets. These organisms had a brain and eyes, as do vertebrates, but lack the skull found in craniates.[1] This evidence suggests that vertebrates arose during the Cambrian explosion. Recall that the "Cambrian explosion" is the name given to a relatively brief span of time during the Cambrian period during which many animal groups appeared and rapidly diversified. Most modern animal phyla originated during the Cambrian explosion.

Vertebrates are the largest group of chordates, with more than 62,000 living species. Vertebrates are grouped based on anatomical and physiological traits. More than one classification and naming scheme is used for these animals. Here we will consider the traditional groups Agnatha, Chondrichthyes, Osteichthyes, Amphibia, Reptilia, Aves, and Mammalia, which constitute classes in the subphylum Vertebrata. Many modern authors classify birds within Reptilia, which correctly reflects their evolutionary heritage. We consider them separately only for convenience. Further, we will consider hagfishes and lampreys together as jawless fishes, the agnathans, although emerging classification schemes separate them into chordate jawless fishes (the hagfishes) and vertebrate jawless fishes (the lampreys).

Animals that possess jaws are known as gnathostomes, which means "jawed mouth." Gnathostomes include fishes and tetrapods—amphibians, reptiles, birds, and mammals. Tetrapods can be further divided into two groups: amphibians and amniotes. Amniotes are animals whose eggs are adapted for terrestrial living, and this group includes mammals, reptiles, and birds. Amniotic embryos, developing in either an externally shed egg or an egg carried by the female, are provided with a water-retaining environment and are protected by amniotic membranes.



Summary

The characteristic features of Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail. Chordata contains two clades of invertebrates: Urochordata (tunicates) and Cephalochordata (lancelets), together with the vertebrates in Vertebrata. Most tunicates live on the ocean floor and are suspension feeders. Lancelets are suspension feeders that feed on phytoplankton and other microorganisms. Vertebrata is named for the vertebral column, which is a feature of almost all members of this clade.

Art Connections

Figure 5.8.2.2: Which of the following statements about common features of chordates is true?

A. The dorsal hollow nerve cord is part of the chordate central nervous system.
B. In vertebrate fishes, the pharyngeal slits become the gills.
C. Humans are not chordates because humans do not have a tail.
D. Vertebrates do not have a notochord at any point in their development; instead, they have a vertebral column.

Answer

A

Footnotes

1. 1 Chen, J. Y., Huang, D. Y., and Li, C. W., "An early Cambrian craniate-like chordate," *Nature* 402 (1999): 518–522, doi:10.1038/990080.

Glossary

Cephalochordata
chordate clade whose members possess a notochord, dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail in the adult stage

Chordata
phylum of animals distinguished by their possession of a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail at some point during their development

Craniata
clade composed of chordates that possess a cranium; includes Vertebrata together with hagfishes

cranium
bony, cartilaginous, or fibrous structure surrounding the brain, jaw, and facial bones

dorsal hollow nerve cord
hollow, tubular structure derived from ectoderm, which is located dorsal to the notochord in chordates

lancelet
member of Cephalochordata; named for its blade-like shape

notochord
flexible, rod-shaped support structure that is found in the embryonic stage of all chordates and in the adult stage of some chordates

pharyngeal slit
opening in the pharynx

post-anal tail

muscular, posterior elongation of the body extending beyond the anus in chordates

tetrapod
phylogenetic reference to an organism with a four-footed evolutionary history; includes amphibians, reptiles, birds, and mammals

tunicate
sessile chordate that is a member of Urochordata

Urochordata
clade composed of tunicates

vertebral column
series of separate bones joined together as a backbone

Vertebrata
members of the phylum Chordata that possess a backbone

This page titled 5.8.2: Chordates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

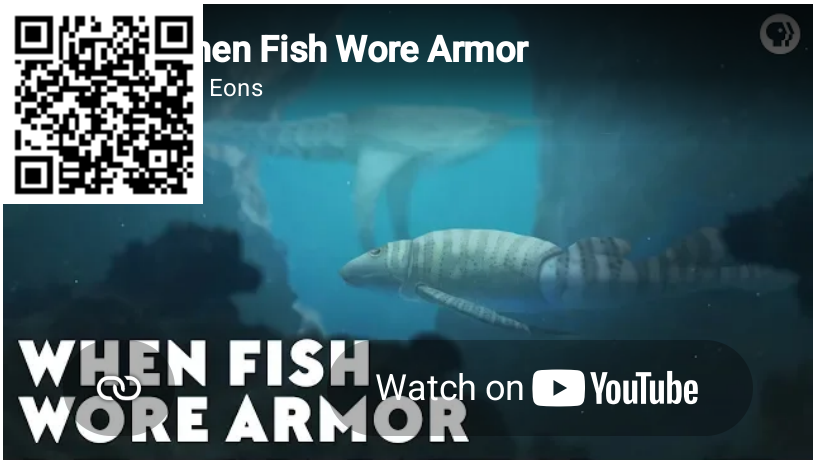
- **29.1: Chordates** by OpenStax is licensed CC BY 4.0.

5.8.3: Fishes

Skills to Develop

- Describe the difference between jawless and jawed fishes
- Discuss the distinguishing features of sharks and rays compared to other modern fishes

Modern fishes include an estimated 31,000 species. Fishes were the earliest vertebrates, with jawless species being the earliest and jawed species evolving later. They are active feeders, rather than sessile, suspension feeders. Jawless fishes—the hagfishes and lampreys—have a distinct cranium and complex sense organs including eyes, distinguishing them from the invertebrate chordates.



Jawless Fishes

Jawless fishes are craniates that represent an ancient vertebrate lineage that arose over one half-billion years ago. In the past, the hagfishes and lampreys were classified together as agnathans. Today, hagfishes and lampreys are recognized as separate clades, primarily because lampreys are true vertebrates, whereas hagfishes are not. A defining feature is the lack of paired lateral appendages (fins). Some of the earliest jawless fishes were the ostracoderms (which translates to “shell-skin”). Ostracoderms were vertebrate fishes encased in bony armor, unlike present-day jawless fishes, which lack bone in their scales.

Myxini: Hagfishes

The clade Myxini includes at least 20 species of hagfishes. Hagfishes are eel-like scavengers that live on the ocean floor and feed on dead invertebrates, other fishes, and marine mammals (Figure 5.8.3.1). Hagfishes are entirely marine and are found in oceans around the world, except for the polar regions. A unique feature of these animals is the slime glands beneath the skin that release mucus through surface pores. This mucus allows the hagfish to escape from the grip of predators. Hagfish can also twist their bodies in a knot to feed and sometimes eat carcasses from the inside out.

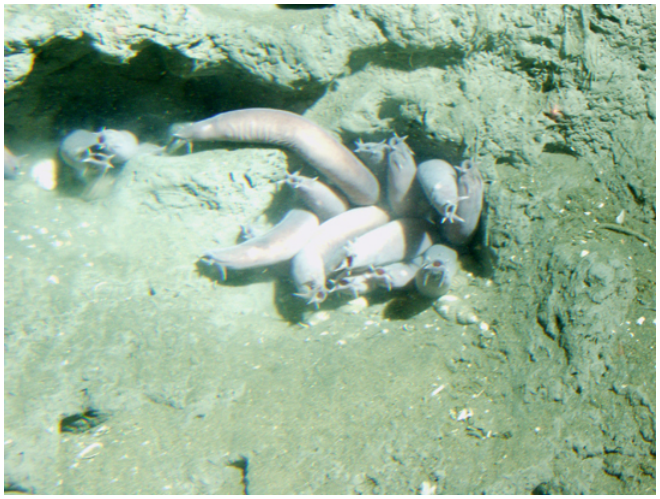


Figure 5.8.3.1: Pacific hagfish are scavengers that live on the ocean floor. (credit: Linda Snook, NOAA/CBNMS)

The skeleton of a hagfish is composed of cartilage, which includes a cartilaginous notochord that runs the length of the body. This notochord provides support to the hagfish's body. Hagfishes do not replace the notochord with a vertebral column during development, as do true vertebrates.



Petromyzontidae: Lampreys

The clade Petromyzontidae includes approximately 35–40 or more species of lampreys. Lampreys are similar to hagfishes in size and shape; however, lampreys possess some vertebral elements. Lampreys lack paired appendages and bone, as do the hagfishes. As adults, lampreys are characterized by a toothed, funnel-like sucking mouth. Many species have a parasitic stage of their life cycle during which they are ectoparasites of fishes (Figure 5.8.3.2).



Figure 5.8.3.2: These parasitic sea lampreys attach to their lake trout host by suction and use their rough tongues to rasp away flesh in order to feed on the trout's blood. (credit: USGS)

Lampreys live primarily in coastal and fresh waters, and have a worldwide distribution, except for in the tropics and polar regions. Some species are marine, but all species spawn in fresh water. Eggs are fertilized externally, and the larvae distinctly differ from the adult form, spending 3 to 15 years as suspension feeders. Once they attain sexual maturity, the adults reproduce and die within days.

Lampreys possess a notochord as adults; however, this notochord is surrounded by a cartilaginous structure called an arcualia, which may resemble an evolutionarily early form of the vertebral column.



Gnathostomes: Jawed Fishes

Gnathostomes or "jaw-mouths" are vertebrates that possess jaws. One of the most significant developments in early vertebrate evolution was the development of the jaw, which is a hinged structure attached to the cranium that allows an animal to grasp and tear its food. The evolution of jaws allowed early gnathostomes to exploit food resources that were unavailable to jawless fishes.

Early gnathostomes also possessed two sets of paired fins, allowing the fishes to maneuver accurately. Pectoral fins are typically located on the anterior body, and pelvic fins on the posterior. Evolution of the jaw and paired fins permitted gnathostomes to expand from the sedentary suspension feeding of jawless fishes to become mobile predators. The ability of gnathostomes to exploit new nutrient sources likely is one reason that they replaced most jawless fishes during the Devonian period. Two early groups of gnathostomes were the acanthodians and placoderms (Figure 5.8.3.3), which arose in the late Silurian period and are now extinct. Most modern fishes are gnathostomes that belong to the clades Chondrichthyes and Osteichthyes.



Figure 5.8.3.3: Dunkleosteous was an enormous placoderm from the Devonian period, 380–360 million years ago. It measured up to 10 meters in length and weighed up to 3.6 tons. (credit: Nobu Tamura)

Chondrichthyes: Cartilaginous Fishes

The clade Chondrichthyes is diverse, consisting of sharks (Figure 5.8.3.4), rays, and skates, together with sawfishes and a few dozen species of fishes called *chimaeras*, or "ghost" sharks." Chondrichthyes are jawed fishes that possess paired fins and a skeleton made of cartilage. This clade arose approximately 370 million years ago in the early or middle Devonian. They are thought to be descended from the placoderms, which had skeletons made of bone; thus, the cartilaginous skeleton of Chondrichthyes is a later development. Parts of shark skeleton are strengthened by granules of calcium carbonate, but this is not the same as bone.

Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for a part or all of their lives. Most sharks are carnivores that feed on live prey, either swallowing it whole or using their jaws and teeth to tear it into smaller pieces. Shark teeth likely evolved from the jagged scales that cover their skin, called placoid scales. Some species of sharks and rays are suspension feeders that feed on plankton.



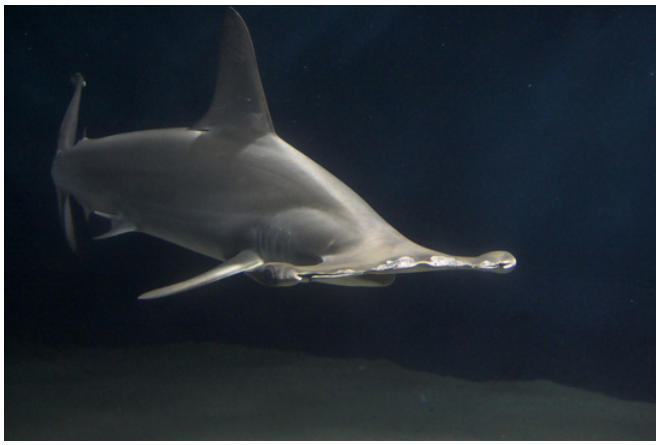


Figure 5.8.3.4: Hammerhead sharks tend to school during the day and hunt prey at night. (credit: Masashi Sugawara)

Sharks have well-developed sense organs that aid them in locating prey, including a keen sense of smell and electroreception, with the latter perhaps the most sensitive of any animal. Organs called ampullae of Lorenzini allow sharks to detect the electromagnetic fields that are produced by all living things, including their prey. Electroreception has only been observed in aquatic or amphibious animals. Sharks, together with most fishes and aquatic and larval amphibians, also have a sense organ called the lateral line, which is used to detect movement and vibration in the surrounding water, and is often considered homologous to "hearing" in terrestrial vertebrates. The lateral line is visible as a darker stripe that runs along the length of a fish's body.

Sharks reproduce sexually, and eggs are fertilized internally. Most species are ovoviviparous: The fertilized egg is retained in the oviduct of the mother's body and the embryo is nourished by the egg yolk. The eggs hatch in the uterus, and young are born alive and fully functional. Some species of sharks are oviparous: They lay eggs that hatch outside of the mother's body. Embryos are protected by a shark egg case or "mermaid's purse" (Figure 5.8.3.5) that has the consistency of leather. The shark egg case has tentacles that snag in seaweed and give the newborn shark cover. A few species of sharks are viviparous: The young develop within the mother's body and she gives live birth.

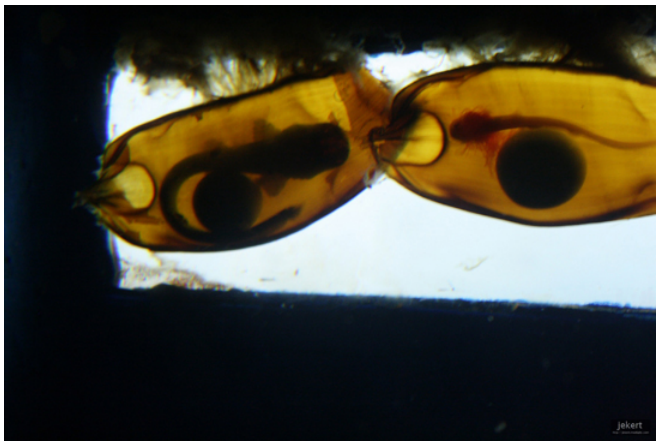
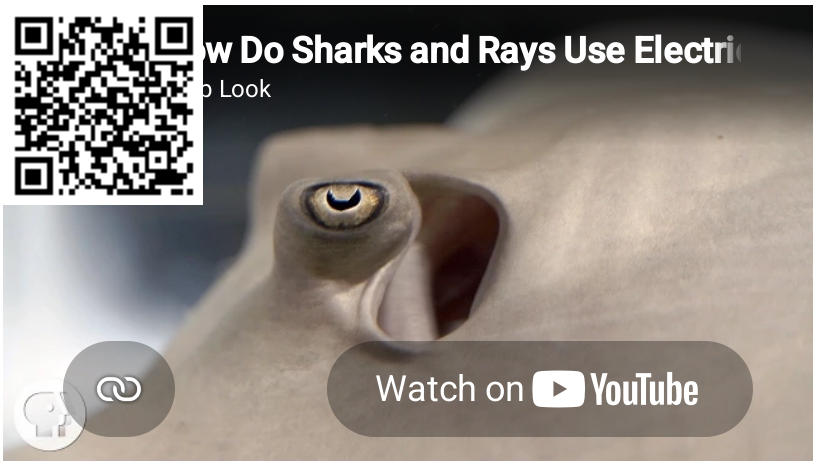


Figure 5.8.3.5: Shark embryos are clearly visible through these transparent egg cases. The round structure is the yolk that nourishes the growing embryo. (credit: Jek Bacarisas)

Rays and skates comprise more than 500 species and are closely related to sharks. They can be distinguished from sharks by their flattened bodies, pectoral fins that are enlarged and fused to the head, and gill slits on their ventral surface (Figure 5.8.3.6). Like sharks, rays and skates have a cartilaginous skeleton. Most species are marine and live on the sea floor, with nearly a worldwide distribution.



Figure 5.8.3.6: This stingray blends into the sandy bottom of the ocean floor. (credit: "Sailn1"/Flickr)



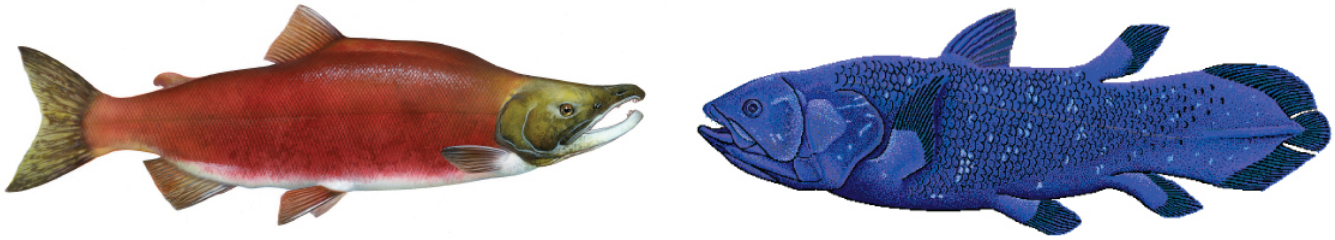
Osteichthyes: Bony Fishes

Members of the clade Osteichthyes, also called bony fishes, are characterized by a bony skeleton. The vast majority of present-day fishes belong to this group, which consists of approximately 30,000 species, making it the largest class of vertebrates in existence today.

Nearly all bony fishes have an ossified skeleton with specialized bone cells (osteocytes) that produce and maintain a calcium phosphate matrix. This characteristic has only reversed in a few groups of Osteichthyes, such as sturgeons and paddlefish, which have primarily cartilaginous skeletons. The skin of bony fishes is often covered by overlapping scales, and glands in the skin secrete mucus that reduces drag when swimming and aids the fish in osmoregulation. Like sharks, bony fishes have a lateral line system that detects vibrations in water.

All bony fishes use gills to breathe. Water is drawn over gills that are located in chambers covered and ventilated by a protective, muscular flap called the operculum. Many bony fishes also have a swim bladder, a gas-filled organ that helps to control the buoyancy of the fish. Bony fishes are further divided into two extant clades: Actinopterygii (ray-finned fishes) and Sarcopterygii (lobe-finned fishes).

Actinopterygii, the ray-finned fishes, include many familiar fishes—tuna, bass, trout, and salmon (Figure 5.8.3.7), among others. Ray-finned fishes are named for their fins that are webs of skin supported by bony spines called rays. In contrast, the fins of Sarcopterygii are fleshy and lobed, supported by bone (Figure 5.8.3.7). Living members of this clade include the less-familiar lungfishes and coelacanths.



(a) (b)

Figure 5.8.3.7: The (a) sockeye salmon and (b) coelacanth are both bony fishes of the Osteichthyes clade. The coelacanth, sometimes called a lobe-finned fish, was thought to have gone extinct in the Late Cretaceous period, 100 million years ago, until one was discovered in 1938 near the Comoros Islands between Africa and Madagascar. (credit a: modification of work by Timothy Knepp, USFWS; credit b: modification of work by Robbie Cada)



Summary

The earliest vertebrates that diverged from the invertebrate chordates were the jawless fishes. Fishes with jaws (gnathostomes) evolved later. Jaws allowed early gnathostomes to exploit new food sources. Agnathans include the hagfishes and lampreys. Hagfishes are eel-like scavengers that feed on dead invertebrates and other fishes. Lampreys are characterized by a toothed, funnel-like sucking mouth, and most species are parasitic on other fishes. Gnathostomes include the cartilaginous fishes and the bony fishes, as well as all other tetrapods. Cartilaginous fishes include sharks, rays, skates, and ghost sharks. Most cartilaginous fishes live in marine habitats, with a few species living in fresh water for part or all of their lives. The vast majority of present-day fishes belong to the clade Osteichthyes, which consists of approximately 30,000 species. Bony fishes can be divided into two clades: ray-finned fishes, virtually all extant species) and Sarcopterygii (lobe-finned fishes, comprising fewer than 10 extant species but which are the ancestors of tetrapods).



Glossary

Actinopterygii
ray-finned fishes

ampulla of Lorenzini
sensory organ that allows sharks to detect electromagnetic fields produced by living things

Chondrichthyes
jawed fish with paired fins and a skeleton made of cartilage

gnathostome
jawed fish

hagfish
eel-like jawless fish that live on the ocean floor and are scavengers

lamprey
jawless fish characterized by a toothed, funnel-like, sucking mouth

lateral line
sense organ that runs the length of a fish's body; used to detect vibration in the water

Myxini
hagfishes

Osteichthyes
bony fish

ostracoderm
one of the earliest jawless fish covered in bone

Petromyzontidae
clade of lampreys

Sarcopterygii
lobe-finned fish

swim bladder
in fishes, a gas filled organ that helps to control the buoyancy of the fish

---

This page titled 5.8.3: Fishes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

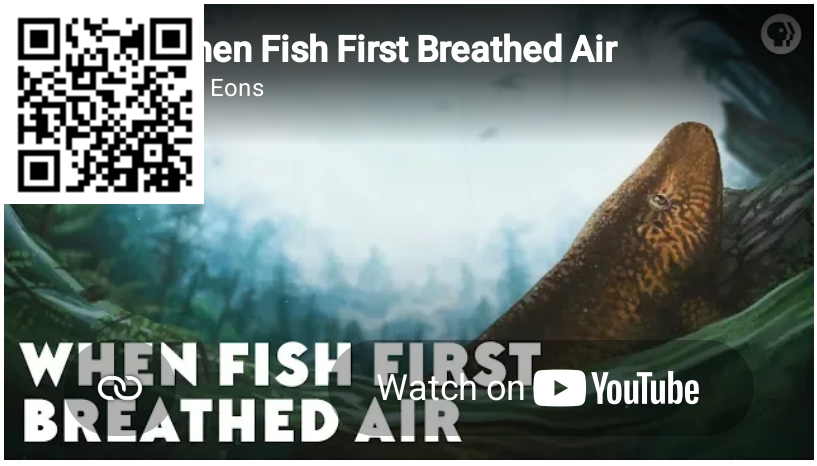
- **29.2: Fishes** by OpenStax is licensed CC BY 4.0.

5.8.4: Amphibians

Skills to Develop

- Describe the important difference between the life cycle of amphibians and the life cycles of other vertebrates
- Distinguish between the characteristics of Urodela, Anura, and Apoda
- Describe the evolutionary history of amphibians

Amphibians are vertebrate tetrapods. Amphibia includes frogs, salamanders, and caecilians. The term amphibian loosely translates from the Greek as “dual life,” which is a reference to the metamorphosis that many frogs and salamanders undergo and their mixture of aquatic and terrestrial environments in their life cycle. Amphibians evolved during the Devonian period and were the earliest terrestrial tetrapods.



Characteristics of Amphibians

As tetrapods, most amphibians are characterized by four well-developed limbs. Some species of salamanders and all caecilians are functionally limbless; their limbs are vestigial. An important characteristic of extant amphibians is a moist, permeable skin that is achieved via mucus glands that keep the skin moist; thus, exchange of oxygen and carbon dioxide with the environment can take place through it (cutaneous respiration). Additional characteristics of amphibians include pedicellate teeth—teeth in which the root and crown are calcified, separated by a zone of noncalcified tissue—and a papilla amphibiorum and papilla basilaris, structures of the inner ear that are sensitive to frequencies below and above 10,00 hertz, respectively. Amphibians also have an auricular operculum, which is an extra bone in the ear that transmits sounds to the inner ear. All extant adult amphibians are carnivorous, and some terrestrial amphibians have a sticky tongue that is used to capture prey.

Evolution of Amphibians

The fossil record provides evidence of the first tetrapods: now-extinct amphibian species dating to nearly 400 million years ago. Evolution of tetrapods from fishes represented a significant change in body plan from one suited to organisms that respired and swam in water, to organisms that breathed air and moved onto land; these changes occurred over a span of 50 million years during the Devonian period. One of the earliest known tetrapods is from the genus *Acanthostega*. *Acanthostega* was aquatic; fossils show that it had gills similar to fishes. However, it also had four limbs, with the skeletal structure of limbs found in present-day tetrapods, including amphibians. Therefore, it is thought that *Acanthostega* lived in shallow waters and was an intermediate form between lobe-finned fishes and early, fully terrestrial tetrapods. What preceded *Acanthostega*?

In 2006, researchers published news of their discovery of a fossil of a “tetrapod-like fish,” *Tiktaalik roseae*, which seems to be an intermediate form between fishes having fins and tetrapods having limbs (Figure 5.8.4.1). *Tiktaalik* likely lived in a shallow water environment about 375 million years ago.[1]

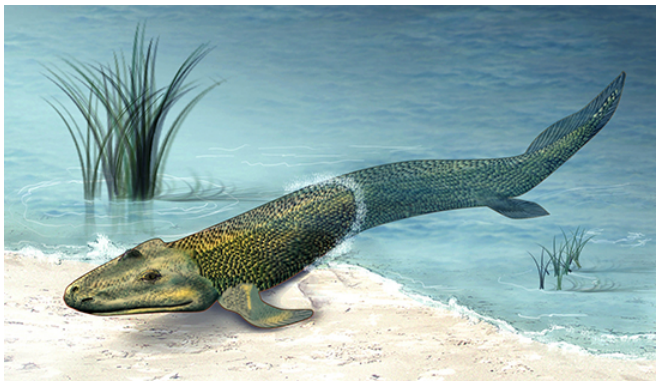


Figure 5.8.4.1: The recent fossil discovery of *Tiktaalik roseae* suggests evidence for an animal intermediate to finned fish and legged tetrapods. (credit: Zina Deretsky, National Science Foundation)

The early tetrapods that moved onto land had access to new nutrient sources and relatively few predators. This led to the widespread distribution of tetrapods during the early Carboniferous period, a period sometimes called the “age of the amphibians.”



Modern Amphibians

Amphibia comprises an estimated 6,770 extant species that inhabit tropical and temperate regions around the world. Amphibians can be divided into three clades: Urodela (“tailed-ones”), the salamanders; Anura (“tail-less ones”), the frogs; and Apoda (“legless ones”), the caecilians.

Urodela: Salamanders

Salamanders are amphibians that belong to the order Urodela. Living salamanders (Figure 5.8.4.1) include approximately 620 species, some of which are aquatic, other terrestrial, and some that live on land only as adults. Adult salamanders usually have a generalized tetrapod body plan with four limbs and a tail. They move by bending their bodies from side to side, called lateral undulation, in a fish-like manner while “walking” their arms and legs fore and aft. It is thought that their gait is similar to that used by early tetrapods. Respiration differs among different species. The majority of salamanders are lungless, and respiration occurs through the skin or through external gills. Some terrestrial salamanders have primitive lungs; a few species have both gills and lungs.

Unlike frogs, virtually all salamanders rely on internal fertilization of the eggs. The only male amphibians that possess copulatory structures are the caecilians, so fertilization among salamanders typically involves an elaborate and often prolonged courtship. Such a courtship allows the successful transfer of sperm from male to female via a spermatophore. Development in many of the most highly evolved salamanders, which are fully terrestrial, occurs during a prolonged egg stage, with the eggs guarded by the mother. During this time, the gilled larval stage is found only within the egg capsule, with the gills being resorbed, and metamorphosis being completed, before hatching. Hatchlings thus resemble tiny adults.

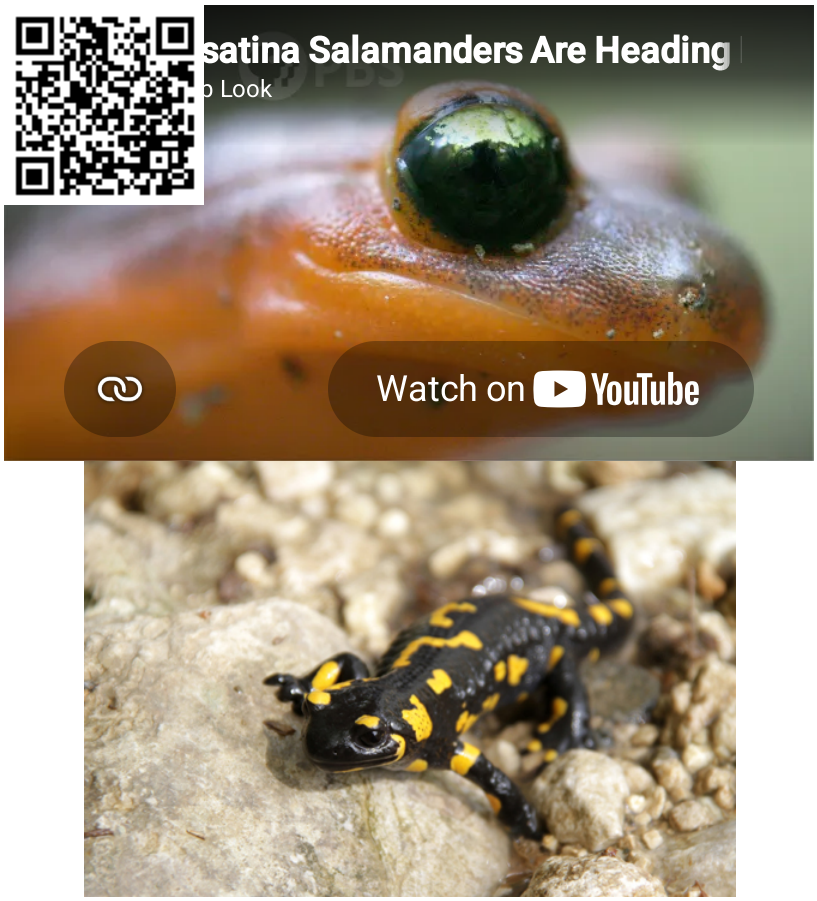


Figure 5.8.4.2: Most salamanders have legs and a tail, but respiration varies among species. (credit: Valentina Storti)

Anura: Frogs

Frogs are amphibians that belong to the order Anura (Figure 5.8.4.3). Anurans are among the most diverse groups of vertebrates, with approximately 5,965 species that occur on all of the continents except Antarctica. Anurans have a body plan that is more specialized for movement. Adult frogs use their hind limbs to jump on land. Frogs have a number of modifications that allow them to avoid predators, including skin that acts as camouflage. Many species of frogs and salamanders also release defensive chemicals from glands in the skin that are poisonous to predators.



Figure 5.8.4.3: The Australian green tree frog is a nocturnal predator that lives in the canopies of trees near a water source.

Frog eggs are fertilized externally, and like other amphibians, frogs generally lay their eggs in moist environments. A moist environment is required as eggs lack a shell and thus dehydrate quickly in dry environments. Frogs demonstrate a great diversity of parental behaviors, with some species laying many eggs and exhibiting little parental care, to species that carry eggs and tadpoles

on their hind legs or backs. The life cycle of frogs, as other amphibians, consists of two distinct stages: the larval stage followed by metamorphosis to an adult stage. The larval stage of a frog, the tadpole, is often a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. At the end of the tadpole stage, frogs undergo metamorphosis into the adult form (Figure 5.8.4.4). During this stage, the gills, tail, and lateral line system disappear, and four limbs develop. The jaws become larger and are suited for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop. These changes during metamorphosis allow the larvae to move onto land in the adult stage.

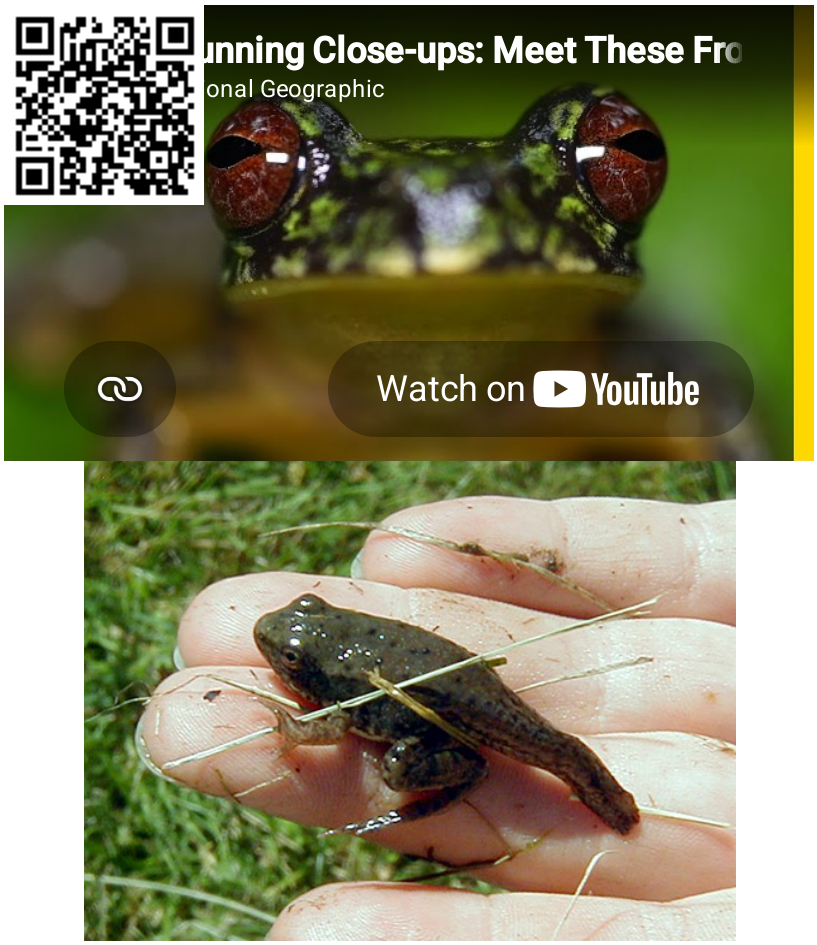


Figure 5.8.4.4: A juvenile frog metamorphoses into a frog. Here, the frog has started to develop limbs, but its tadpole tail is still evident.

Apoda: Caecilians

An estimated 185 species comprise caecilians, a group of amphibians that belong to the order Apoda. Although they are vertebrates, a complete lack of limbs leads to their resemblance to earthworms in appearance. They are adapted for a soil-burrowing or aquatic lifestyle, and they are nearly blind. These animals are found in the tropics of South America, Africa, and Southern Asia. They have vestigial limbs, evidence that they evolved from a legged ancestor.



Evolution Connection: The Paleozoic Era and the Evolution of Vertebrates

The climate and geography of Earth was vastly different during the Paleozoic Era, when vertebrates arose, as compared to today. The Paleozoic spanned from approximately 542 to 251 million years ago. The landmasses on Earth were very different from those of today. Laurentia and Gondwana were continents located near the equator that subsumed much of the current day landmasses in a different configuration (Figure 5.8.4.5). At this time, sea levels were very high, probably at a level that hasn't been reached since. As the Paleozoic progressed, glaciations created a cool global climate, but conditions warmed near the end of the first half of the Paleozoic. During the latter half of the Paleozoic, the landmasses began moving together, with the initial formation of a large northern block called Laurasia. This contained parts of what is now North America, along with Greenland, parts of Europe, and Siberia. Eventually, a single supercontinent, called Pangaea, was formed, starting in the latter third of the Paleozoic. Glaciations then began to affect Pangaea's climate, affecting the distribution of vertebrate life.

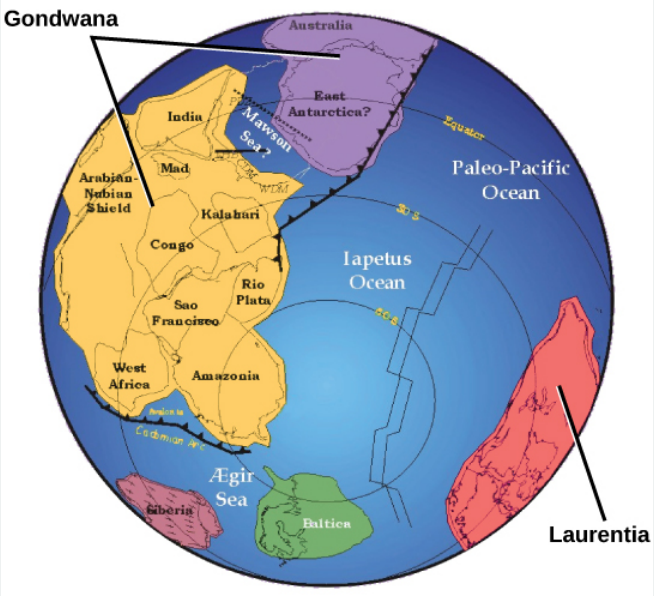


Figure 5.8.4.5: During the Paleozoic Era, around 550 million years ago, the continent Gondwana formed. Both Gondwana and the continent Laurentia were located near the equator.

During the early Paleozoic, the amount of carbon dioxide in the atmosphere was much greater than it is today. This may have begun to change later, as land plants became more common. As the roots of land plants began to infiltrate rock and soil began to form, carbon dioxide was drawn out of the atmosphere and became trapped in the rock. This reduced the levels of carbon dioxide and increased the levels of oxygen in the atmosphere, so that by the end of the Paleozoic, atmospheric conditions were similar to those of today.

As plants became more common through the latter half of the Paleozoic, microclimates began to emerge and ecosystems began to change. As plants and ecosystems continued to grow and become more complex, vertebrates moved from the water to land. The presence of shoreline vegetation may have contributed to the movement of vertebrates onto land. One hypothesis suggests that the fins of aquatic vertebrates were used to maneuver through this vegetation, providing a precursor to the movement of fins on land and the development of limbs. The late Paleozoic was a time of diversification of vertebrates, as amniotes emerged and became two different lines that gave rise, on one hand, to mammals, and, on the other hand, to reptiles and birds. Many marine vertebrates became extinct near the end of the Devonian period, which ended about 360 million years ago, and both marine and terrestrial vertebrates were decimated by a mass extinction in the early Permian period about 250 million years ago.

Link to Learning



View Earth's Paleogeography: Continental Movements Through Time to see changes in Earth as life evolved.

Summary

As tetrapods, most amphibians are characterized by four well-developed limbs, although some species of salamanders and all caecilians are limbless. The most important characteristic of extant amphibians is a moist, permeable skin used for cutaneous respiration. The fossil record provides evidence of amphibian species, now extinct, that arose over 400 million years ago as the first tetrapods. Amphibia can be divided into three clades: salamanders (Urodela), frogs (Anura), and caecilians (Apoda). The life cycle of frogs, like the majority of amphibians, consists of two distinct stages: the larval stage and metamorphosis to an adult stage. Some species in all orders bypass a free-living larval stage.

Footnotes

1. 1 Daeschler, E. B., Shubin, N. H., and Jenkins, F. J. "A Devonian tetrapod-like fish and the evolution of the tetrapod body plan," *Nature* 440 (2006): 757–763, doi:10.1038/nature04639, http://www.nature.com/nature/journal/v440/n7085/abs/nature04639.html.

Glossary

Acanthostega
one of the earliest known tetrapods

Amphibia
frogs, salamanders, and caecilians

Anura

frogs

Apoda
caecilians

caecilian
legless amphibian that belongs to the clade Apoda

cutaneous respiration
gas exchange through the skin

frog
tail-less amphibian that belongs to the clade Anura

salamander
tailed amphibian that belongs to the clade Urodela

tadpole
larval stage of a frog

Urodela
salamanders

This page titled 5.8.4: Amphibians is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.3: Amphibians** by OpenStax is licensed CC BY 4.0.

5.8.5: Reptiles

Skills to Develop

- Describe the main characteristics of amniotes
- Explain the difference between anapsids, synapsids, and diapsids, and give an example of each
- Identify the characteristics of reptiles
- Discuss the evolution of reptiles

The amniotes —reptiles, birds, and mammals—are distinguished from amphibians by their terrestrially adapted egg, which is protected by amniotic membranes. The evolution of amniotic membranes meant that the embryos of amniotes were provided with their own aquatic environment, which led to less dependence on water for development and thus allowed the amniotes to branch out into drier environments. This was a significant development that distinguished them from amphibians, which were restricted to moist environments due their shell-less eggs. Although the shells of various amniotic species vary significantly, they all allow retention of water. The shells of bird eggs are composed of calcium carbonate and are hard, but fragile. The shells of reptile eggs are leathery and require a moist environment. Most mammals do not lay eggs (except for monotremes). Instead, the embryo grows within the mother's body; however, even with this internal gestation, amniotic membranes are still present.



Characteristics of Amniotes

The amniotic egg is the key characteristic of amniotes. In amniotes that lay eggs, the shell of the egg provides protection for the developing embryo while being permeable enough to allow for the exchange of carbon dioxide and oxygen. The albumin, or egg white, provides the embryo with water and protein, whereas the fattier egg yolk is the energy supply for the embryo, as is the case with the eggs of many other animals, such as amphibians. However, the eggs of amniotes contain three additional extra-embryonic membranes: the chorion, amnion, and allantois (Figure 5.8.5.1). Extra-embryonic membranes are membranes present in amniotic eggs that are not a part of the body of the developing embryo. While the inner amniotic membrane surrounds the embryo itself, the chorion surrounds the embryo and yolk sac. The chorion facilitates exchange of oxygen and carbon dioxide between the embryo and the egg's external environment. The amnion protects the embryo from mechanical shock and supports hydration. The allantois stores nitrogenous wastes produced by the embryo and also facilitates respiration. In mammals, membranes that are homologous to the extra-embryonic membranes in eggs are present in the placenta.

Art Connection

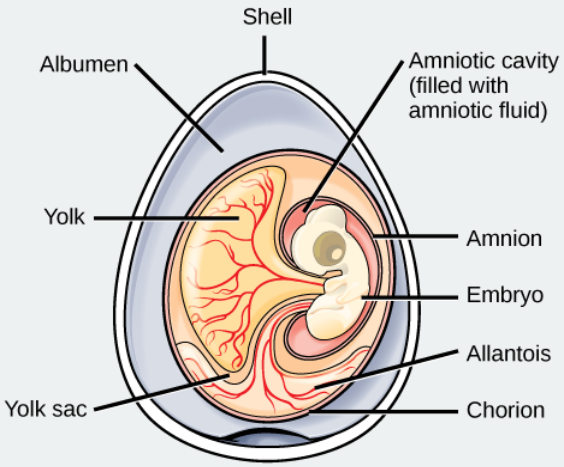


Figure 5.8.5.1: The key features of an amniotic egg are shown.

Which of the following statements about the parts of an egg are false?

A. The allantois stores nitrogenous waste and facilitates respiration.
B. The chorion facilitates gas exchange.
C. The yolk provides food for the growing embryo.
D. The amniotic cavity is filled with albumen.

Additional derived characteristics of amniotes include waterproof skin, due to the presence of lipids, and costal (rib) ventilation of the lungs.

Evolution of Amniotes

The first amniotes evolved from amphibian ancestors approximately 340 million years ago during the Carboniferous period. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids and sauropsids. Synapsids include all mammals, including extinct mammalian species. Synapsids also include therapsids, which were mammal-like reptiles from which mammals evolved. Sauropsids include reptiles and birds, and can be further divided into anapsids and diapsids. The key differences between the synapsids, anapsids, and diapsids are the structures of the skull and the number of temporal fenestrae behind each eye (Figure 5.8.5.2). Temporal fenestrae are post-orbital openings in the skull that allow muscles to expand and lengthen. Anapsids have no temporal fenestrae, synapsids have one, and diapsids have two. Anapsids include extinct organisms and may, based on anatomy, include turtles. However, this is still controversial, and turtles are sometimes classified as diapsids based on molecular evidence. The diapsids include birds and all other living and extinct reptiles.

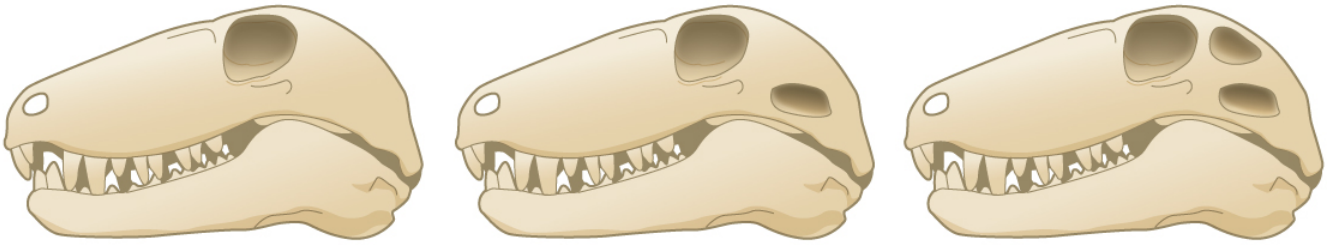


Figure 5.8.5.2: Compare the skulls and temporal fenestrae of anapsids, synapsids, and diapsids. Anapsids have no openings, synapsids have one opening, and diapsids have two openings.

The diapsids diverged into two groups, the Archosauromorpha (“ancient lizard form”) and the Lepidosauromorpha (“scaly lizard form”) during the Mesozoic period (Figure 5.8.5.3). The lepidosaurs include modern lizards, snakes, and tuataras. The archosaurs include modern crocodiles and alligators, and the extinct pterosaurs (“winged lizard”) and dinosaurs (“terrible lizard”). Clade Dinosauria includes birds, which evolved from a branch of dinosaurs.

Art Connection

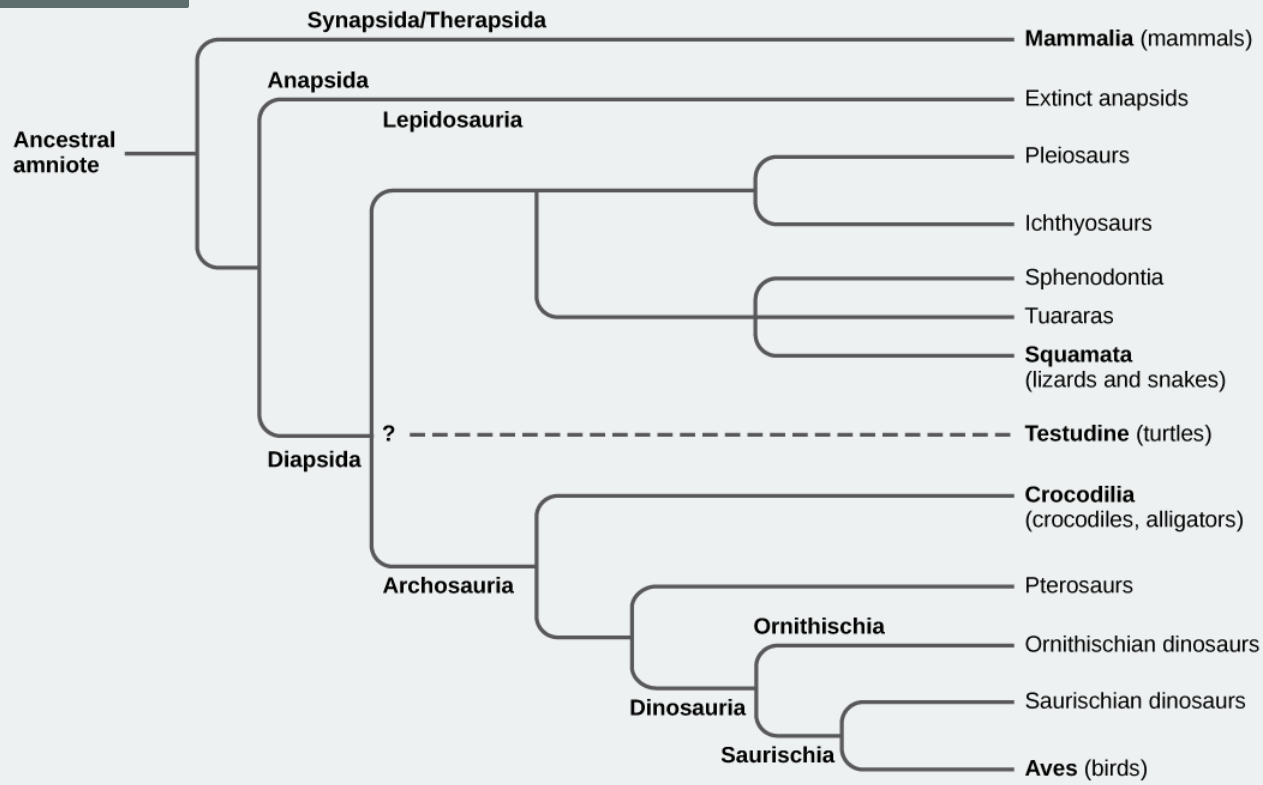


Figure 5.8.5.3: This chart shows the evolution of amniotes. The placement of Testudines (turtles) is currently still debated.

Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

In the past, the most common division of amniotes has been into the classes Mammalia, Reptilia, and Aves. Birds are descended, however, from dinosaurs, so this classical scheme results in groups that are not true clades. We will consider birds as a group distinct from reptiles for the purpose of this discussion with the understanding that this does not completely reflect phylogenetic history and relationships.



Characteristics of Reptiles

Reptiles are tetrapods. Limbless reptiles—snakes and other squamates—have vestigial limbs and, like caecilians, are classified as tetrapods because they are descended from four-limbed ancestors. Reptiles lay eggs enclosed in shells on land. Even aquatic reptiles return to the land to lay eggs. They usually reproduce sexually with internal fertilization. Some species display

ovoviviparity, with the eggs remaining in the mother's body until they are ready to hatch. Other species are viviparous, with the offspring born alive.

One of the key adaptations that permitted reptiles to live on land was the development of their scaly skin, containing the protein keratin and waxy lipids, which reduced water loss from the skin. This occlusive skin means that reptiles cannot use their skin for respiration, like amphibians, and thus all breathe with lungs.

Reptiles are ectotherms, animals whose main source of body heat comes from the environment. This is in contrast to endotherms, which use heat produced by metabolism to regulate body temperature. In addition to being ectothermic, reptiles are categorized as poikilotherms, or animals whose body temperatures vary rather than remain stable. Reptiles have behavioral adaptations to help regulate body temperature, such as basking in sunny places to warm up and finding shady spots or going underground to cool down. The advantage of ectothermy is that metabolic energy from food is not required to heat the body; therefore, reptiles can survive on about 10 percent of the calories required by a similarly sized endotherm. In cold weather, some reptiles such as the garter snake brumate. Brumation is similar to hibernation in that the animal becomes less active and can go for long periods without eating, but differs from hibernation in that brumating reptiles are not asleep or living off fat reserves. Rather, their metabolism is slowed in response to cold temperatures, and the animal is very sluggish.

Evolution of Reptiles

Reptiles originated approximately 300 million years ago during the Carboniferous period. One of the oldest known amniotes is Casineria, which had both amphibian and reptilian characteristics. One of the earliest undisputed reptiles was Hylonomus. Soon after the first amniotes appeared, they diverged into three groups—synapsids, anapsids, and diapsids—during the Permian period. The Permian period also saw a second major divergence of diapsid reptiles into archosaurs (predecessors of crocodilians and dinosaurs) and lepidosaurs (predecessors of snakes and lizards). These groups remained inconspicuous until the Triassic period, when the archosaurs became the dominant terrestrial group due to the extinction of large-bodied anapsids and synapsids during the Permian-Triassic extinction. About 250 million years ago, archosaurs radiated into the dinosaurs and the pterosaurs.

Although they are sometimes mistakenly called dinosaurs, the pterosaurs were distinct from true dinosaurs (Figure 5.8.5.4). Pterosaurs had a number of adaptations that allowed for flight, including hollow bones (birds also exhibit hollow bones, a case of convergent evolution). Their wings were formed by membranes of skin that attached to the long, fourth finger of each arm and extended along the body to the legs.



Figure 5.8.5.4: Pterosaurs, which existed from the late Triassic to the Cretaceous period (210 to 65.5 million years ago), possessed wings but are not believed to have been capable of powered flight. Instead, they may have been able to soar after launching from cliffs. (credit: Mark Witton, Darren Naish)

The dinosaurs were a diverse group of terrestrial reptiles with more than 1,000 species identified to date. Paleontologists continue to discover new species of dinosaurs. Some dinosaurs were quadrupeds (Figure 5.8.5.5); others were bipeds. Some were carnivorous, whereas others were herbivorous. Dinosaurs laid eggs, and a number of nests containing fossilized eggs have been found. It is not known whether dinosaurs were endotherms or ectotherms. However, given that modern birds are endothermic, the

dinosaurs that served as ancestors to birds likely were endothermic as well. Some fossil evidence exists for dinosaurian parental care, and comparative biology supports this hypothesis since the archosaur birds and crocodilians display parental care.

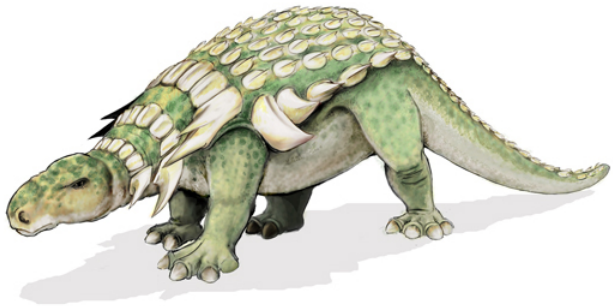
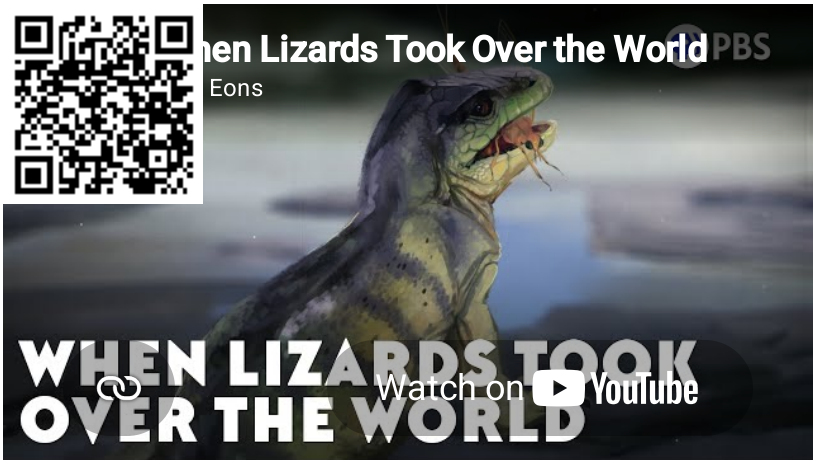


Figure 5.8.5.5: Edmontonia was an armored dinosaur that lived in the late Cretaceous period, 145.5 to 65.6 million years ago. (credit: Mariana Ruiz Villareal)

Dinosaurs dominated the Mesozoic Era, which was known as the "age of reptiles." The dominance of dinosaurs lasted until the end of the Cretaceous, the last period of the Mesozoic Era. The Cretaceous-Tertiary extinction resulted in the loss of most of the large-bodied animals of the Mesozoic Era. Birds are the only living descendants of one of the major clades of dinosaurs.



Modern Reptiles

Class Reptilia includes many diverse species that are classified into four living clades. These are the 25 species of Crocodilia, 2 species of Sphenodontia, approximately 9,200 Squamata species, and the Testudines, with about 325 species.

Crocodilia

Crocodilia ("small lizard") arose with a distinct lineage by the middle Triassic; extant species include alligators, crocodiles, and caimans. Crocodilians (Figure 5.8.5.6) live throughout the tropics and subtropics of Africa, South America, Southern Florida, Asia, and Australia. They are found in freshwater, saltwater, and brackish habitats, such as rivers and lakes, and spend most of their time in water. Some species are able to move on land due to their semi-erect posture.



Figure 5.8.5.6: Crocodilians, such as this Siamese crocodile (*Crocodylus siamensis*), provide parental care for their offspring. (credit: Keshav Mukund Kandhadai)



Sphenodontia

Sphenodontia (“wedge tooth”) arose in the Mesozoic era and includes only one living genus, *Tuatara*, comprising two species that are found in New Zealand (Figure 5.8.5.7). Tuataras measure up to 80 centimeters and weigh about 1 kilogram. Although quite lizard-like in gross appearance, several unique features of the skull and jaws clearly define them and distinguish the group from the squamates.



Figure 5.8.5.7: This tuatara from New Zealand may resemble a lizard but belongs to a distinct lineage, the Sphenodontidae family. (credit: Sid Mosdell)



Squamata

Squamata (“scaly”) arose in the late Permian, and extant species include lizards and snakes. Both are found on all continents except Antarctica. Lizards and snakes are most closely related to tuataras, both groups having evolved from a lepidosaurian ancestor. Squamata is the largest extant clade of reptiles (Figure 5.8.5.8). Most lizards differ from snakes by having four limbs, although these have been variously lost or significantly reduced in at least 60 lineages. Snakes lack eyelids and external ears, which are present in lizards. Lizard species range in size from chameleons and geckos, which are a few centimeters in length, to the Komodo dragon, which is about 3 meters in length. Most lizards are carnivorous, but some large species, such as iguanas, are herbivores.



Figure 5.8.5.8: This Jackson’s chameleon (*Trioceros jacksonii*) blends in with its surroundings.

Snakes are thought to have descended from either burrowing lizards or aquatic lizards over 100 million years ago (Figure 5.8.5.9). Snakes comprise about 3,000 species and are found on every continent except Antarctica. They range in size from 10 centimeter-long thread snakes to 10 meter-long pythons and anacondas. All snakes are carnivorous and eat small animals, birds, eggs, fish, and insects. The snake body form is so specialized that, in its general morphology, a “snake is a snake.” Their specializations all point to snakes having evolved to feed on relatively large prey (even though some current species have reversed this trend). Although variations exist, most snakes have a skull that is very flexible, involving eight rotational joints. They also differ from other squamates by having mandibles (lower jaws) without either bony or ligamentous attachment anteriorly. Having this connection via skin and muscle allows for great expansion of the gape and independent motion of the two sides—both advantages in swallowing big items.



Figure 5.8.5.9: The garter snake belongs to the genus *Thamnophis*, the most widely distributed reptile genus in North America. (credit: Steve Jurvetson)



Testudines

Turtles are members of the clade Testudines (“having a shell”) (Figure 5.8.5.10). Turtles are characterized by a bony or cartilaginous shell. The shell consists of the ventral surface called the plastron and the dorsal surface called the carapace, which develops from the ribs. The plastron is made of scutes or plates; the scutes can be used to differentiate species of turtles. The two clades of turtles are most easily recognized by how they retract their necks. The dominant group, which includes all North American species, retracts its neck in a vertical S-curve. Turtles in the less speciose clade retract the neck with a horizontal curve.

Turtles arose approximately 200 million years ago, predating crocodiles, lizards, and snakes. Similar to other reptiles, turtles are ectotherms. They lay eggs on land, although many species live in or near water. None exhibit parental care. Turtles range in size from the speckled padloper tortoise at 8 centimeters (3.1 inches) to the leatherback sea turtle at 200 centimeters (over 6 feet). The term “turtle” is sometimes used to describe only those species of Testudines that live in the sea, with the terms “tortoise” and “terrapin” used to refer to species that live on land and in fresh water, respectively.



Figure 5.8.5.10: The African spurred tortoise (*Geochelone sulcata*) lives at the southern edge of the Sahara Desert. It is the third largest tortoise in the world. (credit: Jim Bowen)





Summary

The amniotes are distinguished from amphibians by the presence of a terrestrially adapted egg protected by amniotic membranes. The amniotes include reptiles, birds, and mammals. The early amniotes diverged into two main lines soon after the first amniotes arose. The initial split was into synapsids (mammals) and sauropsids. Sauropsids can be further divided into anapsids (turtles) and diapsids (birds and reptiles). Reptiles are tetrapods either having four limbs or descending from such. Limbless reptiles (snakes) are classified as tetrapods, as they are descended from four-limbed organisms. One of the key adaptations that permitted reptiles to live

on land was the development of scaly skin containing the protein keratin, which prevented water loss from the skin. Reptilia includes four living clades: Crocodilia (crocodiles and alligators), Sphenodontia (tuataras), Squamata (lizards and snakes), and Testudines (turtles).

Art Connections

Figure 5.8.5.1: Which of the following statements about the parts of an egg are false?

A. The allantois stores nitrogenous waste and facilitates respiration.
B. The chorion facilitates gas exchange.
C. The yolk provides food for the growing embryo.
D. The amniotic cavity is filled with albumen.

Answer

D

Figure 5.8.5.3: Members of the order Testudines have an anapsid-like skull with one opening. However, molecular studies indicate that turtles descended from a diapsid ancestor. Why might this be the case?

Answer

The ancestor of modern Testudines may at one time have had a second opening in the skull, but over time this might have been lost.

Glossary

amniote
animal that produces a terrestrially adapted egg protected by amniotic membranes

allantois
membrane of the egg that stores nitrogenous wastes produced by the embryo; also facilitates respiration

amnion
membrane of the egg that protects the embryo from mechanical shock and prevents dehydration

anapsid
animal having no temporal fenestrae in the cranium

archosaur
modern crocodilian or bird, or an extinct pterosaur or dinosaur

brumation
period of much reduced metabolism and torpor that occurs in any ectotherm in cold weather

Casineria
one of the oldest known amniotes; had both amphibian and reptilian characteristics

chorion
membrane of the egg that surrounds the embryo and yolk sac

Crocodilia
crocodiles and alligators

diapsid

animal having two temporal fenestrae in the cranium

Hylonomus
one of the earliest reptiles

lepidosaur
modern lizards, snakes, and tuataras

sauropsid
reptile or bird

Sphenodontia
clade of tuataras

Squamata
clade of lizards and snakes

synapsid
mammal having one temporal fenestra

temporal fenestra
non-orbital opening in the skull that may allow muscles to expand and lengthen

Testudines
order of turtles

This page titled 5.8.5: Reptiles is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.4: Reptiles** by OpenStax is licensed CC BY 4.0.

5.8.6: Birds

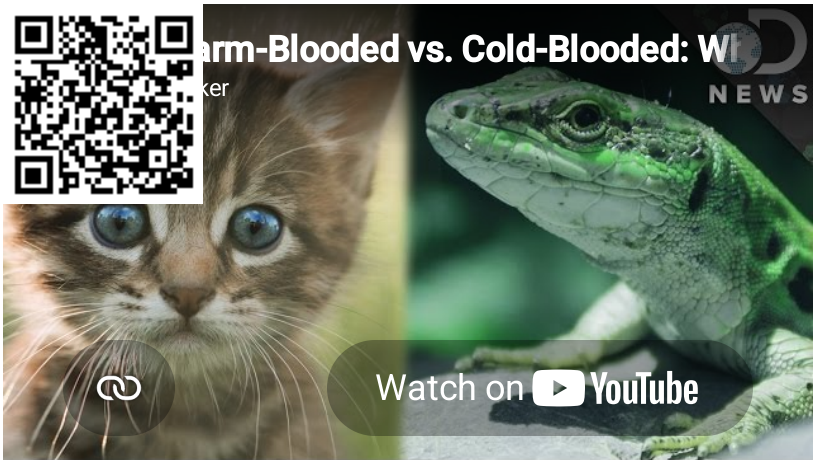
Skills to Develop

- Describe the evolutionary history of birds
- Describe the derived characteristics in birds that facilitate flight

The most obvious characteristic that sets birds apart from other modern vertebrates is the presence of feathers, which are modified scales. While vertebrates like bats fly without feathers, birds rely on feathers and wings, along with other modifications of body structure and physiology, for flight.

Characteristics of Birds

Birds are endothermic, and because they fly, they require large amounts of energy, necessitating a high metabolic rate. Like mammals, which are also endothermic, birds have an insulating covering that keeps heat in the body: feathers. Specialized feathers called down feathers are especially insulating, trapping air in spaces between each feather to decrease the rate of heat loss. Certain parts of a bird's body are covered in down feathers, and the base of other feathers have a downy portion, whereas newly hatched birds are covered in down.



Feathers not only act as insulation but also allow for flight, enabling the lift and thrust necessary to become airborne. The feathers on a wing are flexible, so the collective feathers move and separate as air moves through them, reducing the drag on the wing. Flight feathers are asymmetrical, which affects airflow over them and provides some of the lifting and thrusting force required for flight (Figure 5.8.6.1). Two types of flight feathers are found on the wings, primary feathers and secondary feathers. Primary feathers are located at the tip of the wing and provide thrust. Secondary feathers are located closer to the body, attach to the forearm portion of the wing and provide lift. Contour feathers are the feathers found on the body, and they help reduce drag produced by wind resistance during flight. They create a smooth, aerodynamic surface so that air moves smoothly over the bird's body, allowing for efficient flight.



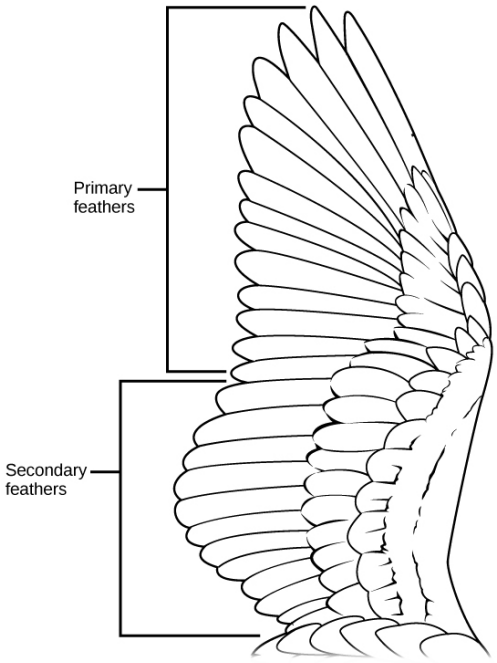


Figure 5.8.6.1: Primary feathers are located at the wing tip and provide thrust; secondary feathers are located close to the body and provide lift.

Flapping of the entire wing occurs primarily through the actions of the chest muscles, the pectoralis and the supracoracoideus. These muscles are highly developed in birds and account for a higher percentage of body mass than in most mammals. These attach to a blade-shaped keel, like that of a boat, located on the sternum. The sternum of birds is larger than that of other vertebrates, which accommodates the large muscles required to generate enough upward force to generate lift with the flapping of the wings. Another skeletal modification found in most birds is the fusion of the two clavicles (collarbones), forming the furcula or wishbone. The furcula is flexible enough to bend and provide support to the shoulder girdle during flapping.

An important requirement of flight is a low body weight. As body weight increases, the muscle output required for flying increases. The largest living bird is the ostrich, and while it is much smaller than the largest mammals, it is flightless. For birds that do fly, reduction in body weight makes flight easier. Several modifications are found in birds to reduce body weight, including pneumatization of bones. Pneumatic bones are bones that are hollow, rather than filled with tissue (Figure 5.8.6.2). They contain air spaces that are sometimes connected to air sacs, and they have struts of bone to provide structural reinforcement. Pneumatic bones are not found in all birds, and they are more extensive in large birds than in small birds. Not all bones of the skeleton are pneumatic, although the skulls of almost all birds are.

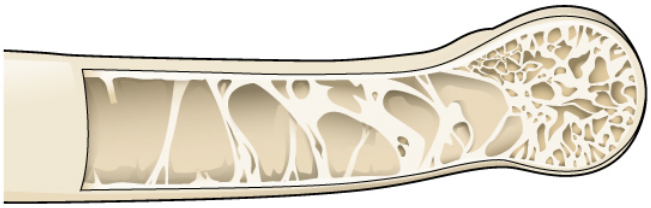


Figure 5.8.6.2: Many birds have hollow, pneumatic bones, which make flight easier.

Other modifications that reduce weight include the lack of a urinary bladder. Birds possess a cloaca, a structure that allows water to be reabsorbed from waste back into the bloodstream. Uric acid is not expelled as a liquid but is concentrated into urate salts, which are expelled along with fecal matter. In this way, water is not held in the urinary bladder, which would increase body weight. Most bird species only possess one ovary rather than two, further reducing body mass.

The air sacs that extend into bones to form pneumatic bones also join with the lungs and function in respiration. Unlike mammalian lungs in which air flows in two directions, as it is breathed in and out, airflow through bird lungs travels in one direction (Figure 5.8.6.3). Air sacs allow for this unidirectional airflow, which also creates a cross-current exchange system with the blood. In a cross-current or counter-current system, the air flows in one direction and the blood flows in the opposite direction, creating a very efficient means of gas exchange.

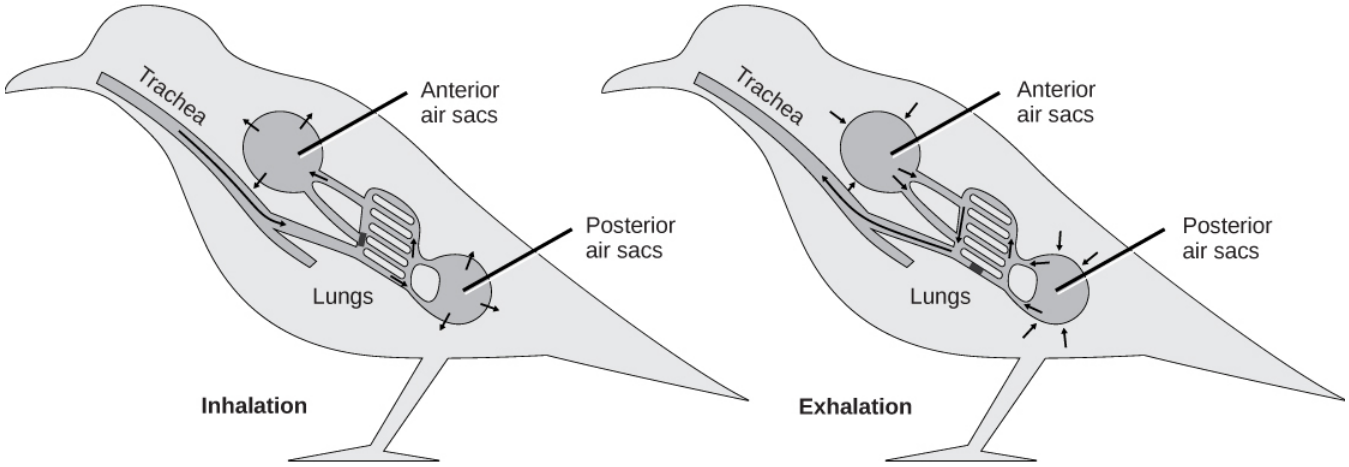


Figure 5.8.6.3: Avian respiration is an efficient system of gas exchange with air flowing unidirectionally. During inhalation, air passes from the trachea into posterior air sacs, then through the lungs to anterior air sacs. The air sacs are connected to the hollow interior of bones. During exhalation, air from air sacs passes into the lungs and out the trachea. (credit: modification of work by L. Shyamal)

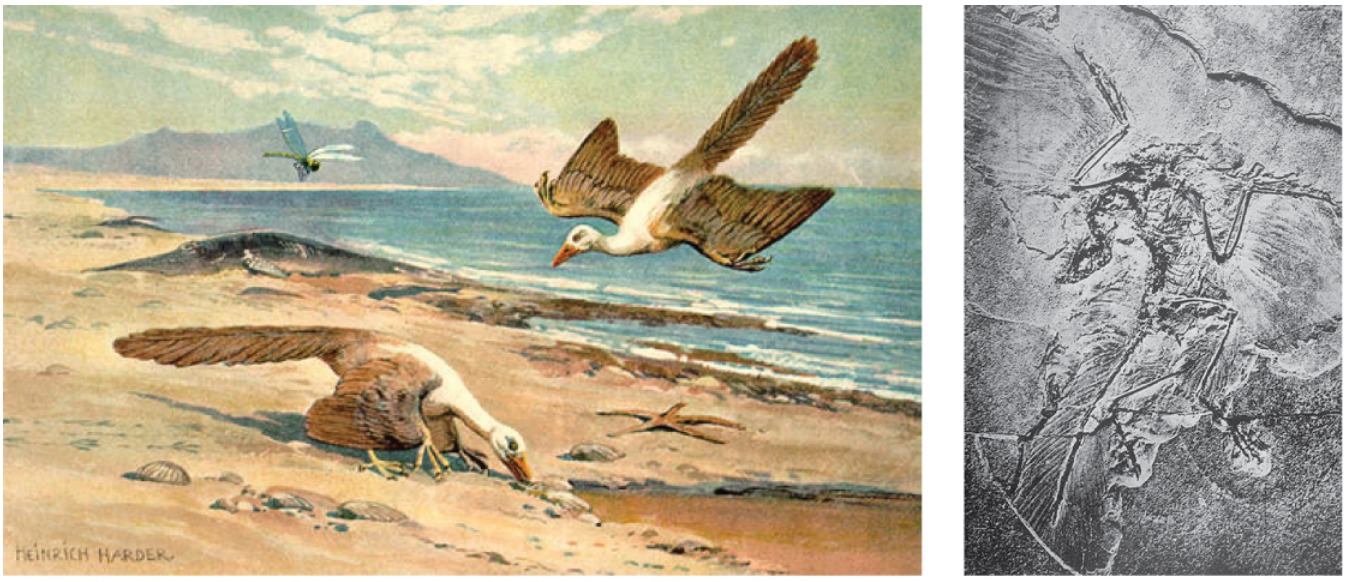
Evolution of Birds



The evolutionary history of birds is still somewhat unclear. Due to the fragility of bird bones, they do not fossilize as well as other vertebrates. Birds are diapsids, meaning they have two fenestrations or openings in their skulls. Birds belong to a group of diapsids called the archosaurs, which also includes crocodiles and dinosaurs. It is commonly accepted that birds evolved from dinosaurs.

Dinosaurs (including birds) are further subdivided into two groups, the Saurischia ("lizard like") and the Ornithischia ("bird like"). Despite the names of these groups, it was not the bird-like dinosaurs that gave rise to modern birds. Rather, Saurischia diverged into two groups: One included the long-necked herbivorous dinosaurs, such as Apatosaurus. The second group, bipedal predators called theropods, includes birds. This course of evolution is suggested by similarities between theropod fossils and birds, specifically in the structure of the hip and wrist bones, as well as the presence of the wishbone, formed by the fusing of the clavicles.

One important fossil of an animal intermediate to dinosaurs and birds is *Archaeopteryx*, which is from the Jurassic period (Figure 5.8.6.4). *Archaeopteryx* is important in establishing the relationship between birds and dinosaurs, because it is an intermediate fossil, meaning it has characteristics of both dinosaurs and birds. Some scientists propose classifying it as a bird, but others prefer to classify it as a dinosaur. The fossilized skeleton of *Archaeopteryx* looks like that of a dinosaur, and it had teeth whereas birds do not, but it also had feathers modified for flight, a trait associated only with birds among modern animals. Fossils of older feathered dinosaurs exist, but the feathers do not have the characteristics of flight feathers.



(a) (b)

Figure 5.8.6.4: (a) *Archaeopteryx* lived in the late Jurassic Period around 150 million years ago. It had teeth like a dinosaur, but had (b) flight feathers like modern birds, which can be seen in this fossil.

It is still unclear exactly how flight evolved in birds. Two main theories exist, the arboreal ("tree") hypothesis and the terrestrial ("land") hypothesis. The arboreal hypothesis posits that tree-dwelling precursors to modern birds jumped from branch to branch using their feathers for gliding before becoming fully capable of flapping flight. In contrast to this, the terrestrial hypothesis holds that running was the stimulus for flight, as wings could be used to improve running and then became used for flapping flight. Like the question of how flight evolved, the question of how endothermy evolved in birds still is unanswered. Feathers provide insulation, but this is only beneficial if body heat is being produced internally. Similarly, internal heat production is only viable if insulation is present to retain that heat. It has been suggested that one or the other—feathers or endothermy—evolved in response to some other selective pressure.

During the Cretaceous period, a group known as the Enantiornithes was the dominant bird type (Figure 5.8.6.5). Enantiornithes means "opposite birds," which refers to the fact that certain bones of the feet are joined differently than the way the bones are joined in modern birds. These birds formed an evolutionary line separate from modern birds, and they did not survive past the Cretaceous. Along with the Enantiornithes, Ornithurae birds (the evolutionary line that includes modern birds) were also present in the Cretaceous. After the extinction of Enantiornithes, modern birds became the dominant bird, with a large radiation occurring during the Cenozoic Era. Referred to as Neornithes ("new birds"), modern birds are now classified into two groups, the

Paleognathae (“old jaw”) or ratites, a group of flightless birds including ostriches, emus, rheas, and kiwis, and the Neognathae (“new jaw”), which includes all other birds.

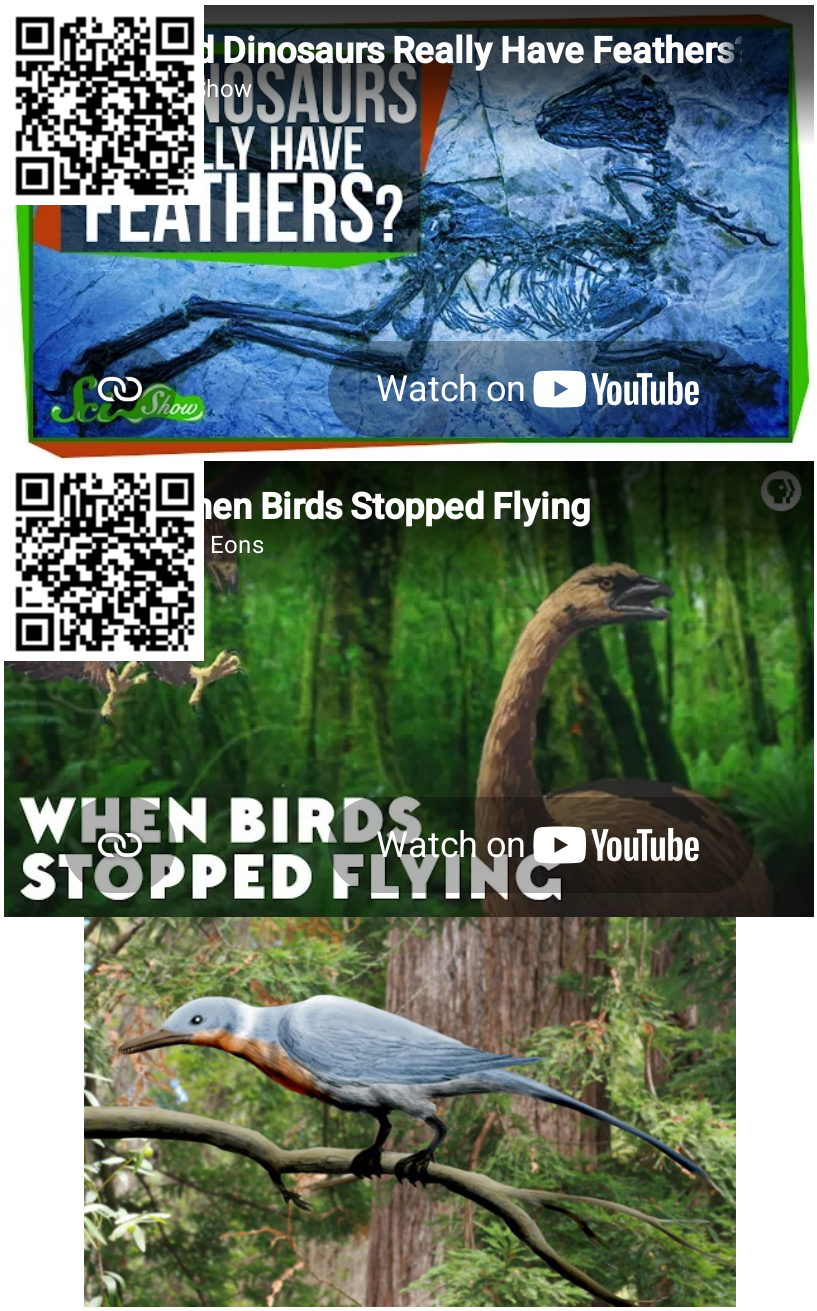


Figure 5.8.6.5: Shanweiniao cooperorum was a species of Enantiornithes that did not survive past the Cretaceous period. (credit: Nobu Tamura)

Career Connection: Veterinarian

Veterinarians treat diseases, disorders, and injuries in animals, primarily vertebrates. They treat pets, livestock, and animals in zoos and laboratories. Veterinarians usually treat dogs and cats, but also treat birds, reptiles, rabbits, and other animals that are kept as pets. Veterinarians that work with farms and ranches treat pigs, goats, cows, sheep, and horses.

Veterinarians are required to complete a degree in veterinary medicine, which includes taking courses in animal physiology, anatomy, microbiology, and pathology, among many other courses. The physiology and biochemistry of different vertebrate species differ greatly.

Veterinarians are also trained to perform surgery on many different vertebrate species, which requires an understanding of the vastly different anatomies of various species. For example, the stomach of ruminants like cows has four compartments versus one compartment for non-ruminants. Birds also have unique anatomical adaptations that allow for flight.

Some veterinarians conduct research in academic settings, broadening our knowledge of animals and medical science. One area of research involves understanding the transmission of animal diseases to humans, called zoonotic diseases. For example, one area of great concern is the transmission of the avian flu virus to humans. One type of avian flu virus, H5N1, is a highly pathogenic strain that has been spreading in birds in Asia, Europe, Africa, and the Middle East. Although the virus does not cross over easily to humans, there have been cases of bird-to-human transmission. More research is needed to understand how this virus can cross the species barrier and how its spread can be prevented.

Summary

Birds are endothermic, meaning they produce their own body heat and regulate their internal temperature independently of the external temperature. Feathers not only act as insulation but also allow for flight, providing lift with secondary feathers and thrust with primary feathers. Pneumatic bones are bones that are hollow rather than filled with tissue, containing air spaces that are sometimes connected to air sacs. Airflow through bird lungs travels in one direction, creating a cross-current exchange with the blood. Birds are diapsids and belong to a group called the archosaurs. Birds are thought to have evolved from theropod dinosaurs. The oldest known fossil of a bird is that of *Archaeopteryx*, which is from the Jurassic period. Modern birds are now classified into two groups, Paleognathae and Neognathae.

Glossary

Archaeopteryx
transition species from dinosaur to bird from the Jurassic period

contour feather
feather that creates an aerodynamic surface for efficient flight

down feather
feather specialized for insulation

Enantiornithes
dominant bird group during the Cretaceous period

flight feather
feather specialized for flight

furcula
wishbone formed by the fusing of the clavicles

Neognathae
birds other than the Paleognathae

Neornithes
modern birds

Paleognathae
ratites; flightless birds, including ostriches and emus

pneumatic bone
air-filled bone

primary feather

feather located at the tip of the wing that provides thrust

secondary feather

feather located at the base of the wing that provides lift

theropod

dinosaur group ancestral to birds

This page titled 5.8.6: Birds is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.5: Birds** by OpenStax is licensed CC BY 4.0.

5.8.7: Mammals

Skills to Develop

- Name and describe the distinguishing features of the three main groups of mammals
- Describe the proposed line of descent that produced mammals
- List some derived features that may have arisen in response to mammals' need for constant, high-level metabolism

Mammals are vertebrates that possess hair and mammary glands. Several other characteristics are distinctive to mammals, including certain features of the jaw, skeleton, integument, and internal anatomy. Modern mammals belong to three clades: monotremes, marsupials, and eutherians (or placental mammals).



Characteristics of Mammals

The presence of hair is one of the most obvious signs of a mammal. Although it is not very extensive on certain species, such as whales, hair has many important functions for mammals. Mammals are endothermic, and hair provides insulation to retain heat generated by metabolic work. Hair traps a layer of air close to the body, retaining heat. Along with insulation, hair can serve as a sensory mechanism via specialized hairs called vibrissae, better known as whiskers. These attach to nerves that transmit information about sensation, which is particularly useful to nocturnal or burrowing mammals. Hair can also provide protective coloration or be part of social signaling, such as when an animal's hair stands "on end."

Mammalian integument, or skin, includes secretory glands with various functions. Sebaceous glands produce a lipid mixture called sebum that is secreted onto the hair and skin for water resistance and lubrication. Sebaceous glands are located over most of the body. Eccrine glands produce sweat, or perspiration, which is mainly composed of water. In most mammals, eccrine glands are limited to certain areas of the body, and some mammals do not possess them at all. However, in primates, especially humans, sweat figures prominently in thermoregulation, regulating the body through evaporative cooling. Sweat glands are located over most of the body surface in primates. Apocrine glands, or scent glands, secrete substances that are used for chemical communication, such as in skunks. Mammary glands produce milk that is used to feed newborns. While male monotremes and eutherians possess mammary glands, male marsupials do not. Mammary glands likely are modified sebaceous or eccrine glands, but their evolutionary origin is not entirely clear.



The skeletal system of mammals possesses many unique features. The lower jaw of mammals consists of only one bone, the dentary. The jaws of other vertebrates are composed of more than one bone. In mammals, the dentary bone joins the skull at the squamosal bone, while in other vertebrates, the quadrate bone of the jaw joins with the articular bone of the skull. These bones are present in mammals, but they have been modified to function in hearing and form bones in the middle ear (Figure 5.8.7.1). Other vertebrates possess only one middle ear bone, the stapes. Mammals have three: the malleus, incus, and stapes. The malleus originated from the articular bone, whereas the incus originated from the quadrate bone. This arrangement of jaw and ear bones aids in distinguishing fossil mammals from fossils of other synapsids.

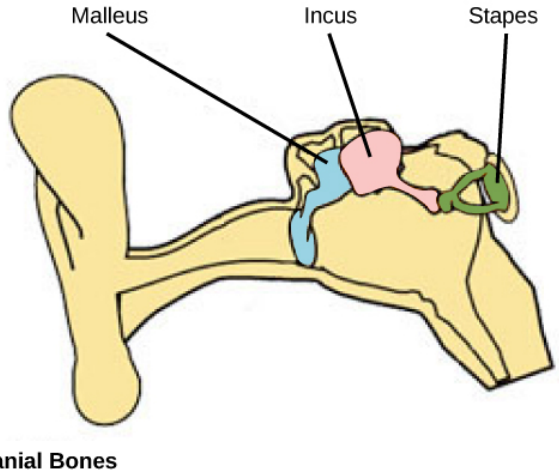


Figure 5.8.7.1: Bones of the mammalian inner ear are modified from bones of the jaw and skull. (credit: NCI)

The adductor muscle that closes the jaw is composed of two muscles in mammals: the temporalis and the masseter. These allow side-to-side movement of the jaw, making chewing possible, which is unique to mammals. Most mammals have heterodont teeth, meaning that they have different types and shapes of teeth rather than just one type and shape of tooth. Most mammals are diphyodonts, meaning that they have two sets of teeth in their lifetime: deciduous or “baby” teeth, and permanent teeth. Other vertebrates are polyphyodonts, that is, their teeth are replaced throughout their entire life.

Mammals, like birds, possess a four-chambered heart. Mammals also have a specialized group of cardiac fibers located in the walls of their right atrium called the sinoatrial node, or pacemaker, which determines the rate at which the heart beats. Mammalian erythrocytes (red blood cells) do not have nuclei, whereas the erythrocytes of other vertebrates are nucleated.

The kidneys of mammals have a portion of the nephron called the loop of Henle or nephritic loop, which allows mammals to produce urine with a high concentration of solutes, higher than that of the blood. Mammals lack a renal portal system, which is a system of veins that moves blood from the hind or lower limbs and region of the tail to the kidneys. Renal portal systems are present in all other vertebrates except jawless fishes. A urinary bladder is present in all mammals.

Mammalian brains have certain characteristics that differ from other vertebrates. In some, but not all mammals, the cerebral cortex, the outermost part of the cerebrum, is highly folded, allowing for a greater surface area than is possible with a smooth cortex. The

optic lobes, located in the midbrain, are divided into two parts in mammals, whereas other vertebrates possess a single, undivided lobe. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

Evolution of Mammals

Mammals are synapsids, meaning they have a single opening in the skull. They are the only living synapsids, as earlier forms became extinct by the Jurassic period. The early non-mammalian synapsids can be divided into two groups, the pelycosaurs and the therapsids. Within the therapsids, a group called the cynodonts are thought to be the ancestors of mammals (Figure 5.8.7.2).

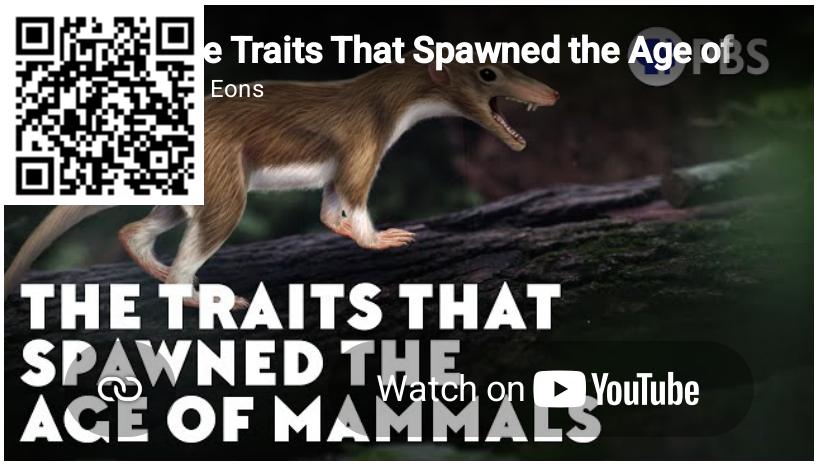


Figure 5.8.7.2: Cynodonts, which first appeared in the Late Permian period 260 million years ago, are thought to be the ancestors of modern mammals. (credit: Nobu Tamura)

A key characteristic of synapsids is endothermy, rather than the ectothermy seen in most other vertebrates. The increased metabolic rate required to internally modify body temperature went hand in hand with changes to certain skeletal structures. The later synapsids, which had more evolved characteristics unique to mammals, possess cheeks for holding food and heterodont teeth, which are specialized for chewing, mechanically breaking down food to speed digestion and releasing the energy needed to produce heat. Chewing also requires the ability to chew and breathe at the same time, which is facilitated by the presence of a secondary palate. A secondary palate separates the area of the mouth where chewing occurs from the area above where respiration occurs, allowing breathing to proceed uninterrupted during chewing. A secondary palate is not found in pelycosaurs but is present in cynodonts and mammals. The jawbone also shows changes from early synapsids to later ones. The zygomatic arch, or cheekbone, is present in mammals and advanced therapsids such as cynodonts, but is not present in pelycosaurs. The presence of the zygomatic arch suggests the presence of the masseter muscle, which closes the jaw and functions in chewing.

In the appendicular skeleton, the shoulder girdle of therian mammals is modified from that of other vertebrates in that it does not possess a procoracoid bone or an interclavicle, and the scapula is the dominant bone.

Mammals evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period, some 205 million years ago. Early mammals were small, about the size of a small rodent. Mammals first began to diversify in the Mesozoic Era, from the Jurassic to the Cretaceous periods, although most of these mammals were extinct by the end of the Mesozoic. During the Cretaceous period, another radiation of mammals began and continued through the Cenozoic Era, about 65 million years ago.



Living Mammals

The eutherians, or placental mammals, and the marsupials together comprise the clade of therian mammals. Monotremes, or metatherians, form their sister clade.

There are three living species of monotremes: the platypus and two species of echidnas, or spiny anteaters. The leathery-beaked platypus belongs to the family Ornithorhynchidae (“bird beak”), whereas echidnas belong to the family Tachyglossidae (“sticky tongue”) (Figure 5.8.7.3). The platypus and one species of echidna are found in Australia, and the other species of echidna is found in New Guinea. Monotremes are unique among mammals as they lay eggs, rather than giving birth to live young. The shells of their eggs are not like the hard shells of birds, but are a leathery shell, similar to the shells of reptile eggs. Monotremes have no teeth.

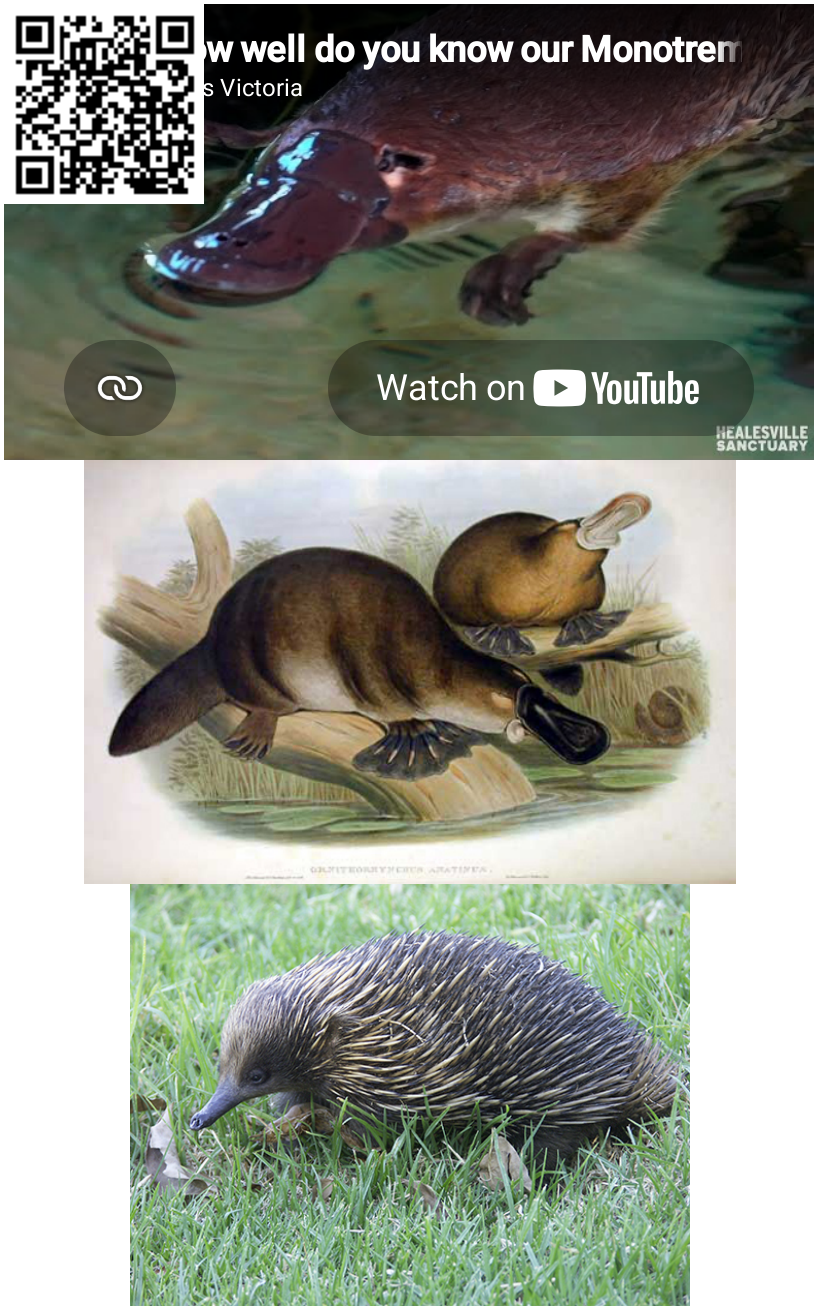


Figure 5.8.7.3: (a) The platypus, a monotreme, possesses a leathery beak and lays eggs rather than giving birth to live young. (b) The echidna is another monotreme. (credit b: modification of work by Barry Thomas)

Marsupials are found primarily in Australia, though the opossum is found in North America. Australian marsupials include the kangaroo, koala, bandicoot, Tasmanian devil (Figure 5.8.7.4), and several other species. Most species of marsupials possess a pouch in which the very premature young reside after birth, receiving milk and continuing to develop. Marsupials differ from eutherians in that there is a less complex placental connection: The young are born at an extremely early age and latch onto the nipple within the pouch.

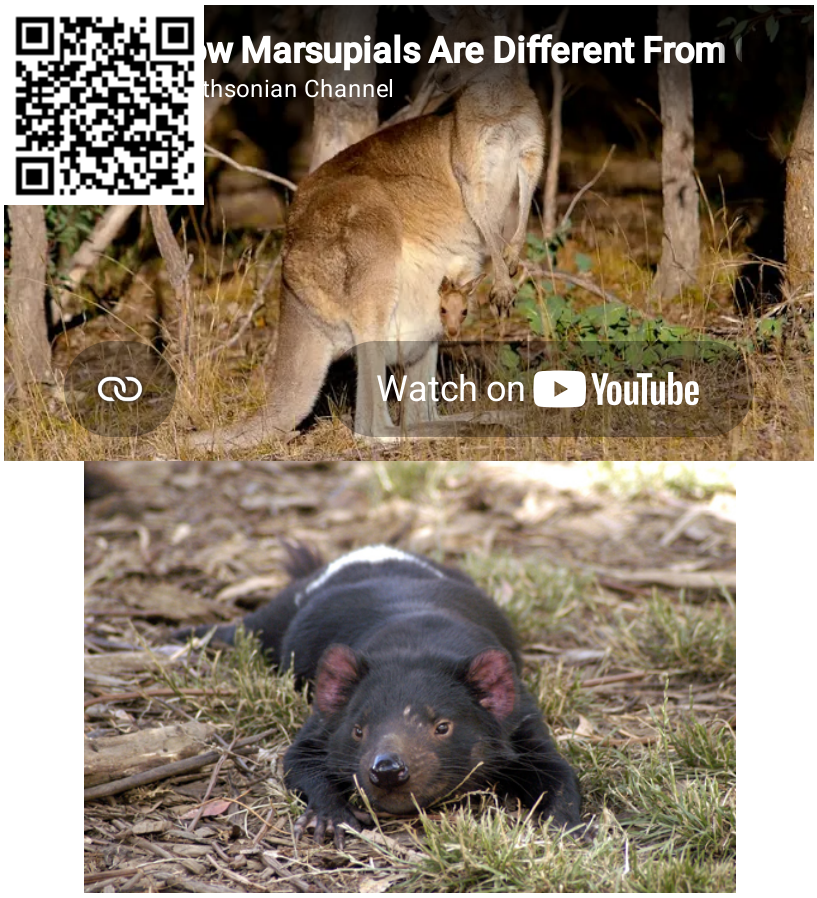
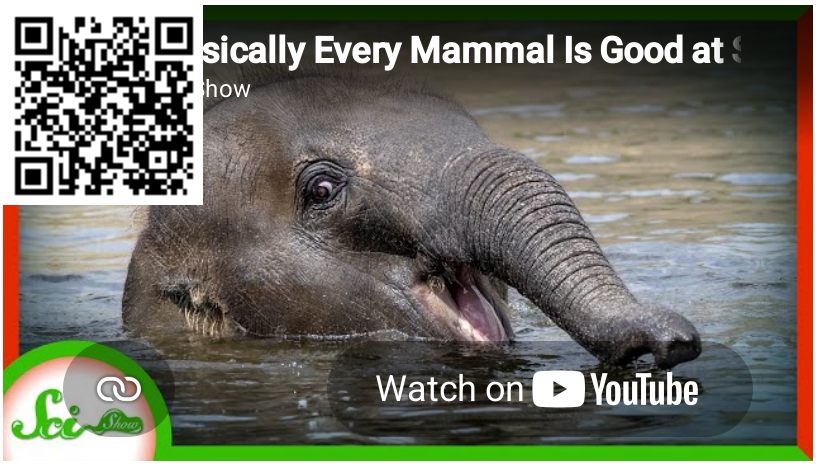


Figure 5.8.7.4: The Tasmanian devil is one of several marsupials native to Australia. (credit: Wayne McLean)

Eutherians are the most widespread of the mammals, occurring throughout the world. There are 18 to 20 orders of placental mammals. Some examples are Insectivora, the insect eaters; Edentata, the toothless anteaters; Rodentia, the rodents; Cetacea, the aquatic mammals including whales; Carnivora, carnivorous mammals including dogs, cats, and bears; and Primates, which includes humans. Eutherian mammals are sometimes called placental mammals because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange. While other mammals possess a less complex placenta or briefly have a placenta, all eutherians possess a complex placenta during gestation.



Summary

Mammals in general are vertebrates that possess hair and mammary glands. The mammalian integument includes various secretory glands, including sebaceous glands, eccrine glands, apocrine glands, and mammary glands. Mammals are synapsids, meaning that they have a single opening in the skull. A key characteristic of synapsids is endothermy rather than the ectothermy seen in other vertebrates. Mammals probably evolved from therapsids in the late Triassic period, as the earliest known mammal fossils are from the early Jurassic period. There are three groups of mammals living today: monotremes, marsupials, and eutherians. Monotremes are unique among mammals as they lay eggs, rather than giving birth to young. Eutherian mammals are sometimes called placental mammals, because all species possess a complex placenta that connects a fetus to the mother, allowing for gas, fluid, and nutrient exchange.

Glossary

apocrine gland
: scent gland that secretes substances that are used for chemical communication

dentary
: single bone that comprises the lower jaw of mammals

diphyodont
: refers to the possession of two sets of teeth in a lifetime

eccrine gland
: sweat gland

eutherian mammal
: mammal that possesses a complex placenta, which connects a fetus to the mother; sometimes called placental mammals

heterodont tooth
: different types of teeth that are modified for different purposes

mammal
: one of the groups of endothermic vertebrates that possesses hair and mammary glands

mammary gland
: in female mammals, a gland that produces milk for newborns

marsupial

one of the groups of mammals that includes the kangaroo, koala, bandicoot, Tasmanian devil, and several other species; young develop within a pouch

monotreme

egg-laying mammal

Ornithorhynchidae

clade that includes the duck-billed platypus

sebaceous gland

in mammals, a skin gland that produce a lipid mixture called *sebum*

Tachyglossidae

clade that includes the echidna or spiny anteater

This page titled 5.8.7: Mammals is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.6: Mammals** by OpenStax is licensed CC BY 4.0.

5.8.8: The Evolution of Primates

Skills to Develop

- Describe the derived features that distinguish primates from other animals
- Explain why scientists are having difficulty determining the true lines of descent in hominids

Order Primates of class Mammalia includes lemurs, tarsiers, monkeys, apes, and humans. Non-human primates live primarily in the tropical or subtropical regions of South America, Africa, and Asia. They range in size from the mouse lemur at 30 grams (1 ounce) to the mountain gorilla at 200 kilograms (441 pounds). The characteristics and evolution of primates is of particular interest to us as it allows us to understand the evolution of our own species.

Characteristics of Primates

All primate species possess adaptations for climbing trees, as they all descended from tree-dwellers. This arboreal heritage of primates has resulted in hands and feet that are adapted for brachiation, or climbing and swinging through trees. These adaptations include, but are not limited to: 1) a rotating shoulder joint, 2) a big toe that is widely separated from the other toes and thumbs, which are widely separated from fingers (except humans), which allow for gripping branches, 3) stereoscopic vision, two overlapping fields of vision from the eyes, which allows for the perception of depth and gauging distance. Other characteristics of primates are brains that are larger than those of most other mammals, claws that have been modified into flattened nails, typically only one offspring per pregnancy, and a trend toward holding the body upright.

Order Primates is divided into two groups: prosimians and anthropoids. Prosimians include the bush babies of Africa, the lemurs of Madagascar, and the lorises, pottos, and tarsiers of Southeast Asia. Anthropoids include monkeys, apes, and humans. In general, prosimians tend to be nocturnal (in contrast to diurnal anthropoids) and exhibit a smaller size and smaller brain than anthropoids.

Evolution of Primates

The first primate-like mammals are referred to as proto-primates. They were roughly similar to squirrels and tree shrews in size and appearance. The existing fossil evidence (mostly from North Africa) is very fragmented. These proto-primates remain largely mysterious creatures until more fossil evidence becomes available. The oldest known primate-like mammals with a relatively robust fossil record is *Plesiadapis* (although some researchers do not agree that *Plesiadapis* was a proto-primate). Fossils of this primate have been dated to approximately 55 million years ago. Plesiadapiforms were proto-primates that had some features of the teeth and skeleton in common with true primates. They were found in North America and Europe in the Cenozoic and went extinct by the end of the Eocene.

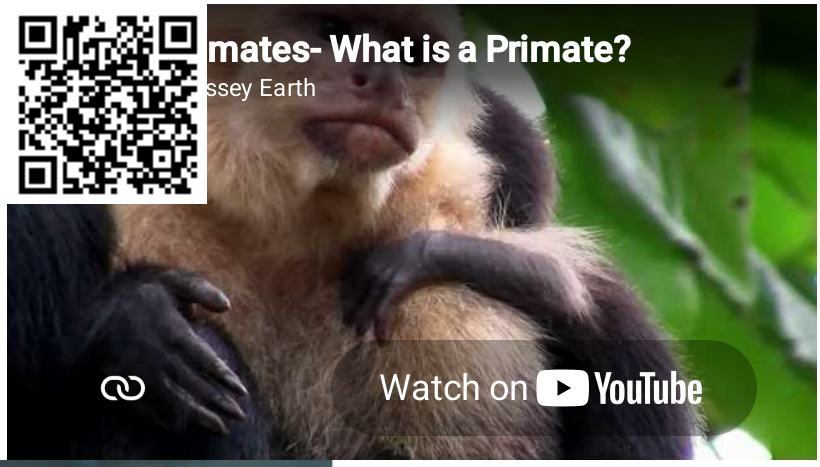
The first true primates were found in North America, Europe, Asia, and Africa in the Eocene Epoch. These early primates resembled present-day prosimians such as lemurs. Evolutionary changes continued in these early primates, with larger brains and eyes, and smaller muzzles being the trend. By the end of the Eocene Epoch, many of the early prosimian species went extinct due either to cooler temperatures or competition from the first monkeys.

Anthropoid monkeys evolved from prosimians during the Oligocene Epoch. By 40 million years ago, evidence indicates that monkeys were present in the New World (South America) and the Old World (Africa and Asia). New World monkeys are also called Platyrrhini—a reference to their broad noses (Figure 5.8.8.1). Old World monkeys are called Catarrhini—a reference to their narrow noses. There is still quite a bit of uncertainty about the origins of the New World monkeys. At the time the platyrrhines arose, the continents of South American and Africa had drifted apart. Therefore, it is thought that monkeys arose in the Old World and reached the New World either by drifting on log rafts or by crossing land bridges. Due to this reproductive isolation, New World monkeys and Old World monkeys underwent separate adaptive radiations over millions of years. The New World monkeys are all arboreal, whereas Old World monkeys include arboreal and ground-dwelling species.

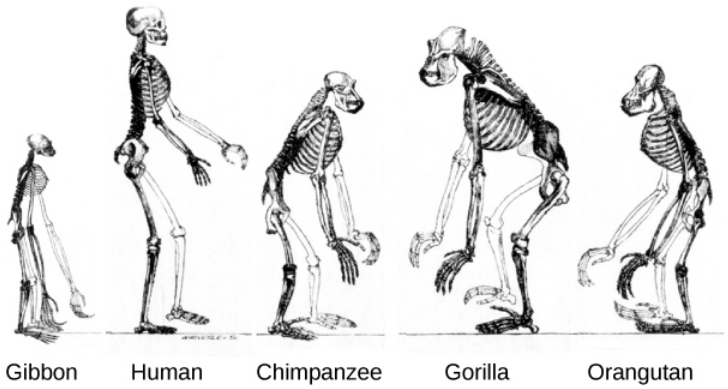


Figure 5.8.8.1: The howler monkey is native to Central and South America. It makes a call that sounds like a lion roaring. (credit: Xavi Talleda)

Apes evolved from the catarrhines in Africa midway through the Cenozoic, approximately 25 million years ago. Apes are generally larger than monkeys and they do not possess a tail. All apes are capable of moving through trees, although many species spend most their time on the ground. Apes are more intelligent than monkeys, and they have relatively larger brains proportionate to body size. The apes are divided into two groups. The lesser apes comprise the family Hylobatidae, including gibbons and siamangs. The great apes include the genera *Pan* (chimpanzees and bonobos) (Figure 5.8.8.2a), *Gorilla* (gorillas), *Pongo* (orangutans), and *Homo* (humans) (Figure 5.8.8.2b). The very arboreal gibbons are smaller than the great apes; they have low sexual dimorphism (that is, the genders are not markedly different in size); and they have relatively longer arms used for swinging through trees.







(a) (b)

Figure 5.8.8.2: The (a) chimpanzee is one of the great apes. It possesses a relatively large brain and has no tail. (b) All great apes have a similar skeletal structure. (credit a: modification of work by Aaron Logan; credit b: modification of work by Tim Vickers)

Human Evolution

The family Hominidae of order Primates includes the hominoids: the great apes (Figure 5.8.8.3). Evidence from the fossil record and from a comparison of human and chimpanzee DNA suggests that humans and chimpanzees diverged from a common hominoid ancestor approximately 6 million years ago. Several species evolved from the evolutionary branch that includes humans, although our species is the only surviving member. The term hominin is used to refer to those species that evolved after this split of the primate line, thereby designating species that are more closely related to humans than to chimpanzees. Hominins were predominantly bipedal and include those groups that likely gave rise to our species—including *Australopithecus*, *Homo habilis*, and *Homo erectus*—and those non-ancestral groups that can be considered "cousins" of modern humans, such as Neanderthals. Determining the true lines of descent in hominins is difficult. In years past, when relatively few hominin fossils had been recovered, some scientists believed that considering them in order, from oldest to youngest, would demonstrate the course of evolution from early hominins to modern humans. In the past several years, however, many new fossils have been found, and it is clear that there was often more than one species alive at any one time and that many of the fossils found (and species named) represent hominin species that died out and are not ancestral to modern humans.



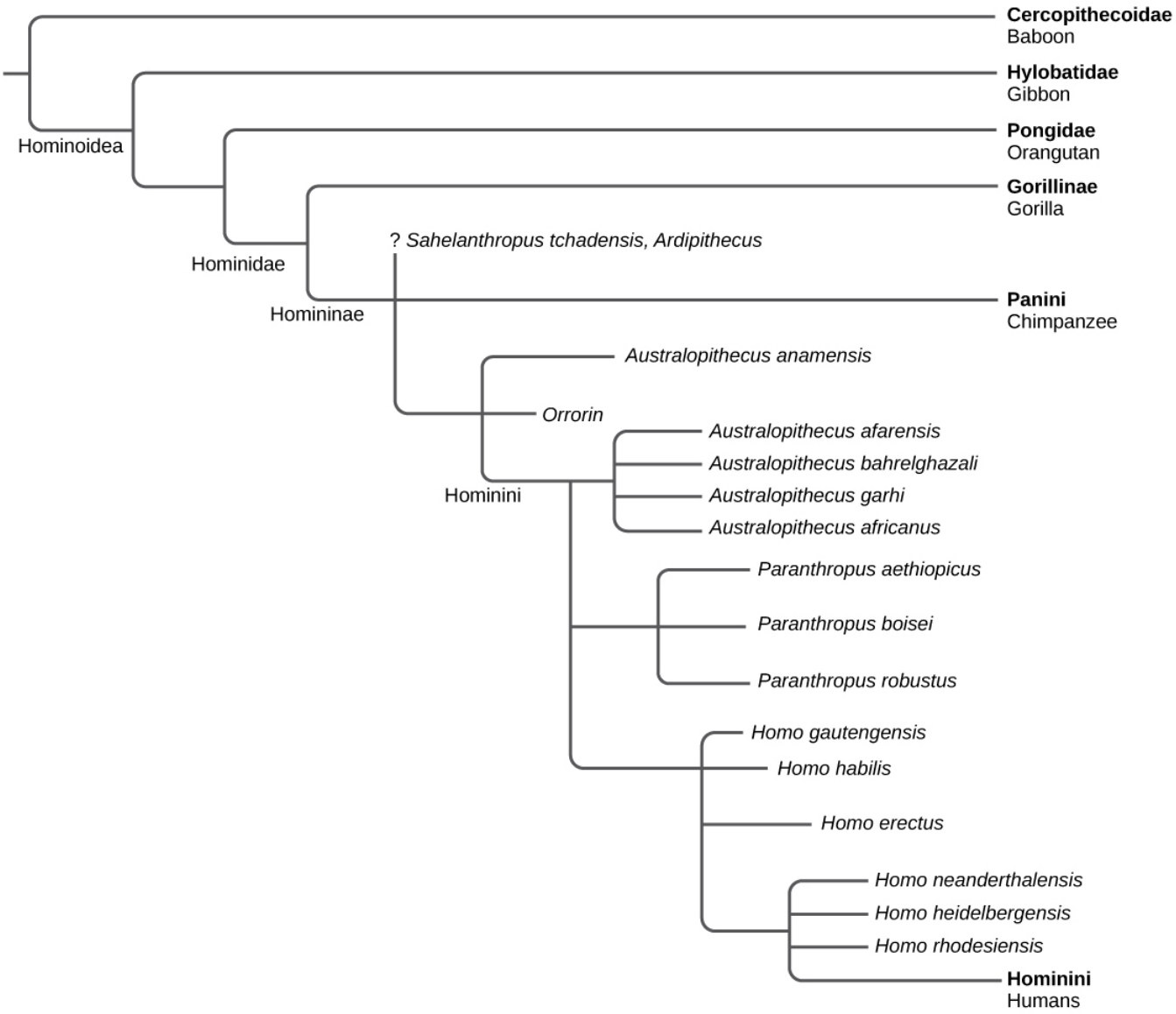


Figure 5.8.8.3: This chart shows the evolution of modern humans.

Very Early Hominins

Three species of very early hominids have made news in the past few years. The oldest of these, *Sahelanthropus tchadensis*, has been dated to nearly 7 million years ago. There is a single specimen of this genus, a skull that was a surface find in Chad. The fossil, informally called “Toumai,” is a mosaic of primitive and evolved characteristics, and it is unclear how this fossil fits with the picture given by molecular data, namely that the line leading to modern humans and modern chimpanzees apparently bifurcated about 6 million years ago. It is not thought at this time that this species was an ancestor of modern humans.

A second, younger species, *Orrorin tugenensis*, is also a relatively recent discovery, found in 2000. There are several specimens of *Orrorin*. It is not known whether *Orrorin* was a human ancestor, but this possibility has not been ruled out. Some features of *Orrorin* are more similar to those of modern humans than are the australopiths, although *Orrorin* is much older.

A third genus, *Ardipithecus*, was discovered in the 1990s, and the scientists who discovered the first fossil found that some other scientists did not believe the organism to be a biped (thus, it would not be considered a hominid). In the intervening years, several more specimens of *Ardipithecus*, classified as two different species, demonstrated that the organism was bipedal. Again, the status of this genus as a human ancestor is uncertain.

Early Hominins: Genus *Australopithecus*

Australopithecus (“southern ape”) is a genus of hominin that evolved in eastern Africa approximately 4 million years ago and went extinct about 2 million years ago. This genus is of particular interest to us as it is thought that our genus, genus *Homo*, evolved from *Australopithecus* about 2 million years ago (after likely passing through some transitional states). *Australopithecus* had a number of characteristics that were more similar to the great apes than to modern humans. For example, sexual dimorphism was more exaggerated than in modern humans. Males were up to 50 percent larger than females, a ratio that is similar to that seen in modern gorillas and orangutans. In contrast, modern human males are approximately 15 to 20 percent larger than females. The brain size of *Australopithecus* relative to its body mass was also smaller than modern humans and more similar to that seen in the great apes. A key feature that *Australopithecus* had in common with modern humans was bipedalism, although it is likely that *Australopithecus* also spent time in trees. Hominin footprints, similar to those of modern humans, were found in Laetoli, Tanzania and dated to 3.6 million years ago. They showed that hominins at the time of *Australopithecus* were walking upright.

There were a number of *Australopithecus* species, which are often referred to as *australopiths*. *Australopithecus anamensis* lived about 4.2 million years ago. More is known about another early species, *Australopithecus afarensis*, which lived between 3.9 and 2.9 million years ago. This species demonstrates a trend in human evolution: the reduction of the dentition and jaw in size. *A. afarensis* (Figure 5.8.8.4) had smaller canines and molars compared to apes, but these were larger than those of modern humans. Its brain size was 380–450 cubic centimeters, approximately the size of a modern chimpanzee brain. It also had prognathic jaws, which is a relatively longer jaw than that of modern humans. In the mid-1970s, the fossil of an adult female *A. afarensis* was found in the Afar region of Ethiopia and dated to 3.24 million years ago (Figure 5.8.8.5). The fossil, which is informally called “Lucy,” is significant because it was the most complete australopith fossil found, with 40 percent of the skeleton recovered.



(a) (b)

Figure 5.8.8.4: The skull of (a) *Australopithecus afarensis*, an early hominid that lived between two and three million years ago, resembled that of (b) modern humans but was smaller with a sloped forehead and prominent jaw.



Figure 5.8.8.5: This adult female *Australopithecus afarensis* skeleton, nicknamed Lucy, was discovered in the mid 1970s. (credit: "120"/Wikimedia Commons)

Australopithecus africanus lived between 2 and 3 million years ago. It had a slender build and was bipedal, but had robust arm bones and, like other early hominids, may have spent significant time in trees. Its brain was larger than that of *A. afarensis* at 500 cubic centimeters, which is slightly less than one-third the size of modern human brains. Two other species, *Australopithecus bahrelghazali* and *Australopithecus garhi*, have been added to the roster of australopiths in recent years.

A Dead End: Genus *Paranthropus*

The australopiths had a relatively slender build and teeth that were suited for soft food. In the past several years, fossils of hominids of a different body type have been found and dated to approximately 2.5 million years ago. These hominids, of the genus *Paranthropus*, were relatively large and had large grinding teeth. Their molars showed heavy wear, suggesting that they had a coarse and fibrous vegetarian diet as opposed to the partially carnivorous diet of the australopiths. *Paranthropus* includes *Paranthropus robustus* of South Africa, and *Paranthropus aethiopicus* and *Paranthropus boisei* of East Africa. The hominids in this genus went extinct more than 1 million years ago and are not thought to be ancestral to modern humans, but rather members of an evolutionary branch on the hominin tree that left no descendants.

Early Hominins: Genus *Homo*

The human genus, *Homo*, first appeared between 2.5 and 3 million years ago. For many years, fossils of a species called *H. habilis* were the oldest examples in the genus *Homo*, but in 2010, a new species called *Homo gautengensis* was discovered and may be older. Compared to *A. africanus*, *H. habilis* had a number of features more similar to modern humans. *H. habilis* had a jaw that was

less prognathic than the australopiths and a larger brain, at 600–750 cubic centimeters. However, *H. habilis* retained some features of older hominin species, such as long arms. The name *H. habilis* means “handy man,” which is a reference to the stone tools that have been found with its remains.

Link to Learning



Visit this site for a video about Smithsonian paleontologist Briana Pobiner explaining the link between hominin eating of meat and evolutionary trends.

H. erectus appeared approximately 1.8 million years ago (Figure 5.8.8.6). It is believed to have originated in East Africa and was the first hominin species to migrate out of Africa. Fossils of *H. erectus* have been found in India, China, Java, and Europe, and were known in the past as “Java Man” or “Peking Man.” *H. erectus* had a number of features that were more similar to modern humans than those of *H. habilis*. *H. erectus* was larger in size than earlier hominins, reaching heights up to 1.85 meters and weighing up to 65 kilograms, which are sizes similar to those of modern humans. Its degree of sexual dimorphism was less than earlier species, with males being 20 to 30 percent larger than females, which is close to the size difference seen in our species. *H. erectus* had a larger brain than earlier species at 775–1,100 cubic centimeters, which compares to the 1,130–1,260 cubic centimeters seen in modern human brains. *H. erectus* also had a nose with downward-facing nostrils similar to modern humans, rather than the forward facing nostrils found in other primates. Longer, downward-facing nostrils allow for the warming of cold air before it enters the lungs and may have been an adaptation to colder climates. Artifacts found with fossils of *H. erectus* suggest that it was the first hominin to use fire, hunt, and have a home base. *H. erectus* is generally thought to have lived until about 50,000 years ago.



Figure 5.8.8.6: Homo erectus had a prominent brow and a nose that pointed downward rather than forward.

Humans: *Homo sapiens*

A number of species, sometimes called archaic *Homo sapiens*, apparently evolved from *H. erectus* starting about 500,000 years ago. These species include *Homo heidelbergensis*, *Homo rhodesiensis*, and *Homo neanderthalensis*. These archaic *H. sapiens* had a brain size similar to that of modern humans, averaging 1,200–1,400 cubic centimeters. They differed from modern humans by having a thick skull, a prominent brow ridge, and a receding chin. Some of these species survived until 30,000–10,000 years ago, overlapping with modern humans (Figure 5.8.8.7).

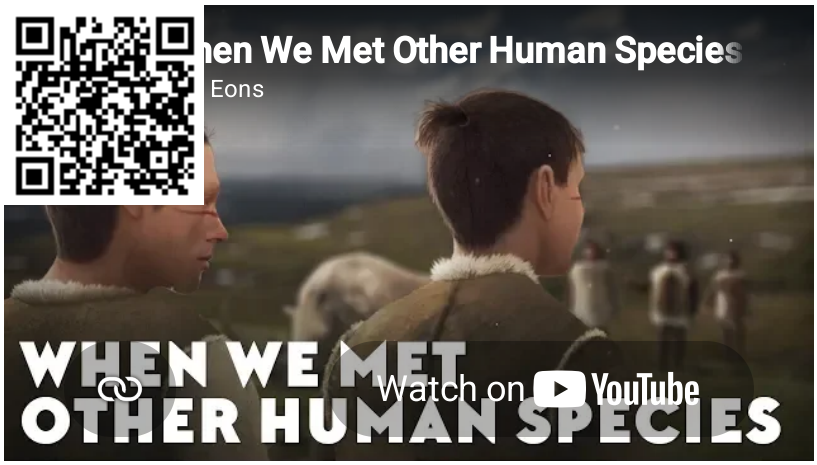


Figure 5.8.8.7: The *Homo neanderthalensis* used tools and may have worn clothing.

There is considerable debate about the origins of anatomically modern humans or *Homo sapiens sapiens*. As discussed earlier, *H. erectus* migrated out of Africa and into Asia and Europe in the first major wave of migration about 1.5 million years ago. It is thought that modern humans arose in Africa from *H. erectus* and migrated out of Africa about 100,000 years ago in a second major migration wave. Then, modern humans replaced *H. erectus* species that had migrated into Asia and Europe in the first wave.

This evolutionary timeline is supported by molecular evidence. One approach to studying the origins of modern humans is to examine mitochondrial DNA (mtDNA) from populations around the world. Because a fetus develops from an egg containing its mother's mitochondria (which have their own, non-nuclear DNA), mtDNA is passed entirely through the maternal line. Mutations in mtDNA can now be used to estimate the timeline of genetic divergence. The resulting evidence suggests that all modern humans have mtDNA inherited from a common ancestor that lived in Africa about 160,000 years ago. Another approach to the molecular understanding of human evolution is to examine the Y chromosome, which is passed from father to son. This evidence suggests that all men today inherited a Y chromosome from a male that lived in Africa about 140,000 years ago.





Summary

All primate species possess adaptations for climbing trees, as they all probably descended from tree-dwellers, although not all species are arboreal. Other characteristics of primates are brains that are larger than those of other mammals, claws that have been modified into flattened nails, typically only one young per pregnancy, stereoscopic vision, and a trend toward holding the body upright. Primates are divided into two groups: prosimians and anthropoids. Monkeys evolved from prosimians during the Oligocene Epoch. Apes evolved from catarrhines in Africa during the Miocene Epoch. Apes are divided into the lesser apes and the greater apes. Hominins include those groups that gave rise to our species, such as *Australopithecus* and *H. erectus*, and those groups that can be considered "cousins" of humans, such as Neanderthals. Fossil evidence shows that hominins at the time of *Australopithecus* were walking upright, the first evidence of bipedal hominins. A number of species, sometimes called archaic *H. sapiens*, evolved from *H. erectus* approximately 500,000 years ago. There is considerable debate about the origins of anatomically modern humans or *H. sapiens sapiens*.

Glossary

anthropoid
: monkeys, apes, and humans

Australopithecus
: genus of hominins that evolved in eastern Africa approximately 4 million years ago

brachiation
: movement through trees branches via suspension from the arms

Catarrhini
: clade of Old World monkeys

Gorilla
: genus of gorillas

hominin
: species that are more closely related to humans than chimpanzees

hominoid
: pertaining to great apes and humans

Homo
: genus of humans

Homo sapiens sapiens

anatomically modern humans

Hylobatidae
family of gibbons

Pan
genus of chimpanzees and bonobos

Platyrrhini
clade of New World monkeys

Plesiadapis
oldest known primate-like mammal

Pongo
genus of orangutans

Primates
order of lemurs, tarsiers, monkeys, apes, and humans

prognathic jaw
long jaw

prosimian
division of primates that includes bush babies of Africa, lemurs of Madagascar, and lorises, pottos, and tarsiers of Southeast Asia

stereoscopic vision
two overlapping fields of vision from the eyes that produces depth perception

---

This page titled 5.8.8: The Evolution of Primates is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.7: The Evolution of Primates** by OpenStax is licensed CC BY 4.0.

5.8.E: Vertebrates (Exercises)

29.1: Chordates

Review Questions

Which of the following is *not* contained in phylum Chordata?

A. Cephalochordata
B. Echinodermata
C. Urochordata
D. Vertebrata

Answer

B

Which group of invertebrates is most closely related to vertebrates?

A. cephalochordates
B. echinoderms
C. arthropods
D. urochordates

Answer

A

Free Response

What are the characteristic features of the chordates?

Answer

The characteristic features of the phylum Chordata are a notochord, a dorsal hollow nerve cord, pharyngeal slits, and a post-anal tail.

29.2: Fishes

Review Questions

Members of Chondrichthyes differ from members of Osteichthyes by having a _____.

A. jaw
B. bony skeleton
C. cartilaginous skeleton
D. two sets of paired fins

Answer

C

Members of Chondrichthyes are thought to be descended from fishes that had _____.

A. a cartilaginous skeleton
B. a bony skeleton
C. mucus glands

D. slime glands

Answer

B

Free Response

What can be inferred about the evolution of the cranium and vertebral column from examining hagfishes and lampreys?

Answer

Comparison of hagfishes with lampreys shows that the cranium evolved first in early vertebrates, as it is seen in hagfishes, which evolved earlier than lampreys. This was followed by evolution of the vertebral column, a primitive form of which is seen in lampreys and not in hagfishes.

Why did gnathostomes replace most agnathans?

Answer

Evolution of the jaw and paired fins permitted gnathostomes to diversify from the sedentary suspension feeding of agnathans to a mobile predatory lifestyle. The ability of gnathostomes to utilize new nutrient sources may be one reason why the gnathostomes replaced most agnathans.

29.3: Amphibians

Review Questions

Which of the following is *not* true of *Acanthostega*?

A. It was aquatic.
B. It had gills.
C. It had four limbs.
D. It laid shelled eggs.

Answer

D

Frogs belong to which order?

A. Anura
B. Urodela
C. Caudata
D. Apoda

Answer

A

Free Response

Explain why frogs are restricted to a moist environment.

Answer

A moist environment is required, as frog eggs lack a shell and dehydrate quickly in dry environments.

Describe the differences between the larval and adult stages of frogs.

Answer

The larval stage of frogs is the tadpole, which is usually a filter-feeding herbivore. Tadpoles usually have gills, a lateral line system, long-finned tails, and lack limbs. In the adult form, the gills and lateral line system disappear, and four limbs develop. The jaws grow larger, suitable for carnivorous feeding, and the digestive system transforms into the typical short gut of a predator. An eardrum and air-breathing lungs also develop.

29.4: Reptiles

Review Questions

During the Mesozoic period, diapsids diverged into_____.

A. pterosaurs and dinosaurs
B. mammals and reptiles
C. lepidosaurs and archosaurs
D. Testudines and Sphenodontia

Answer

C

Squamata includes_____.

A. crocodiles and alligators
B. turtles
C. tuataras
D. lizards and snakes

Answer

D

Free Response

Describe the functions of the three extra-embryonic membranes present in amniotic eggs.

Answer

The chorion facilitates the exchange of oxygen and carbon dioxide gases between the embryo and the surrounding air. The amnion protects the embryo from mechanical shock and prevents dehydration. The allantois stores nitrogenous wastes produced by the embryo and facilitates respiration.

What characteristics differentiate lizards and snakes?

Answer

Lizards differ from snakes by having eyelids, external ears, and less kinematic skulls.

29.5: Birds

Review Questions

A bird or feathered dinosaur is _____.

A. Neornithes

B. *Archaeopteryx*
C. Enantiornithes
D. Paleognathae

Answer

B

Which of the following feather types helps to reduce drag produced by wind resistance during flight?

A. flight feathers
B. primary feathers
C. secondary feathers
D. contour feathers

Answer

D

Free Response

Explain why birds are thought to have evolved from theropod dinosaurs.

Answer

This is suggested by similarities observed between theropod fossils and birds, specifically in the design of the hip and wrist bones, as well as the presence of a furcula, or wishbone, formed by the fusing of the clavicles.

Describe three skeletal adaptations that allow for flight in birds.

Answer

The sternum of birds is larger than that of other vertebrates, which accommodates the force required for flapping. Another skeletal modification is the fusion of the clavicles, forming the furcula or wishbone. The furcula is flexible enough to bend during flapping and provides support to the shoulder girdle during flapping. Birds also have pneumatic bones that are hollow rather than filled with tissue.

29.6: Mammals

Review Questions

Eccrine glands produce _____.

A. sweat
B. lipids
C. scents
D. milk

Answer

A

Monotremes include:

A. kangaroos
B. koalas
C. bandicoots

D. platypuses

Answer

D

Free Response

Describe three unique features of the mammalian skeletal system.

Answer

The lower jaw of mammals consists of only one bone, the dentary. The dentary bone joins the skull at the squamosal bone. Mammals have three bones of the middle ear. The adductor muscle that closes the jaw is composed of two muscles in mammals. Most mammals have heterodont teeth.

Describe three characteristics of the mammalian brain that differ from other vertebrates.

Answer

In some mammals, the cerebral cortex is highly folded, allowing for greater surface area than a smooth cortex. The optic lobes are divided into two parts in mammals. Eutherian mammals also possess a specialized structure that links the two cerebral hemispheres, called the corpus callosum.

29.7: The Evolution of Primates

Review Questions

Which of the following is *not* an anthropoid?

A. lemurs
B. monkeys
C. apes
D. humans

Answer

A

Which of the following is part of a clade believed to have died out, leaving no descendants?

A. *Paranthropus robustus*
B. *Australopithecus africanus*
C. *Homo erectus*
D. *Homo sapiens sapiens*

Answer

A

Free Response

How did archaic *Homo sapiens* differ from anatomically modern humans?

Answer

Archaic *Homo sapiens* differed from modern humans by having a thick skull and a prominent brow ridge, and lacking a prominent chin.

Why is it so difficult to determine the sequence of hominin ancestors that have led to modern *Homo sapiens*?

Answer

The immediate ancestors of humans were *Australopithecus*. All people past and present, along with the australopithecines, are hominins. We share the adaptation of being habitually bipedal. The earliest australopithecines very likely did not evolve until 5 million years ago. The primate fossil record for this crucial transitional period leading to australopithecines is still sketchy and somewhat confusing. By about 2.5 million years ago, there were at least two evolutionary lines of hominins descended from early australopithecines.

This page titled 5.8.E: Vertebrates (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **29.E: Vertebrates (Exercises)** by OpenStax is licensed CC BY 4.0.

CHAPTER OVERVIEW

5.9: Plantae

Seedless plants reproduce and spread through spores, but do not flower or seed to replicate.

5.9.1: Kingdom Plantae - Evolution and Phylogeny

5.9.2: Kingdom Plantae - Adaptations

5.9.E1: Seedless Plants (Exercises)

5.9.E2: Seed Plants (Exercises)

Contributors and Attributions

- Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 5.9: Plantae is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

Kingdom Plantae - Evolution and Phylogeny

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 90 minutes.
- Optional Activities are embedded.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to Unit 3.4.8, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify the challenges to life on land for plants
- Describe the timeline of plant evolution and the impact of land plants on other living things
- Identify the main characteristics of bryophytes
- Identify the new traits that first appear in pterophytes
- Describe the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- State which period saw the first appearance of gymnosperms and explain when they were the dominant plant life
- List the four groups of modern-day gymnosperms and provide examples of each
- Explain why angiosperms are the dominant form of plant life in most terrestrial ecosystems
- Describe the two main groups of flowering plants

Introduction

The kingdom **Plantae** constitutes large and varied groups of organisms. All are eukaryotic, multicellular with differentiated tissues, and photosynthetic. There are more than 300,000 species of cataloged plants. Of these, more than 260,000 are seed plants. Mosses, ferns, conifers, and flowering plants are all members of the plant kingdom.

Evolutionary History of Plants

The major event to mark the Ordovician, more than 500 Ma, was the colonization of land by the ancestors of modern land plants. Fossilized cells, cuticles, and spores of early land plants have been dated as far back as the Ordovician period in the early Paleozoic era. The oldest-known vascular plants have been identified in deposits from the Devonian. One of the richest sources of information is the Rhynie chert, a sedimentary rock deposit found in Rhynie, Scotland, where embedded fossils of some of the earliest vascular plants have been identified (Figure 5.9.1.1).

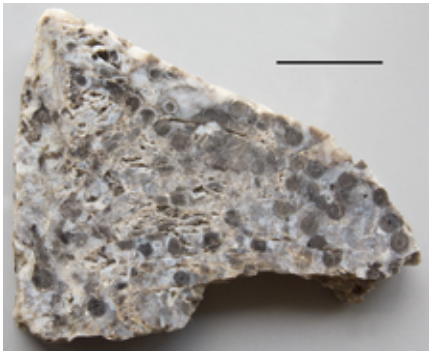




Figure 5.9.1.1: This Rhynie chert contains fossilized material from vascular plants. The circles seen in the rock on the left are the cross sections of the root-like structures called rhizoids seen in the model on the right. Credit left: Peter Coxhead CC-BY-SA 3.0; right: Matteo De Stefano/MUSE CC-BY-SA 3.0.

Current evolutionary thought holds that green algae and land-dwelling plants are monophyletic. The evolutionary transition from water to land imposed severe constraints on plants. They had to develop strategies to avoid dehydration, disperse reproductive cells, support themselves without water, and capture and filter sunlight. These adaptations were required for the colonization of land begun by the **bryophytes** (seedless, non-vascular plants) and their ancestors. While seed plants developed adaptations that allowed them to populate even arid habitats, full independence from water did not happen in all plants. Most seedless plants still require a moist environment.

An incredible variety of seedless plants populates the terrestrial landscape (Figure 5.9.1.2). Mosses may grow on a tree trunk, and horsetails may display their jointed stems and spindly leaves across the forest floor. Ferns dominate some forest floors. Today, seedless plants represent only a small fraction of the plants in our environment; yet, three hundred million years ago, seedless plants dominated the landscape and grew in the enormous swampy forests of the Carboniferous period. Their decomposition created large deposits of coal that we mine today.



Figure 5.9.1.2: Seedless plants, like these horsetails (*Equisetum* sp.), thrive in damp, shaded environments under a tree canopy where dryness is rare. (credit: modification of work by Jerry Kirkhart)

Seeds and pollen, two critical adaptations, distinguish the seed plants from other (seedless) vascular plants. Seed plants, such as conifers and flowering plants, do not rely on water for reproduction like the seedless plants do (Figure 5.9.1.3). They play an integral role in all aspects of life on the planet, shaping the physical terrain, influencing the climate, and maintaining life as we know it.

Fossils place the earliest distinct seed plants at about 350 Ma. The first reliable record of **gymnosperms** (the cone-bearing plants) dates their appearance to the Pennsylvanian period, about 319 Ma. Gymnosperms dominated the landscape in the early (Triassic) and middle (Jurassic) Mesozoic era. **Angiosperms** (the flowering plants) surpassed gymnosperms by the middle of the Cretaceous (about 100 Ma) in the late Mesozoic era, and today are the most abundant plant group in most terrestrial biomes.



(a) (b) (c) (d)

Figure 5.9.1.3: Seed plants dominate the landscape and play an integral role in human societies. (a) Palm trees grow along the shoreline; (b) wheat is a crop grown in most of the world; (c) the flower of the cotton plant produces fibers that are woven into fabric; (d) the potent alkaloids of the beautiful opium poppy have influenced human life both as a medicinal remedy and as a dangerously addictive drug. (credit a: modification of work by Ryan Kozie; credit b: modification of work by Stephen Ausmus; credit c: modification of work by David Nance; credit d: modification of work by Jolly Janner)

The Major Divisions (i.e. Phyla) of Land Plants

The green algae and land plants are grouped together into a subphylum called the Streptophytina, and thus are called Streptophytes. In a further division, land plants are classified into two major groups (knowns as **Divisions** rather than phyla) according to the absence or presence of vascular tissue, as detailed in Figures 5.9.1.4.

Plants that lack **vascular tissue** (the bryophytes), which is formed of specialized cells for the transport of water and nutrients, are referred to as non-vascular plants. Liverworts, mosses, and hornworts are **seedless, non-vascular plants** that likely appeared early in land plant evolution. Vascular plants developed a network of cells that conduct water and solutes.

The first vascular plants (the **tracheophytes**) appeared in the late Ordovician and were probably similar to **lycophytes**, which include club mosses (not to be confused with the mosses) and the **pterophytes** (ferns, horsetails, and whisk ferns). Lycophytes and pterophytes are referred to as **seedless vascular plants**, because they do not produce seeds.

The seed plants, or **spermatophytes**, form the largest group of all existing plants, and hence dominate the landscape. Seed plants include gymnosperms, most notably conifers, which produce “naked seeds,” and the most successful of all plants, the angiosperms, which produce flowers. Angiosperms protect their seeds inside chambers at the center of a flower; the walls of the chamber later develop into a fruit.

The evolutionary history of the development of each of these groups is detailed in the cladogram in Figure 5.9.1.5. Each taxa is described in more detail below.

STREPTOPHYTES: THE GREEN PLANTS								
Charophytes	Embryophytes: The Land Plants							
	Non Vascular			Vascular				
	Seedless Plants Bryophytes			Seedless Plants		Seed Plants Spermatophytes		
				Lycophytes	Pterophytes			
	Liver-worts	Horn-worts	Mosses	Club Mosses	Whisk Ferns	Gymno-sperms	Angio-sperms	
				Quillworts	Horsetails			
				Spike Mosses	Ferns			

Figure 5.9.1.4: This table shows the major divisions of green plants.

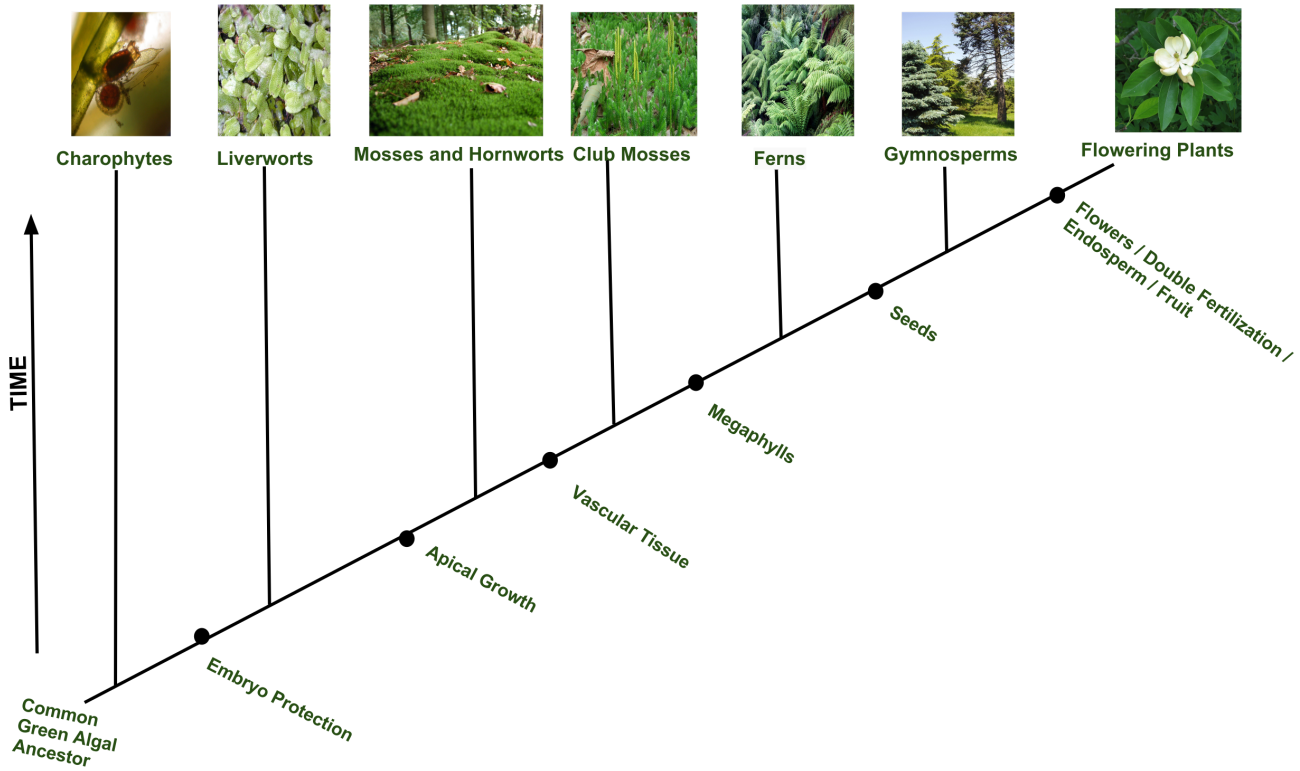


Figure 5.9.1.5: Evolutionary history of the kingdom Plantae.
Laurenprue216; CC-BY-SA 3.0

? Optional Activity 5.9.1.1

Figure 5.9.1.4: Which of the following statements about plant divisions is false?

A. Lycophytes and pterophytes are seedless vascular plants.
B. All vascular plants produce seeds.

C. All nonvascular embryophytes are bryophytes.
D. Seed plants include angiosperms and gymnosperms.

Answer

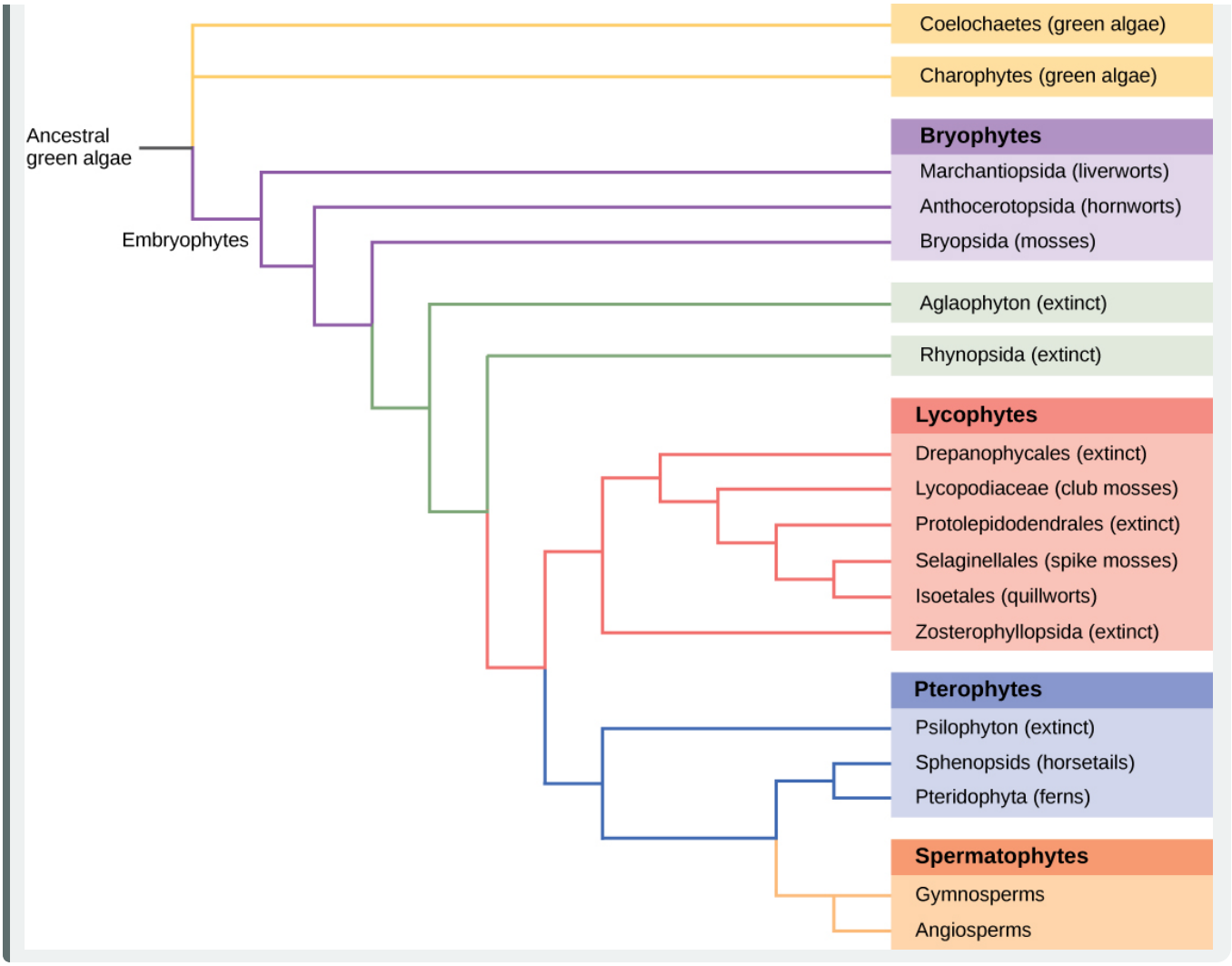
B.

Evolution Connection: Algae and Evolutionary Paths to Photosynthesis

Some scientists consider all algae to be plants, while others assert that only the **Charophytes** belong in the kingdom Plantae. These divergent opinions are related to the different evolutionary paths to photosynthesis selected for in different types of algae. While all algae are photosynthetic—that is, they contain some form of a chloroplast—they did not all become photosynthetic via the same path.

The ancestors to the green algae became photosynthetic by engulfing, but not metabolising, a green, photosynthetic bacterium about 1.65 billion years ago. That algal line evolved into the Charophytes, and eventually into the modern mosses, ferns, gymnosperms, and angiosperms. Their evolutionary trajectory was relatively straight and monophyletic. In contrast, the other algae—red, brown, golden, stramenopiles, and so on—all became photosynthetic by secondary, or even tertiary, endosymbiotic events; that is, they endosymbiosed cells that had already endosymbiosed a cyanobacterium. These latecomers to photosynthesis are parallels to the Charophytes in terms of autotrophy, but they did not expand to the same extent as the Charophytes, nor did they colonize the land.

The different views on whether all algae are Plantae arise from how these evolutionary paths are viewed. Scientists who solely track evolutionary straight lines, consider only the Charophytes as plants. To biologists who cast a broad net over living things that share a common characteristic (in this case, photosynthetic eukaryotes), all algae are plants.



? Optional Activity 5.9.1.2

What evolved first: eukaryotic cells or cells capable of photosynthesis?

Answer

Bacteria capable of photosynthesis (cyanobacteria) evolved first and were engulfed by larger bacterial cells without being degraded. These photosynthetic cells evolved a mutualistic relationship with their hosts and are now known as chloroplasts within some eukaryotic cells.

The Seedless Plants

Bryophytes (Non-Vascular, Seedless Plants)

Bryophytes are the group of plants that are the closest extant relatives of early terrestrial plants. The first bryophytes (liverworts) most likely appeared in the Ordovician period, about 450 million years ago. Because of the lack of lignin and other resistant structures in these plants, the likelihood of bryophytes forming fossils is rather small. By the Silurian period, however, vascular plants had spread through the continents. This compelling fact is used as evidence that non-vascular plants must have preceded the Silurian period.

Today, more than 25,000 species of bryophytes thrive in mostly damp habitats, although some live in deserts. They constitute the major flora of inhospitable environments like the tundra, where their small size and tolerance to desiccation offer distinct

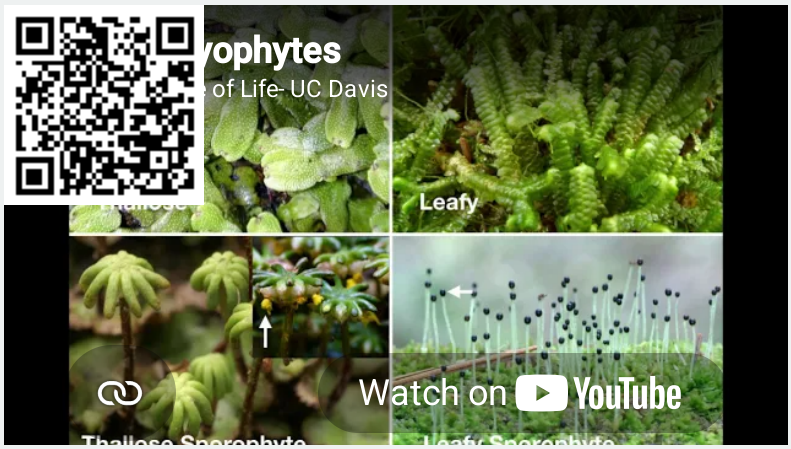
advantages. They generally lack lignin and do not have **tracheids** (xylem cells specialized for forming conduits inside the plant to conduct water). Rather, water and nutrients circulate inside specialized conducting cells. Although the term non-tracheophyte is more accurate, bryophytes are commonly called nonvascular plants.

In a bryophyte, all the conspicuous vegetative organs—including the photosynthetic leaf-like structures, the thallus, stem, and the rhizoid that anchors the plant to its substrate—belong to the haploid organism or **gametophyte**. The **sporophyte** (the diploid organism) is barely noticeable. The gametes formed by bryophytes swim with a flagellum, as do gametes in a few of the tracheophytes. The **sporangium**, the multicellular sexual reproductive structure, is present in bryophytes and absent in the majority of algae. The bryophyte embryo also remains attached to the parent plant, which protects and nourishes it. This is a characteristic of land plants.

Bryophytes may have been successful at the transition from an aquatic habitat to land, but they are still dependent on water for reproduction and absorb moisture and nutrients through the gametophyte surface. The lack of roots for absorbing water and minerals from the soil, as well as a lack of reinforced conducting cells, limits bryophytes to small sizes. Although they may survive in reasonably dry conditions, they cannot reproduce and expand their habitat range in the absence of water.

The bryophytes are divided into three phyla: the liverworts (**Marchantiophyta**), the hornworts (**Anthocerotophyta**), and the mosses (**Bryophyta**).

Video



Learn more about Bryophytes in this 8-minute video.
Questions after watching: How would you recognize a bryophyte next time you go on a hike in the forest? What are their distinctive features? If they have no root system, how do they take in water? What about other nutrients?

Video



Hank introduces us to nonvascular plants - liverworts, hornworts & mosses - which have bizarre features, kooky habits, and unique sex lives. Nonvascular plants inherited their reproductive cycle from algae, but have perfected it to the point where it is now used by all plants in one way or another.

The Seedless Vascular Plants

Video



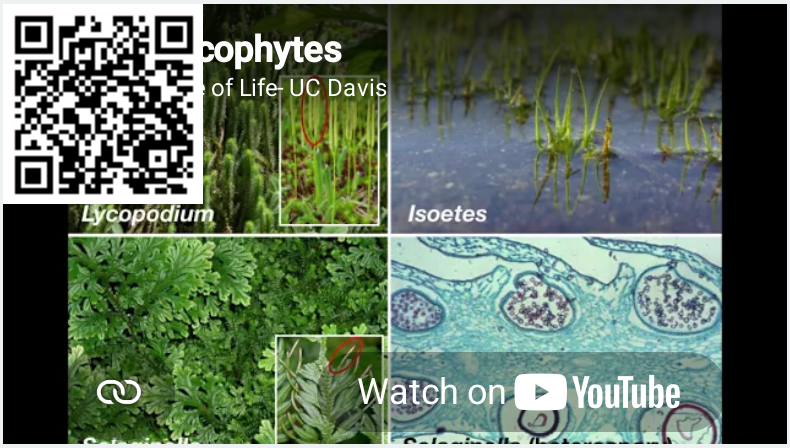
Hank introduces us to one of the most diverse and important families in the tree of life - the vascular plants. These plants have found tremendous success and their secret is also their defining trait: conductive tissues that can take food and water from one part of a plant to another part.

The vascular plants, or tracheophytes, are the dominant and most conspicuous group of land plants. More than 260,000 species of tracheophytes represent more than 90 percent of Earth's vegetation. Several evolutionary innovations explain their success and their ability to spread to all habitats. Vascular plants can achieve enormous heights, thus competing successfully for light. Photosynthetic organs become leaves. Pipe-like cells or vascular tissues transport water, minerals, and macromolecules (especially carbohydrates) throughout the organism.

By the late Devonian period, plants had evolved vascular tissue, well-defined leaves, and root systems. With these advantages, plants increased in height and size. During the Carboniferous period, swamp forests of club mosses (**Lycopodiophyta**) and ferns, horsetails, and whisk ferns (**Pteridophyta**), with some specimens reaching heights of more than 30 m, covered most of the land. These forests gave rise to the extensive coal deposits that gave the Carboniferous its name.

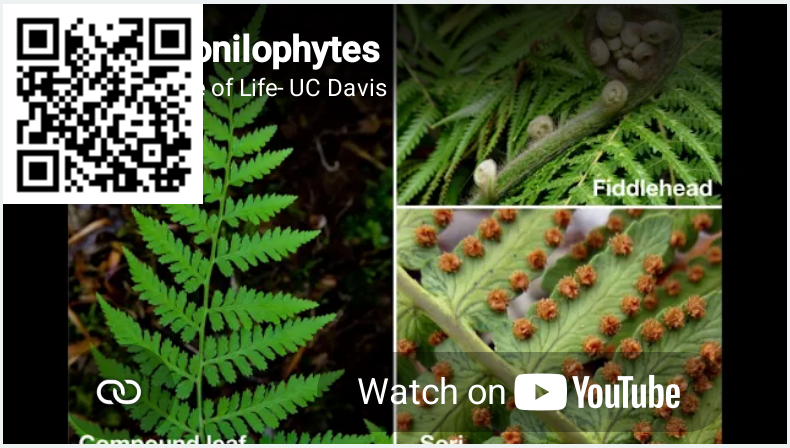
Water is still required for the fertilization of *seedless vascular plants*, and most favor a moist environment as the sperm must swim on a layer of moisture to reach the egg. This step in reproduction explains why ferns and their relatives are more abundant in damp environments. Modern-day seedless tracheophytes include club mosses, horsetails, ferns, and whisk ferns. In seedless vascular plants, the diploid sporophyte is the dominant phase of the lifecycle. The gametophyte is now an inconspicuous, but still independent, organism. Throughout plant evolution, there is an evident reversal of roles in the dominant phase of the lifecycle.

Video



Learn more about lycophytes in this 5.5-minute video.
Questions after watching: What's unique about the "plumbing system" of lycophytes? What is the most significant impact that lycophytes have had on our society?

Video



In this 7-minute video, you will learn more about monilophytes (a smaller clade of the Pteridophyta).
Question after watching: How are monilophytes different to the lycophytes you just heard about in the last video?

Gymnosperms

The fossil plant *Elkinsia polymorpha*, a "seed fern" from the Devonian period, about 400 Ma, is considered the earliest seed plant currently known. Seed ferns produced their seeds along their branches without specialized structures (Figure 5.9.1.6). They are the first true seed plants due to structures called **cupules** that enclose and protect the **ovule**, the female gametophyte, and associated tissues, which then developed into a seed upon fertilization. Seed plants resembling modern tree ferns became more numerous and diverse in the swamps of the Carboniferous period.

Following the wet Mississippian and Pennsylvanian periods, which were dominated by giant fern trees, the Permian period was dry. This gave a reproductive edge to seed plants, which are better adapted to survive dry spells. The Ginkgoales, a group of gymnosperms with only one surviving species, *Gingko biloba*, were the first gymnosperms to appear during the lower Jurassic. Gymnosperms expanded in the Mesozoic era (about 240 Ma), supplanting ferns in the landscape, and reaching their greatest diversity during this time. The Jurassic period was as much the age of the cycads (palm-tree-like gymnosperms) as the age of the dinosaurs. Gingkoales and the more familiar conifers also dotted the landscape.

Gymnosperms, meaning “naked seeds,” are a diverse group of seed plants and are paraphyletic. Their characteristics include naked seeds, separate female and male gametes, pollination by wind, and tracheids (which transport water and solutes in the vascular system). Gymnosperm seeds are not enclosed in an **ovary**; rather, they are exposed on cones or modified leaves. **Sporophylls** are specialized leaves that produce sporangia. The term **strobilus** describes a tight arrangement of sporophylls around a central stalk, as seen in cones. Some seeds are enveloped by sporophyte tissues upon maturation.

Modern gymnosperms are classified into four taxa: **Coniferophyta** (the conifers), **Cycadophyta** (the cycads), and **Ginkgophyta** (the ginko) are similar in their production of **secondary cambium** (cells that generate the vascular system of the trunk or stem and are partially specialized for water transportation) and their pattern of seed development. However, the three phyla are not closely related phylogenetically to each other. **Gnetophyta** (a group of 70 species of three genera) are considered the closest group to angiosperms because they produce true xylem tissue with vessel elements.



Figure 5.9.1.6: This fossilized leaf is from *Glossopteris*, a seed fern that thrived during the Permian age (290–240 million years ago). (credit: D.L. Schmidt, USGS)

Although angiosperms (flowering plants) are the major form of plant life in most biomes, gymnosperms still dominate some ecosystems, such as the taiga (boreal forests - see Unit 4.4.3) and the alpine forests at higher mountain elevations because of their adaptation to cold temperatures and dry growth conditions (Figure 5.9.1.7).



Figure 5.9.1.7: This boreal forest (taiga) has low-lying plants and conifer trees. Government of Canada: Boreal Forest

Angiosperms (The Flowering Plants)

Undisputed fossil records place the massive appearance and diversification of angiosperms in the middle to late Mesozoic era. Angiosperms (“seed in a vessel”) produce a flower containing male and/or female reproductive structures. Fossil evidence indicates that flowering plants first appeared in the Lower Cretaceous, about 125 million years ago, and were rapidly diversifying by the Middle Cretaceous, about 100 Ma (Figure 5.9.1.8). Earlier traces of angiosperms are scarce but fossilized pollen recovered from Jurassic geological material has been attributed to possible angiosperms. A few early Cretaceous rocks show clear imprints of leaves resembling angiosperm leaves. By the mid-Cretaceous, a staggering number of diverse flowering plants crowd the fossil record. The same geological period is also marked by the appearance of many modern groups of insects, including pollinating insects that likely played a key role in ecology and the evolution of flowering plants.

Although several hypotheses have been offered to explain this sudden profusion and variety of flowering plants, none have garnered the consensus of paleobotanists (scientists who study ancient plants). New data in comparative genomics and paleobotany have, however, shed some light on the evolution of angiosperms. Rather than being derived from gymnosperms, angiosperms formed a sister clade that developed in parallel with the gymnosperms. The two innovative structures of flowers and fruit represent

an improved reproductive strategy that served to protect the embryo, while increasing genetic variability and range. Paleobotanists debate whether angiosperms evolved from small woody bushes, or were basal angiosperms related to tropical grasses. Both views draw support from cladistics studies, and the so-called woody magnoliid hypothesis, which proposes that the early ancestors of angiosperms were shrubs, also offers molecular biological evidence.



Figure 5.9.1.8: This leaf imprint shows a *Ficus speciosissima*, an angiosperm that flourished during the Cretaceous period. (credit: W. T. Lee, USGS)

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems. With more than 250,000 species, the angiosperm phylum (Anthophyta) is second only to insects in terms of diversification. The success of angiosperms is due to two novel reproductive structures: flowers and fruit (Figure 5.9.1.9). The function of the **flower** is to facilitate **pollination**, which helps plants mix up their genes with that of other plants to produce offspring. Flowers also provide protection for the ovule and developing embryo inside a receptacle. The function of the **fruit** is seed dispersal. They also protect the developing seed and assist with germination. Different fruit structures or tissues on fruit—such as sweet flesh, wings, parachutes, or spines that grab—reflect the dispersal strategies that help spread seeds.



Figure 5.9.1.9: These flowers grow in the Sunken Gardens at Butchart Gardens in Victoria, BC. Flowering plants dominate terrestrial landscapes. The vivid colors of flowers are an adaptation to pollination by animals such as insects and birds. Jeffrey Beall; CC BY-ND 2.0.

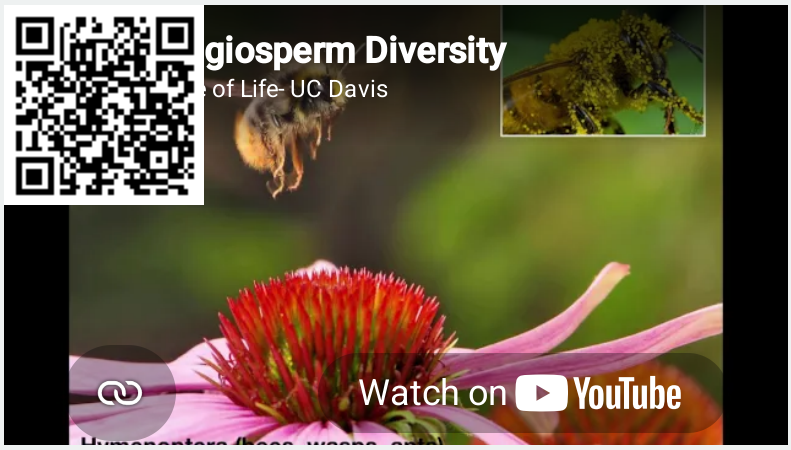
Angiosperms are classified in a single phylum: the Anthophyta. Modern angiosperms appear to be a monophyletic group, which means that they originate from a single ancestor. Flowering plants are divided into two major groups, according to the structure of the **cotyledons** (the first leaves formed after germination), veins (the vascular tissue of xylem and phloem), pollen grains (haploid sperm cells), and other structures such as flower petal numbers (Table 5.9.1.1). **Monocots** include grasses and lilies, and **eudicots** or

dicots form a polyphyletic group. **Basal angiosperms** are a group of plants that are believed to have branched off before the separation into monocots and eudicots because they exhibit traits from both groups. They are categorized separately in many classification schemes. The *Magnoliidae* (magnolia trees, laurels, and water lilies) and the *Piperaceae* (peppers) belong to the basal angiosperm group.

Table 5.9.1.1: Comparison of Structural Characteristics of Monocots and Eudicots

Characteristic	Monocot	Eudicot
Cotyledon	One	Two
Veins in Leaves	Parallel	Network (branched)
Stem Vascular Tissue	Scattered	Arranged in ring pattern
Roots	Network of adventitious roots	Tap root with many lateral roots
Pollen	Monosulcate	Trisulcate
Flower Parts	Three or multiple of three	Four, five, multiple of four or five and whorls

Video



Marlene Simon interviews Ernesto Sandoval to review the basic features and diversity of Angiosperms.

Highlight: Sweetgrass (Angiosperm)

"Sweetgrass is a fragrant grass with long, satiny leaves. Also known as vanillagrass, mannagrass, and holy grass, it is well known to [some] Indigenous people in Canada and the United States as a material for baskets, as well as a scent, medicine and smudge. Two closely related species are native to Canada: common sweetgrass (*Hierochloë hirta* subspecies *arctica*) and alpine sweetgrass (*H. alpina*). As a widely used and revered sacred plant, sweetgrass is still harvested today, and continues to play an important role in Indigenous cultures.

Sweetgrass is a perennial grass, in the family Poaceae. Usually placed in the genus *Hierochloë*, it is sometimes included within the genus *Anthoxanthum*. It has often been treated as one species, *Hierochloë odorata*, but currently taxonomists recognize up to four species, two of which grow in Canada: common sweetgrass (*Hierochloë hirta* subspecies *arctica*) and alpine sweetgrass (*H. alpina*).

The flat, bright green leaves can grow [more than] half a meter long, and have a distinctively reddish colour at their base. The flowers are small and greenish, and grow in branching clusters at the top of slender, upright stalks. The seeds are small and often infertile, and rarely germinate to create new plants. Sweetgrass's most common means of reproduction comes from its creeping, underground stems. These stems, known as rhizomes, grow horizontally under the earth, creating dense patches of grass that can be manually divided up to produce new plants.

Sweetgrass thrives in diverse habitats and is circumpolar in distribution. Members of the genus are native to northern Eurasia, Greenland, Iceland, Canada and the United States (except in the south central and southeastern regions). In Canada, common sweetgrass grows near rivers, lake edges, and wet meadows, often forming dense patches, from sea level to subalpine zones. Alpine sweetgrass grows near sea level in the Arctic, and in meadows and on rocky slopes in subalpine and alpine areas in other parts of Canada, especially in the Pacific Coastal and Rocky Mountains."

Adapted from: Turner, N. (2018). Sweetgrass. In *The Canadian Encyclopedia*. Retrieved from https://www.thecanadianencyclopedia.ca/en/article/sweetgrass



"Sweetgrass" (Matt Lavin; CC BY-SA 2.0)

This page titled 5.9.1: Kingdom Plantae - Evolution and Phylogeny is shared under a CC BY-SA license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **25.1: Early Plant Life** by OpenStax is licensed CC BY 4.0.
- **25.0: Prelude to Seedless Plants** by OpenStax is licensed CC BY 4.0.
- **25.3: Bryophytes** by OpenStax is licensed CC BY 4.0.
- **25.4: Seedless Vascular Plants** by OpenStax is licensed CC BY 4.0.
- **26.1: Evolution of Seed Plants** by OpenStax is licensed CC BY 4.0.
- **26.2: Gymnosperms** by OpenStax is licensed CC BY 4.0.
- **26.3: Angiosperms** by OpenStax is licensed CC BY 4.0.

Kingdom Plantae - Adaptations

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to the Unit 3 Glossary, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Discuss the challenges to plant life on land
- Describe the adaptations that allowed plants to colonize the land
- Discuss the importance of adaptations to life on land
- Discuss the type of seeds produced by gymnosperms, as well as other characteristics of gymnosperms
- Describe the main parts of a flower and their purpose
- Detail the life cycle of an angiosperm
- Discuss the two main groups of flowering plants

Introduction

As plants adapted to life on land, they had to contend with several challenges in the terrestrial environment, the largest being a lack of easy access to water as compared to an aquatic environment.

Plant Adaptations to Life on Land

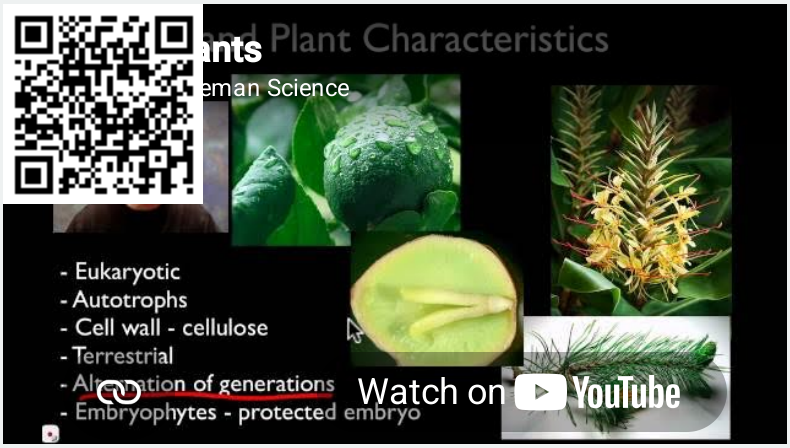
Water has been described as the “universal solvent.” The cell’s interior is a watery soup: in this medium, most small molecules dissolve and diffuse, and the majority of the chemical reactions of metabolism take place. Desiccation, or drying out, is a constant danger for an organism on land when exposed to air. Even when parts of a plant are close to a source of water, the aerial structures are likely to dry out. Water also provides buoyancy to organisms and there is no need for structural support to help the organism maintain a shape or orientation. On land, plants needed to develop structural support since air does not provide the same lift as water. The organism is also subject to bombardment by mutagenic radiation, because air does not filter out as many of the ultraviolet rays of sunlight as water. Additionally, the male gametes must reach the female gametes using new strategies, because swimming is no longer possible. Therefore, both gametes *and* zygotes must be protected from desiccation. The successful land plants developed strategies to deal with all of these challenges. Not all adaptations appeared at once. Some species never moved very far from the aquatic environment, whereas others went on to conquer the driest environments on Earth.

To balance these survival challenges, life on land offers several advantages. First, sunlight is abundant. Water filters sunlight, altering the spectral quality and reducing the amount of light absorbed by the photosynthetic pigment chlorophyll. Soils provide nutrients where the plants grow, rather than depending on currents and diffusion to bring them. Finally, land plants evolved before land animals; therefore, plants were initially able to evolve without herbivores (although they did have pathogens). As some animals evolved to land-dwelling, plants developed strategies to deter predation: from spines and thorns to toxic chemicals.

Early land plants, like the early land animals, did not live very far from an abundant source of water and developed survival strategies to combat dryness. One of these strategies is called tolerance. Many mosses, for example, can dry out to a brown and brittle mat, but as soon as rain or a flood makes water available, mosses will absorb it and are restored to their healthy green appearance. Another strategy is to colonize environments with high humidity, where droughts are uncommon. Ferns, which are considered an early lineage of plants, thrive in damp and cool places such as the understory of temperate forests. Later, plants moved away from moist or aquatic environments using resistance to desiccation, rather than tolerance. These plants, like cacti, minimize the loss of water to such an extent they can survive in extremely dry environments.

The most successful adaptation was the development of new structures that gave plants the advantage when colonizing new and dry environments. Four major adaptations are found in all terrestrial plants: the alternation of generations, a sporangium in which the spores are formed, a gametangium that produces haploid cells, and apical meristem tissue in roots and shoots. The evolution of a waxy cuticle and a cell wall containing **lignin**, a complex polymer impermeable to water, also contributed to the success of land plants. These adaptations are noticeably lacking in the closely related green algae—another reason for the debate over their placement in the plant kingdom.

Video



In this 7.5-minute video from Bozeman Science, you will be taken through an overview of plants, their unique characteristics, and their classification.

Questions after watching: Based on the information you learned in this video, create an evolutionary tree of plants containing the 4 groups: bryophytes, ferns and relatives, gymnosperms, and angiosperms. Include the adaptation that evolved at each node and led to the diversification of the plant groups at the appropriate location.

Alternation of Generations

Alternation of generations describes a life cycle in which an organism has both haploid and diploid multicellular stages (Figure 5.9.2.1).

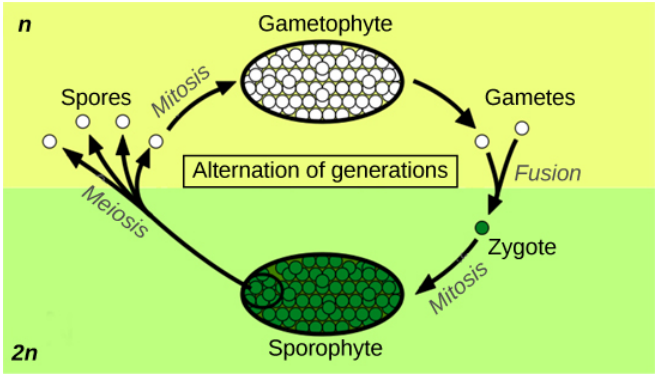


Figure 5.9.2.1: Alternation of generations between the 1*n* gametophyte and 2*n* sporophyte is shown. (credit: Peter Coxhead)

Haplontic refers to a lifecycle in which there is a dominant haploid stage, and **diplontic** refers to a lifecycle in which the diploid is the dominant life stage. Humans are diplontic. Most plants exhibit alternation of generations, which is described as **haplodiplodontic:** the haploid multicellular form, known as a gametophyte, is followed in the development sequence by a multicellular diploid organism: the sporophyte. The gametophyte gives rise to the gametes by mitosis. This can be the most obvious phase of the life cycle of the plant, as in the bryophytes, or it can occur in a microscopic structure, such as a pollen grain, in vascular plants. The sporophyte stage is barely noticeable in the non-vascular plants.

Optional Activity 5.9.2.1

Alternation of generations means that plants produce:

1. only haploid multicellular organisms
2. only diploid multicellular organisms
3. only diploid multicellular organisms with single-celled haploid gametes
4. both haploid and diploid multicellular organisms

Answer

D

Sporangia and Gametangia

Gametangia (singular, gametangium) are structures observed on multicellular haploid gametophytes. In the gametangia, precursor cells give rise to gametes by mitosis. The male gametangium (**antheridium**) releases sperm. Many seedless plants produce sperm equipped with flagella that enable them to swim in a moist environment to the **archegonia**: the female gametangium. The embryo develops inside the archegonium as the sporophyte. Gametangia are prominent in seedless plants, but are very rarely found in seed plants.

The sporophyte bears the sporangia (singular, sporangium): organs that first appeared in the land plants. The term "sporangia" literally means "spore in a vessel," as it is a reproductive sac that contains spores (Figure 5.9.2.2). The spores are later released by the sporangia and disperse in the environment. Two different types of spores are produced in land plants, the megaspore (female) and the microspore (male), resulting in the separation of sexes at different points in the lifecycle.



Figure 5.9.2.2: Spore-producing sacs called sporangia grow at the ends of long, thin stalks in this photo of the moss *Esporangios bryum*. (credit: Javier Martin)

Seedless Plants

The sporophyte of seedless plants is diploid and results from fusion of two gametes. Seedless non-vascular plants produce only one kind of spore and are called **homosporous**. The gametophyte phase is dominant in these plants. After germinating from a spore, the resulting gametophyte produces both male and female gametangia, usually on the same individual. In contrast, heterosporous plants produce two morphologically different types of spores. The male spores are called **microspores**, because of their smaller size, and develop into the male gametophyte; the comparatively larger **megaspores** develop into the female gametophyte. Heterospory is observed in a few seedless vascular plants and in all seed plants.

When the haploid spore germinates in a hospitable environment, it generates a multicellular gametophyte by mitosis. The gametophyte supports the zygote formed from the fusion of gametes and the resulting young sporophyte (vegetative form). The cycle then begins anew.

Seed Plants

Gymnosperms are seed plants that use an exposed seed to reproduce. This contrasts to angiosperms, or flowering plants, that enclose the seeds in fruits or nuts. The life cycle of gymnosperm alternates between sporophyte (2n) and gametophyte (1n) stages. The bulk of their lives are spent in the sporophyte stage, but while they do the organism hosts a female gametophyte. You can think of it as the sex organs of the plant, or its ovaries (Figure 5.9.2.3). All gymnosperms are heterosporous. The male and female

reproductive organs can form in cones or strobili. Male and female sporangia are produced either on the same plant, described as **monoecious** (“one home” or bisexual), or on separate plants, referred to as **dioecious** (“two homes” or unisexual).

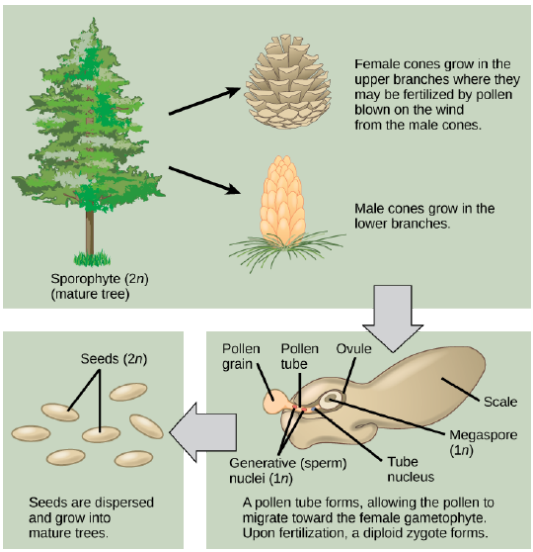


Figure 5.9.2.3: This image shows the life cycle of a conifer. Pollen from male cones blows up into upper branches, where it fertilizes female cones.

Optional Activity 5.9.2.2

Figure 5.9.2.3: At what stage does the diploid zygote form?

A. When the female cone begins to bud from the tree
B. At fertilization
C. When the seeds drop from the tree
D. When the pollen tube begins to grow

Answer

B. The diploid zygote forms after the pollen tube has finished forming, so that the male generative nuclei can fuse with the female gametophyte.

Video



In this 6-minute video, explore the long-distance pollination process of naked seed plants, the gymnosperms. Questions after watching: What is the difference between male cones and female cones in a pine tree? If the gametes of pine trees are inside cones, how do the female and male gametes meet to achieve fertilization?

The adult, or sporophyte, phase is the main phase of an angiosperm's life cycle (Figure 5.9.2.4). Like gymnosperms, angiosperms are heterosporous. Therefore, they generate microspores, which will generate pollen grains as the male gametophytes, and megaspores, which will form an ovule that contains female gametophytes. Inside the anthers' **microsporangia**, male gametophytes divide by meiosis to generate haploid microspores, which, in turn, undergo mitosis and give rise to pollen grains. Each pollen grain contains two cells: one generative cell that will divide into two sperm and a second cell that will become the pollen tube cell. The ovary contains the female **megasporangia** which will give rise to the haploid megaspores.

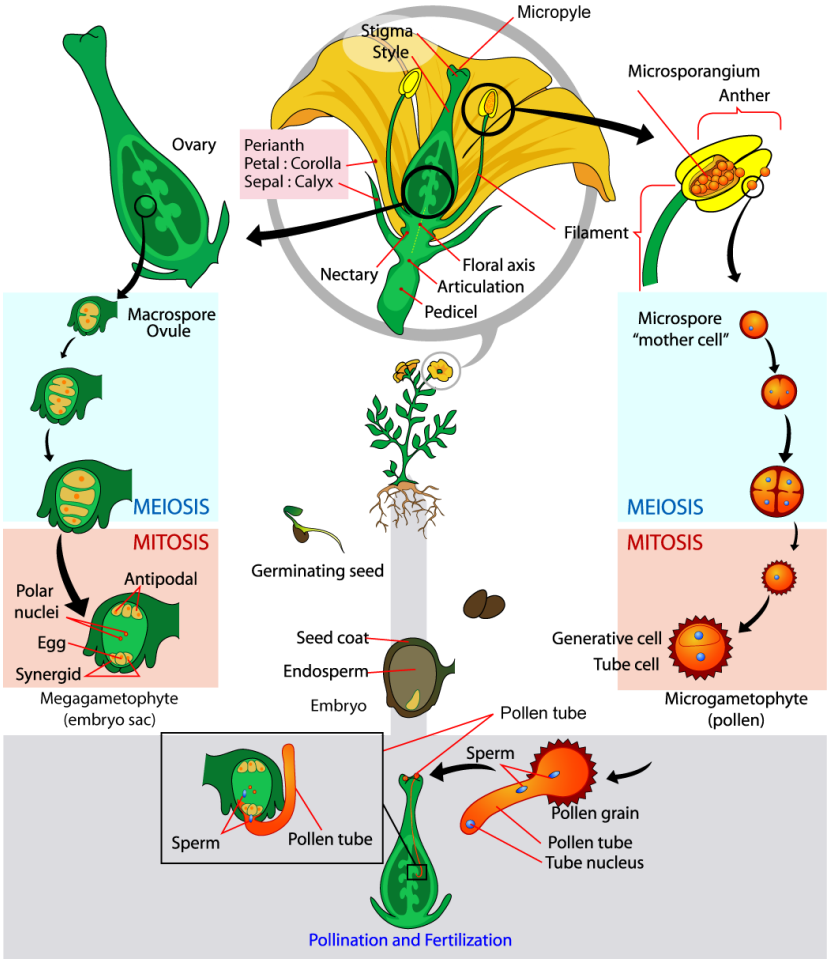


Figure 5.9.2.4: The life cycle of an angiosperm is shown. Anthers and carpels are structures that shelter the actual gametophytes: the pollen grain and embryo sac. Double fertilization is a process unique to angiosperms. (credit: modification of work by Mariana Ruiz Villareal)

Video



Hank gets into the dirty details about vascular plant reproduction: they use the basic alternation of generations developed by nonvascular plants 470 million years ago, but they've tricked it out so that it works a whole lot different compared to the way it did back in the Ordovician swamps where it got its start.

Apical Meristems

Shoots and roots of plants increase in length through rapid cell division in a tissue called the **apical meristem**, which is a small zone of cells found at the shoot tip or root tip (Figure 5.9.2.5). The apical meristem is made of undifferentiated cells that continue to proliferate throughout the life of the plant. Elongation of the shoots and roots allows a plant to access additional space and resources: light in the case of the shoot, and water and minerals in the case of roots. A separate meristem, called the **lateral meristem**, produces cells that increase the diameter of tree trunks.

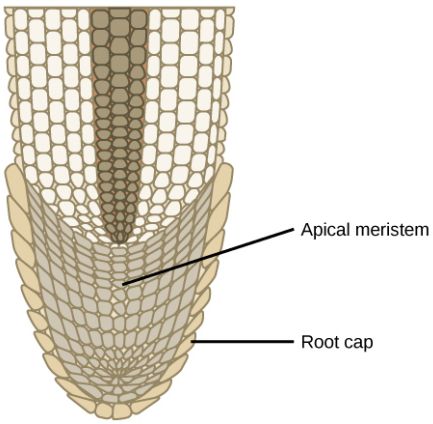


Figure 5.9.2.5: Addition of new cells in a root occurs at the apical meristem. Subsequent enlargement of these cells causes the organ to grow and elongate. The root cap protects the fragile apical meristem as the root tip is pushed through the soil by cell elongation.

Additional Land Plant Adaptations

Seeds and Pollen

Protection of the embryo is a major requirement for land plants. The vulnerable embryo must be sheltered from desiccation and other environmental hazards. In both seedless and seed plants, the female gametophyte provides protection and nutrients to the embryo as it develops into the new generation of sporophyte. This distinguishing feature of land plants gave the group its alternate name of embryophytes.

Unlike bryophyte and fern spores (which are haploid cells dependent on moisture for rapid development of gametophytes), seeds contain a diploid embryo that will germinate into a sporophyte. Storage tissue to sustain growth and a protective coat give seeds their superior evolutionary advantage. Several layers of hardened tissue prevent desiccation, and free reproduction from the need for a constant supply of water. Furthermore, seeds remain in a state of dormancy, induced by desiccation and the hormone abscisic acid, until conditions for growth become favorable. Whether blown by the wind, floating on water, or carried away by animals, seeds are scattered in an expanding geographic range, thus avoiding competition with the parent plant.

Pollen grains are male gametophytes and are carried by wind, water, or a pollinator. The whole structure is protected from desiccation and can reach the female organs without dependence on water, a major evolutionary development for land-based plants. Male gametes reach female gametophyte and the egg cell gamete though a pollen tube: an extension of a cell within the pollen grain. The sperm of modern gymnosperms lack flagella, but in cycads and the *Gingko*, the sperm still possess flagella that allow them to swim down the pollen tube to the female gamete; however, they are enclosed in a pollen grain.

Cuticle

In land plants, a waxy, waterproof cover called a **cuticle** protects the leaves and stems from desiccation. However, the cuticle also prevents intake of carbon dioxide needed for the synthesis of carbohydrates through photosynthesis. To overcome this, **stomata**, or pores that open and close to regulate gases and water vapor, appeared in plants as they moved away from moist environments into drier habitats.

UVB Filters

Water filters ultraviolet-B (UVB) light, which is harmful to all organisms, especially those that must absorb light to survive. This filtering does not occur for land plants. This presented an additional challenge to land colonization, which was met by the evolution of biosynthetic pathways for the synthesis of protective flavonoids and other compounds: pigments that absorb UV wavelengths of light and protect the aerial parts of plants from photodynamic damage.

Secondary Metabolites

Plants cannot avoid being eaten by animals. Instead, they synthesize a large range of poisonous **secondary metabolites**: complex organic molecules such as alkaloids, whose noxious smells and unpleasant taste deter animals. These toxic compounds can also cause severe diseases and even death, thus discouraging predation. Humans have used many of these compounds for centuries as drugs, medications, or spices. In contrast, as plants co-evolved with animals, the development of sweet and nutritious metabolites lured animals into providing valuable assistance in dispersing pollen grains, fruit, or seeds. Plants have been enlisting animals to be their helpers in this way for hundreds of millions of years.

Vascular Tissue: Xylem and Phloem

As plants adapted to dry land and evolved strategies for dealing with the dry environment, new organs and structures made their appearance. Early land plants did not grow more than a few inches off the ground, competing for light on these low mats. By developing a shoot and growing taller, individual plants captured more light. Because air offers substantially less support than water, land plants incorporated more rigid molecules in their stems (and later, tree trunks). In small plants such as single-celled algae, simple diffusion suffices to distribute water and nutrients throughout the organism. However, for plants to evolve larger forms, the evolution of vascular tissue for the distribution of water and solutes was a prerequisite. The vascular system contains xylem and phloem tissues. **Xylem** conducts water and minerals absorbed from the soil up to the shoot, while **phloem** transports food derived from photosynthesis throughout the entire plant. A root system evolved to take up water and minerals from the soil and to anchor the increasingly taller shoot in the soil.

Roots: Support for the Plant

Roots are not well preserved in the fossil record. Nevertheless, it seems that roots appeared later in evolution than vascular tissue. The development of an extensive network of roots represented a significant new feature of vascular plants. Thin **rhizoids** attached bryophytes to the substrate, but these rather flimsy filaments did not provide a strong anchor for the plant; neither did they absorb substantial amounts of water and nutrients. In contrast, roots, with their prominent vascular tissue system, transfer water and minerals from the soil to the rest of the plant. The extensive network of roots that penetrates deep into the soil to reach sources of water also stabilizes trees by acting as a ballast or anchor. The majority of roots establish a symbiotic relationship with fungi, forming mycorrhizae, which benefit the plant by greatly increasing the surface area for absorption of water and soil minerals and nutrients.

Leaves, Sporophylls, and Strobili

The appearance of true leaves in the pterophytes improved plants' photosynthetic efficiency. Leaves capture more sunlight with their increased surface area by employing more chloroplasts to trap light energy and convert it to chemical energy, which is then used to fix atmospheric carbon dioxide into carbohydrates. The carbohydrates are exported to the rest of the plant by the conductive cells of phloem tissue.

In addition to photosynthesis, leaves play another role in the life of plants. Pine cones, mature fronds of ferns, and flowers are all sporophylls, leaves that were modified structurally to bear sporangia. Strobili are cone-like structures that contain sporangia. They are prominent in conifers and are commonly known as pine cones.

Flowers and Fruits

Angiosperms produce their gametes in separate organs, which are usually housed in a flower (Figure 5.9.2.6). Both fertilization and embryo development take place inside this anatomical structure that provides a stable system of sexual reproduction largely sheltered from environmental fluctuations. Flowering plants are the most diverse phylum on Earth after insects; flowers come in a bewildering array of sizes, shapes, colors, smells, and arrangements. Most flowers have a mutualistic pollinator, with the distinctive

features of flowers reflecting the nature of the pollination agent. The relationship between pollinator and flower characteristics is one of the great examples of coevolution.

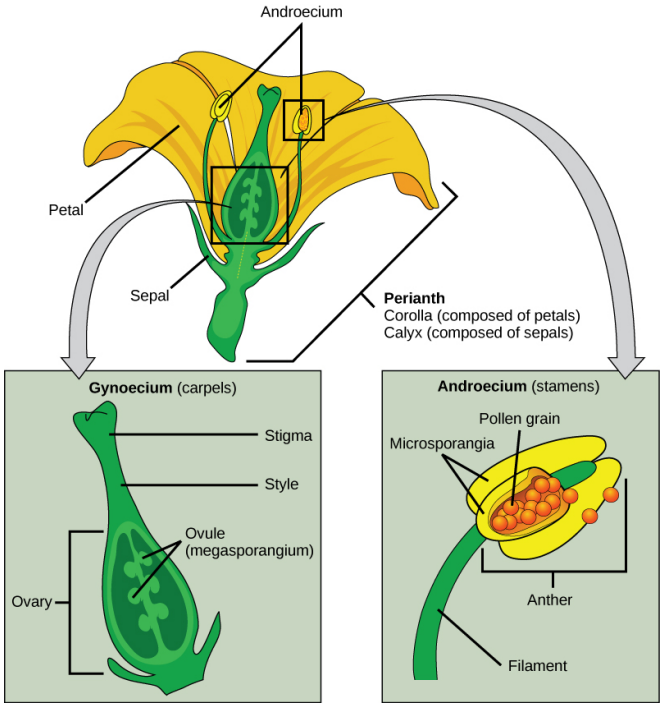


Figure 5.9.2.6: This image depicts the structure of a perfect flower. Perfect flowers produce both male and female floral organs. The flower shown has only one **carpel**, but some flowers have a cluster of carpels. Together, all the carpels make up the **gynoecium**. (credit: modification of work by Mariana Ruiz Villareal)

Following fertilization, the ovule grows into a **seed**. The surrounding tissues of the ovary thicken, developing into a fruit that will protect the seed inside and often ensure its dispersal over a wide geographic range. Not all fruits develop from an ovary; such structures are “false fruits.” Like flowers, fruit can vary tremendously in appearance, size, smell, and taste. Tomatoes, walnut shells, and avocados are all examples of fruit. As with pollen and seeds, fruits also act as agents of dispersal. Some may be carried away by the wind. Many attract animals that will eat the fruit and pass the seeds through their digestive systems, then deposit the seeds in another location. Cockleburs are covered with stiff, hooked spines that can hook into fur (or clothing) and hitch a ride on an animal for long distances. The cockleburs that clung to the velvet trousers of an enterprising Swiss hiker, George de Mestral, inspired his invention of the loop and hook fastener he named Velcro.

? Optional Activity 5.9.2.3

Besides the seed, what other major structure diminishes a plant’s reliance on water for reproduction?

A. flower
B. fruit
C. pollen
D. spore

Answer

C. pollen

Career Connection: Paleobotanist

How organisms acquired traits that allow them to colonize new environments—and how the contemporary ecosystem is shaped—are fundamental questions of evolution. Paleobotany (the study of extinct plants) addresses these questions through the analysis of fossilized specimens retrieved from field studies, reconstituting the morphology of organisms that disappeared long

ago. **Paleobotanists** trace the evolution of plants by following the modifications in plant morphology: shedding light on the connection between existing plants by identifying common ancestors that display the same traits. This field seeks to find transitional species that bridge gaps in the path to the development of modern organisms. Fossils are formed when organisms are trapped in sediments or environments where their shapes are preserved. Paleobotanists collect fossil specimens in the field and place them in the context of the geological sediments and other fossilized organisms surrounding them. The activity requires great care to preserve the integrity of the delicate fossils and the layers of rock in which they are found.

One of the most exciting recent developments in paleobotany is the use of analytical chemistry and molecular biology to study fossils. Preservation of molecular structures requires an environment free of oxygen, since oxidation and degradation of material through the activity of microorganisms depend on its presence. One example of the use of analytical chemistry and molecular biology is the identification of oleanane, a compound that deters pests. Up to this point, oleanane appeared to be unique to flowering plants; however, it has now been recovered from sediments dating from the Permian, much earlier than the current dates given for the appearance of the first flowering plants. Paleobotanists can also study fossil DNA, which can yield a large amount of information, by analyzing and comparing the DNA sequences of extinct plants with those of living and related organisms. Through this analysis, evolutionary relationships can be built for plant lineages.

Some paleobotanists are skeptical of the conclusions drawn from the analysis of molecular fossils. For example, the chemical materials of interest degrade rapidly when exposed to air during their initial isolation, as well as in further manipulations. There is always a high risk of contaminating the specimens with extraneous material, mostly from microorganisms. Nevertheless, as technology is refined, the analysis of DNA from fossilized plants will provide invaluable information on the evolution of plants and their adaptation to an ever-changing environment.

? Optional Activity 5.9.2.4

How did the development of a vascular system contribute to the increase in size of plants?

Answer

Plants became able to transport water and nutrients and not be limited by rates of diffusion. Vascularization allowed the development of leaves, which increased efficiency of photosynthesis and provided more energy for plant growth.

Indigenous Connection

Sweetgrass (*Hierochloe odorata*) is an aromatic angiosperm that belongs to the Order *Poales*, which contains many of the grasses and sedges. It is a hardy perennial monocot that is found from the plains of North America to the Arctic Circle. As an **herbaceous** plant, it grows to approximately 100 cm and reproduces primarily vegetatively through rhizomes, modified stems that grow underground (Figure 5.9.2.7).

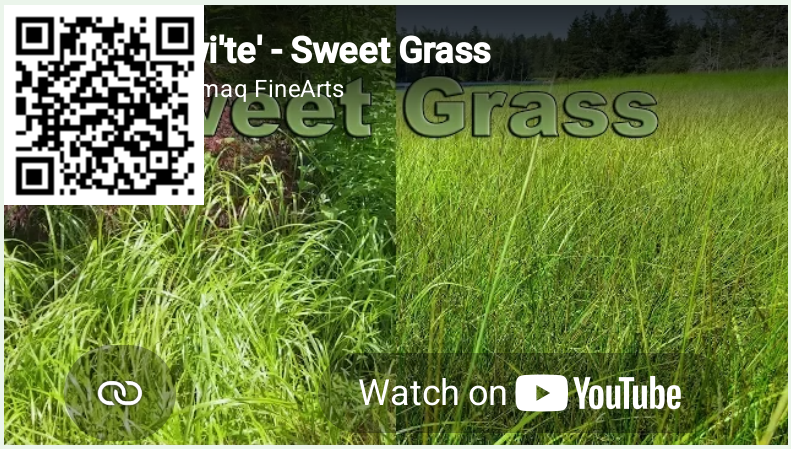


Figure 5.9.2.7: Hierochloe odorata (Sally and Andy Wasowski; CC-BY-SA)

"Sweetgrass is revered as a sacred plant. For many it is a cultural keystone species, reflecting a group's cultural identity and embodying their values and beliefs. Sweetgrass leaves at the harvestable stage are bright green, and, depending on when they are picked and how quickly they are dried, turn light green to straw-coloured. For weaving into baskets, the dried leaves are soaked, and then coiled or twined, alone or with other materials as the foundation. Experienced weavers often mix sweetgrass dried in different ways to create subtle designs, or add a few dyed leaves as coloured decorations.

On the Great Plains of southern Alberta, the Siksika and their relatives have many uses for sweetgrass, which they call *sipátsimo*. They use it as a ceremonial incense during daily prayers, burn it at major tribal events such as the Sundance, and use the smoke to purify tribal dancers. Siksika also used sweetgrass leaves to treat saddle sores on their horses, packed braided sweetgrass leaves into saddles, and fed their horses sweetgrass to give them stamina. They also inhaled sweetgrass smoke or drank an infusion of the plant for colds, coughs and sore throats, and used water in which the stems had been soaked as an eyewash.

Sweetgrass was used to make a hair wash and hair tonic, not only by the Siksika, but by the Nlaka'pamux of British Columbia, who call sweetgrass *xásxast* (literally, 'good-good'). The Nlaka'pamux were said to have traded for sweetgrass braids from the Siksika. Other Interior Salish Peoples, as well as the Ktunaxa of British Columbia, also use sweetgrass for ceremonial and medicinal purposes. On the far West Coast of Canada, the Nuxalk have been using sweetgrass from the estuary of the Bella Coola River for ceremonial purposes for generations; according to some, they also learned about using sweetgrass from the Siksika, who were said to have visited the Nuxalk at some point in the early 20th century."



In this 16-minute video, you will be introduced to the usage and cultural significance of sweetgrass for the Mi'kmaw culture. You will also be introduced to natural history of sweetgrass.
Question after watching: What practice did the indigenous population engaged in that might have contributed to the spread of sweetgrass?

Adapted from: Turner, N. (2018). Sweetgrass. In *The Canadian Encyclopedia*. Retrieved from https://www.thecanadianencyclopedia.ca/en/article/sweetgrass

Biodiversity of Plants

Biodiversity ensures a resource for new food crops and medicines. Plant life balances ecosystems, protects watersheds, mitigates erosion, moderates climate and provides shelter for many animal species. Threats to plant diversity, however, come from many angles. The explosion of the human population, especially in tropical countries where birth rates are highest and economic development is in full swing, is leading to human encroachment into forested areas. To feed the larger population, humans need to obtain arable land, so there is massive clearing of trees. The need for more energy to power larger cities and economic growth therein leads to the construction of dams, the consequent flooding of ecosystems, and increased emissions of pollutants. Other threats to tropical forests come from poachers, who log trees for their precious wood. Ebony and Brazilian rosewood, both on the endangered list, are examples of tree species driven almost to extinction by indiscriminate logging.

The number of plant species becoming extinct is increasing at an alarming rate. Because ecosystems are in a delicate balance, and seed plants maintain close symbiotic relationships with animals—whether predators or pollinators—the disappearance of a single

plant can lead to the extinction of connected animal species. A real and pressing issue is that many plant species have not yet been cataloged, and so their place in the ecosystem is unknown. These unknown species are threatened by logging, habitat destruction, and loss of pollinators. They may become extinct before we have the chance to begin to understand the possible impacts from their disappearance.

This page titled 5.9.2: Kingdom Plantae - Adaptations is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **25.1: Early Plant Life** by OpenStax is licensed CC BY 4.0.
- **26.3: Angiosperms** by OpenStax is licensed CC BY 4.0.
- **26.1: Evolution of Seed Plants** by OpenStax is licensed CC BY 4.0.
- **25.4: Seedless Vascular Plants** by OpenStax is licensed CC BY 4.0.
- **26.4: The Role of Seed Plants** by OpenStax is licensed CC BY 4.0.

5.9.E1: Seedless Plants (Exercises)

25.1: Early Plant Life

Review Questions

The land plants are probably descendants of which of these groups?

A. green algae
B. red algae
C. brown algae
D. angiosperms

Answer

A

Alternation of generations means that plants produce:

A. only haploid multicellular organisms
B. only diploid multicellular organisms
C. only diploid multicellular organisms with single-celled haploid gametes
D. both haploid and diploid multicellular organisms

Answer

D

Which of the following traits of land plants allows them to grow in height?

A. alternation of generations
B. waxy cuticle
C. tracheids
D. sporopollenin

Answer

C

Free Response

Why did land plants lose some of the accessory pigments present in brown and red algae?

Answer

Sunlight is not filtered by water or other algae on land; therefore, there is no need to collect light at additional wavelengths made available by other pigment coloration.

What is the difference between extant and extinct?

Answer

Paleobotanists distinguish between extinct species, which no longer live, and extant species, which are still living.

25.2: Green Algae - Precursors of Land Plants

Review Questions

What characteristic of Charales would enable them to survive a dry spell?

A. sperm with flagella
B. phragmoplasts
C. sporopollenin
D. chlorophyll *a*

Answer

C

Which one of these characteristics is present in land plants and not in Charales?

A. alternation of generations
B. flagellated sperm
C. phragmoplasts
D. plasmodesmata

Answer

A

Free Response

To an alga, what is the main advantage of producing drought-resistant structures?

Answer

It allows for survival through periodic droughts and colonization of environments where the supply of water fluctuates.

25.3: Bryophytes

Review Questions

Which of the following structures is not found in bryophytes?

A. a cellulose cell wall
B. chloroplast
C. sporangium
D. root

Answer

D

Stomata appear in which group of plants?

A. Charales
B. liverworts
C. hornworts
D. mosses

Answer

C

The chromosome complement in a moss protonema is:

A. 1*n*
B. 2*n*
C. 3*n*
D. varies with the size of the protonema

Answer

A

Why do mosses grow well in the Arctic tundra?

A. They grow better at cold temperatures.
B. They do not require moisture.
C. They do not have true roots and can grow on hard surfaces.
D. There are no herbivores in the tundra.

Answer

C

Free Response

In areas where it rains often, mosses grow on roofs. How do mosses survive on roofs without soil?

Answer

Mosses absorb water and nutrients carried by the rain and do not need soil because they do not derive much nutrition from the soil.

What are the three classes of bryophytes?

Answer

The bryophytes are divided into three phyla: the liverworts or Hepaticophyta, the hornworts or Anthocerotophyta, and the mosses or true Bryophyta.

25.4: Seedless Vascular Plants

Review Questions

Microphylls are characteristic of which types of plants?

A. mosses
B. liverworts
C. club mosses
D. ferns

Answer

C

A plant in the understory of a forest displays a segmented stem and slender leaves arranged in a whorl. It is probably a _____.

A. club moss
B. whisk fern
C. fern
D. horsetail

Answer

D

The following structures are found on the underside of fern leaves and contain sporangia:

A. sori
B. rhizomes
C. megaphylls
D. microphylls

Answer

A

The dominant organism in fern is the _____.

A. sperm
B. spore
C. gamete
D. sporophyte

Answer

D

What seedless plant is a renewable source of energy?

A. club moss
B. horsetail
C. sphagnum moss
D. fern

Answer

C

How do mosses contribute to returning nitrogen to the soil?

A. Mosses fix nitrogen from the air.
B. Mosses harbor cyanobacteria that fix nitrogen.
C. Mosses die and return nitrogen to the soil.
D. Mosses decompose rocks and release nitrogen.

Answer

D

Free Response

How did the development of a vascular system contribute to the increase in size of plants?

Answer

Plants became able to transport water and nutrients and not be limited by rates of diffusion. Vascularization allowed the development of leaves, which increased efficiency of photosynthesis and provided more energy for plant growth.

Which plant is considered the most advanced seedless vascular plant and why?

Answer

Ferns are considered the most advanced seedless vascular plants, because they display characteristics commonly observed in seed plants—they form large leaves and branching roots.

This page titled 5.9.E1: Seedless Plants (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **25.E: Seedless Plants (Exercises)** by OpenStax is licensed CC BY 4.0.

5.9.E2: Seed Plants (Exercises)

26.1: Evolution of Seed Plants

The first plants to colonize land were most likely closely related to modern day mosses (bryophytes) and are thought to have appeared about 500 million years ago. They were followed by liverworts (also bryophytes) and primitive vascular plants—the pterophytes—from which modern ferns are derived.

Review Questions

Seed plants are _____.

A. all homosporous.
B. mostly homosporous with some heterosporous.
C. mostly heterosporous with some homosporous.
D. all heterosporous.

Answer

D

Besides the seed, what other major structure diminishes a plant's reliance on water for reproduction?

A. flower
B. fruit
C. pollen
D. spore

Answer

A

In which of the following geological periods would gymnosperms dominate the landscape?

A. Carboniferous
B. Permian
C. Triassic
D. Eocene (present)

Answer

C

Which of the following structures widens the geographic range of a species and is an agent of dispersal?

A. seed
B. flower
C. leaf
D. root

Answer

A

Free Response

The Triassic Period was marked by the increase in number and variety of angiosperms. Insects also diversified enormously during the same period. Can you propose the reason or reasons that could foster coevolution?

Answer

Both pollination and herbivory contributed to diversity, with plants needing to attract some insects and repel others.

What role did the adaptations of seed and pollen play in the development and expansion of seed plants?

Answer

Seeds and pollen allowed plants to reproduce in absence of water. This allowed them to expand their range onto dry land and to survive drought conditions.

26.2: Gymnosperms

Gymnosperms, meaning “naked seeds,” are a diverse group of seed plants and are paraphyletic. Paraphyletic groups are those in which not all members are descendants of a single common ancestor. Their characteristics include naked seeds, separate female and male gametes, pollination by wind, and tracheids (which transport water and solutes in the vascular system).

Review Questions

Which of the following traits characterizes gymnosperms?

A. The plants carry exposed seeds on modified leaves.
B. Reproductive structures are located in a flower.
C. After fertilization, the ovary thickens and forms a fruit.
D. The gametophyte is longest phase of the life cycle.

Answer

A

Megasporocytes will eventually produce which of the following?

A. pollen grain
B. sporophytes
C. male gametophytes
D. female gametophytes

Answer

D

What is the ploidy of the following structures: gametophyte, seed, spore, sporophyte?

A. $1n$, $1n$, $2n$, $2n$
B. $1n$, $2n$, $1n$, $2n$
C. $2n$, $1n$, $2n$, $1n$
D. $2n$, $2n$, $1n$, $1n$

Answer

B

In the northern forests of Siberia, a tall tree is most likely a:

A. conifer
B. cycad
C. *Gingko biloba*
D. gnetophyte

Answer

A

Free Response

The Mediterranean landscape along the sea shore is dotted with pines and cypresses. The weather is not cold, and the trees grow at sea level. What evolutionary adaptation of conifers makes them suitable to the Mediterranean climate?

Answer

The trees are adapted to arid weather, and do not lose as much water due to transpiration as non-conifers.

What are the four modern-day phyla of gymnosperms?

Answer

The four modern-day phyla of gymnosperms are Coniferophyta, Cycadophyta, Gingkophyta, and Gnetophyta.

26.3: Angiosperms

From their humble and still obscure beginning during the early Jurassic period, the angiosperms—or flowering plants—have evolved to dominate most terrestrial ecosystems. With more than 250,000 species, the angiosperm phylum (Anthophyta) is second only to insects in terms of diversification.

Review Questions

Which of the following structures in a flower is not directly involved in reproduction?

A. the style
B. the stamen
C. the sepal
D. the anther

Answer

C

Pollen grains develop in which structure?

A. the anther
B. the stigma
C. the filament
D. the carpel

Answer

A

In the course of double fertilization, one sperm cell fuses with the egg and the second one fuses with _____.

A. the synergids
B. the polar nuclei of the center cell
C. the egg as well
D. the antipodal cells

Answer

B

Corn develops from a seedling with a single cotyledon, displays parallel veins on its leaves, and produces monosulcate pollen. It is most likely:

A. a gymnosperm
B. a monocot
C. a eudicot
D. a basal angiosperm

Answer

B

Free Response

Some cycads are considered endangered species and their trade is severely restricted. Customs officials stop suspected smugglers who claim that the plants in their possession are palm trees, not cycads. How would a botanist distinguish between the two types of plants?

Answer

The resemblance between cycads and palm trees is only superficial. Cycads are gymnosperms and do not bear flowers or fruit. Cycads produce cones: large, female cones that produce naked seeds, and smaller male cones on separate plants. Palms do not.

What are the two structures that allow angiosperms to be the dominant form of plant life in most terrestrial ecosystems?

Answer

Angiosperms are successful because of flowers and fruit. These structures protect reproduction from variability in the environment.

26.4: The Role of Seed Plants

Without seed plants, life as we know it would not be possible. Plants play a key role in the maintenance of terrestrial ecosystems through stabilization of soils, cycling of carbon, and climate moderation. Large tropical forests release oxygen and act as carbon dioxide sinks. Seed plants provide shelter to many life forms, as well as food for herbivores, thereby indirectly feeding carnivores. Plant secondary metabolites are used for medicinal purposes and industrial production.

Review Questions

Which of the following plant structures is not a defense against herbivory?

A. thorns
B. spines
C. nectar
D. alkaloids

Answer

C

White and sweet-smelling flowers with abundant nectar are probably pollinated by

A. bees and butterflies
B. flies
C. birds
D. wind

Answer

A

Abundant and powdery pollen produced by small, indistinct flowers is probably transported by:

A. bees and butterflies
B. flies
C. birds
D. wind

Answer

D

Plants are a source of _____.

A. food
B. fuel
C. medicine
D. all of the above

Answer

D

Free Response

Biosynthesis of nectar and nutrient-rich pollen is energetically very expensive for a plant. Yet, plants funnel large amounts of energy into animal pollination. What are the evolutionary advantages that offset the cost of attracting animal pollinators?

Answer

Using animal pollinators promotes cross-pollination and increases genetic diversity. The odds that the pollen will reach another flower are greatly increased compared with the randomness of wind pollination.

What is biodiversity and why is it important to an ecosystem?

Answer

Biodiversity is the variation in all forms of life. It can refer to variation within a species, within an ecosystem, or on an entire planet. It is important because it ensures a resource for new food crops and medicines. Plant life balances the ecosystems, protects watersheds, mitigates erosion, moderates climate, and provides shelter for many animal species.

This page titled 5.9.E2: Seed Plants (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **26.E: Seed Plants (Exercises)** is licensed CC BY 4.0.

CHAPTER OVERVIEW

5.1: The Origin and Diversity of Life

Learning Objectives

- Identify the major evolutionary leaps at given points in the geologic timeline
- Identify the origins of given taxonomic groupings on the geologic timeline
- Explain possible causes of mass extinction in Earth's history
- Utilize phylogeny and biogeography to identify reasons for the present distribution of various organisms
- Describe the current hypotheses on the origin of life
- Describe the evidence for the evolution of prokaryotes and eukaryotes

5.1.1: Deep Time

5.1.2: Origins of Life

5.1.3: Evidence for Early Life

5.1.4: Eukaryotic Origins

This page titled 5.1: The Origin and Diversity of Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

5.1.1: Deep Time

Deep Time

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify the major time frames on the geologic timeline
- Explain the evidence scientists use to explain the age of the Earth and mass extinctions

Geologic Time

The **geological time scale** in Figure 5.1.1.1 is one of the crowning achievements of science in general and geology in particular. It is a reference and communication system for comparing rocks and fossils found throughout the world and is geology's equivalent of the periodic table of the elements. It is also an important way to help organize when important milestones in the history of life on Earth occurred. For example, a paleontologist can call her colleague and say, "I just found an amazing new trilobite from the Devonian of British Columbia" and her colleague will immediately understand when in geological time that trilobite lived.

Most of the boundaries on the geological time scale correspond to the origination or extinction of particular fossils. Knowing when major groups of fossils first appeared or went extinct is therefore useful for determining the ages of rocks in the field. For example, if someone finds a rock with a trilobite fossil upon it, they will immediately know that the rock is Paleozoic in age, from 541 million years ago (Ma) to 252 Ma, and not older or younger; knowing the species of trilobite allows even greater precision.

The geological time scale provides a global summary of countless small-scale temporal correlations of rock layers made at local and regional scales. It is based almost entirely upon careful observations of the distributions of fossils in time and space.

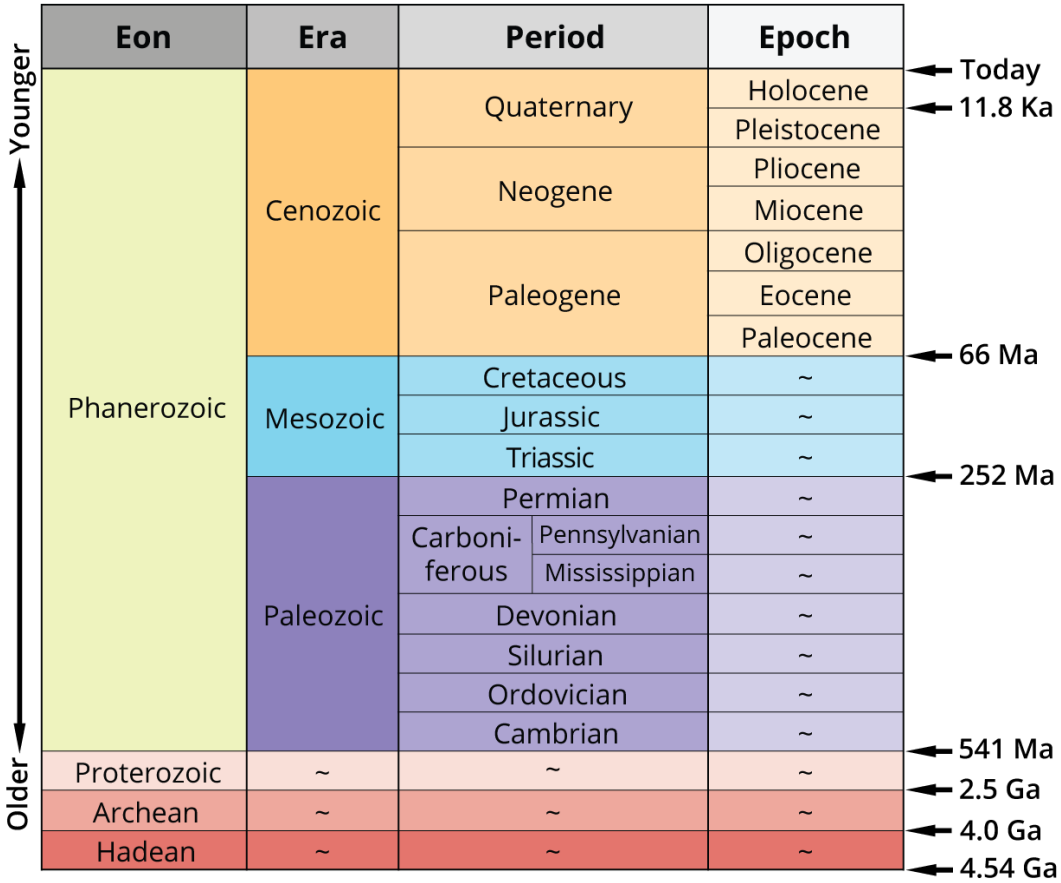


Figure 5.1.1.1: The geological time scale. Ka = thousands of years, Ma = millions of years, and Ga = billions of years. (Jonathan R. Hendricks CC-BY-SA 4.0)

Eons

The **Eon** is the broadest category of geological time. All geologic time is measured in years before the present and are indicated in abbreviated terms: "Ga" indicates billions of years, "Ma" indicates millions of years and, "Ka" indicates thousands of years. The Earth is 4.54 billion years old (4.54 Ga). Earth's history is characterized by four eons; in order from oldest to youngest, these are the Hadeon, Archean, Proterozoic, and Phanerozoic. Collectively, the Hadean, Archean, and Proterozoic are sometimes informally referred to as the **Precambrian**. The Cambrian Period defines the beginning of the Phanerozoic Eon; so, all rocks older than the Cambrian are *Pre*cambrian in age. The Hadean is the oldest Eon on Earth and accounts for the formation of the planet and the origins of life. The Archaean, 4.0 Ga, includes the first prokaryotes and the oldest rocks still in existence. During the Proterozoic, the first multicellular life evolved.

Most of Earth's history is represented by the three Precambrian eons. These older eons tell the story of Earth's beginning, life's origin, and the rise of complex life. The Hadean and Archean are difficult eons to study, however, because they are exposed in very limited places on Earth's surface. Since they are the oldest eons, rocks that are Hadean and Archean in age are often buried far below younger rocks at the Earth's surface. Proterozoic rocks, which span nearly 2 billion years or 42% of Earth's history, are much more accessible. But, until recently, these have received significantly less attention from paleontologists than rocks from the younger, fossil-rich Phanerozoic eon. That is slowly beginning to change, however, as more clues about the origins of complex life begin to be revealed from Proterozoic-aged rocks.

Humans live during the **Phanerozoic**, which means "visible life". This is the interval of geological time characterized by abundant, complex fossilized remains. Being the youngest eon of time, it is also well represented by rocks at Earth's surface. Because of these two factors, most paleontologists and geologists study fossils and rocks from the Phanerozoic eon. The Phanerozoic Eon began 541 Ma (or, 0.541 Ga) and represents only 12% of Earth's history.

Eras

Eons of geological time are subdivided into **Eras**, which are the second-longest units of geological time. The Phanerozoic eon is divided into three eras: the Paleozoic, Mesozoic, and Cenozoic.

Most of our knowledge of the fossil record comes from the three eras of the Phanerozoic eon. The Paleozoic ("old life") Era is characterized by trilobites, the first four-limbed vertebrates, and the origin of land plants. The Mesozoic ("middle life") Era represents the "age of dinosaurs," though is also noteworthy for the first appearances of mammals and flowering plants. Finally, the Cenozoic ("new life") Era is sometimes called the "age of mammals" and is the era we live in today.

As temporal points of reference, it is worth memorizing the ages of the boundaries that separate the three eras of the Phanerozoic Eon. Long before geologists knew these absolute age dates, they realized that the boundaries represent important events in the history of life: **mass extinctions**. For example, many fossils that are commonly found in the youngest Paleozoic rocks are not found in overlying Mesozoic rocks. Similarly, dinosaur fossils found in the youngest Mesozoic rocks are never again found in the overlying Cenozoic rocks. Mass extinctions are when large numbers of species go extinct within a very short period of geologic time. Paleontologists and geologists used these mass extinction events to define these (and other) boundaries within the Phanerozoic portion of the geological time scale. It is therefore no coincidence that some of the major boundaries coincide with mass extinction events.

The older Archean and Proterozoic Eons are similarly divided into several Eras. For example, the youngest Era of the Proterozoic Eon is called the Neoproterozoic. For the sake of simplicity, these older Eras are not included on the time scale shown at the top of this page; they do, however, exist.

Periods

Just as eons are subdivided into eras, Eras are subdivided into units of time called **Periods**. The most well-known of all geological periods is the Jurassic Period of the Mesozoic era. The Paleozoic Era is divided into six Periods. From oldest to youngest, these are the Cambrian (a time of rapid evolution and rise in biodiversity), Ordovician (primitive fish evolve), Silurian (first land plants), Devonian (first amphibians and forests), Carboniferous (massive forests and first reptiles), and Permian (first known mass extinction event). Note that in North America, the Carboniferous is divided into two separate Periods: the Mississippian and the Pennsylvanian. The Mesozoic era is divided into the Triassic (first dinosaurs and mammals), Jurassic (height of dinosaur diversity), and Cretaceous (early flowering plants and extinction of most dinosaurs) Periods. Finally, the Cenozoic Era is divided into three Periods: the Paleogene (evolution of early primates), Neogene (grassy ecosystems dominate plains), and Quaternary (evolution of modern humans).

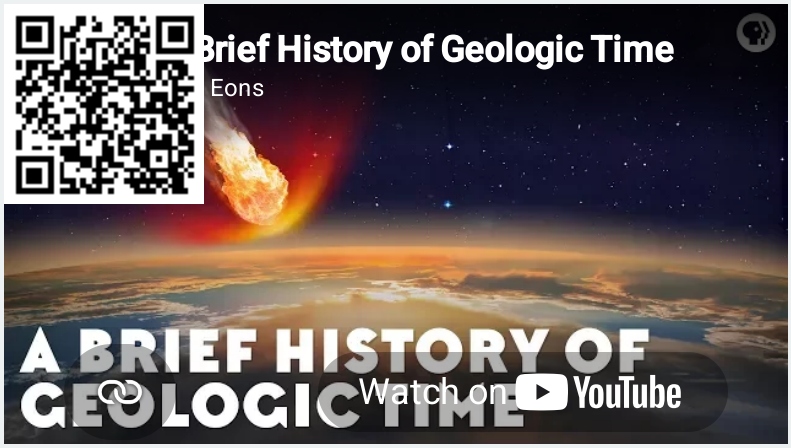
Epochs and Ages

Periods of geological time are subdivided into **Epochs**. In turn, epochs are divided into even narrower units of time called **Ages**. For the sake of simplicity, only the epochs of the Paleogene, Neogene, and Quaternary Periods are shown on the time scale at the top of this page. It is important to note, however, that all of the periods of the Phanerozoic era are subdivided into epochs and ages.

The Paleogene Period is divided into--from oldest to youngest--the Paleocene, Eocene, and Oligocene Epochs. The Neogene is divided into the Miocene and Pliocene Epochs. Finally, the Quaternary is divided into the Pleistocene and Holocene Epochs.

Some geologists think now that humans are having such a notable impact on the Earth and its life, a new, youngest epoch should be added to the Quaternary: the **Anthropocene**. These impacts include the destruction of large swaths of habitat, overexploitation of species, and planetary climate change, among others. These are discussed more in Unit 5. There is still considerable discussion in the geological community about whether this epoch should be added, as well as debate about what characteristics should define its beginning.

Video



This 12-minute video details the geologic record and important events through Earth's history that have shaped life. Question after watching: For each of the eras, eons, epochs, and periods in Figure 5.1.1.1, what is a main characteristic of this time period? Create a concept map, flow chart, table, or annotation of Figure 5.1.1.1.

Video



The first era of the current eon, the Paleozoic Era, is probably the most deceptively fascinating time in Earth's history. This 11-minute video describes it and the conditions of the Permian Extinction.

Question after watching:

Why do scientists say that mass extinctions provide opportunities? Continue to work on the notes that you started with the video above that outlines the major characteristics of each time period.

The Geologic and Evolutionary Record

A remarkable feature of Earth's history is how often evolutionary changes coincided with geologic and climatologic changes. In addition, consider that changes in geology (e.g., mountain formation or lowering of the sea level) can cause changes in climate. Changes in climate, in turn, can cause changes in geology through things like global loss/gain of ice. Geology and climate alter the habitats available for life. Past and present climate change will be covered in depth in Unit 5.

Here, we look at two types of geologic change that have had dramatic effects on life: **continental drift** and the impact of meteors**.**

Theory of Continental Drift

A body of evidence, both geological and biological, supports the conclusion that 200 million years ago, at the start of the Mesozoic era, all the continents were attached to one another in a single landmass, named **Pangaea**, seen in Figure 5.1.1.2. This drawing of

Pangaea is based on a computer-generated fit of the continents as they would look if the sea level were lowered by 1800 meters.

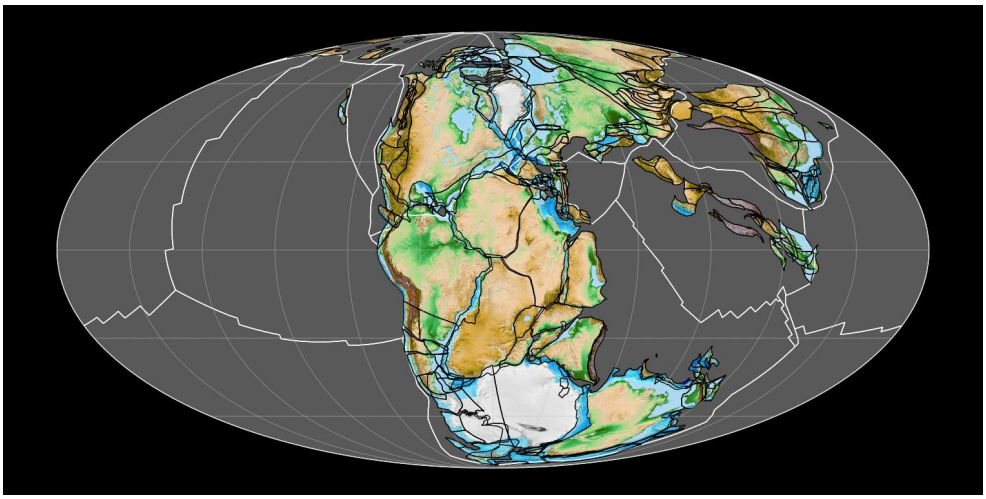


Figure 5.1.1.2: The supercontinent Pangaea in the early Mesozoic (at 200 Ma). The modern continents are highlighted for reference with North America in the upper left-hand corner, South America directly to the south, and Africa to the east. Antarctica is at the bottom with Australia to its right. (Fama Clamosa; CC-BY-SA 4.0)

During the Triassic Period, Pangaea began breaking up, first into two major landmasses:

- **Laurasia** in the Northern Hemisphere
- **Gondwana** in the Southern Hemisphere.

The present continents separated at intervals throughout the Mesozoic and Cenozoic Eras, eventually reaching the positions they have today. Evidence for this theory includes the shape of the continents, the geologic record, and fossils.

Shape of the Continents

The shape of the east coast of South America and the west coast of Africa and are strikingly complementary like puzzle pieces that fit together (Figure 5.1.1.2). This is even more dramatic when one fits the continents together using the boundaries of the continental slopes, (e.g., 1800 meters down), rather than the present-day shorelines.

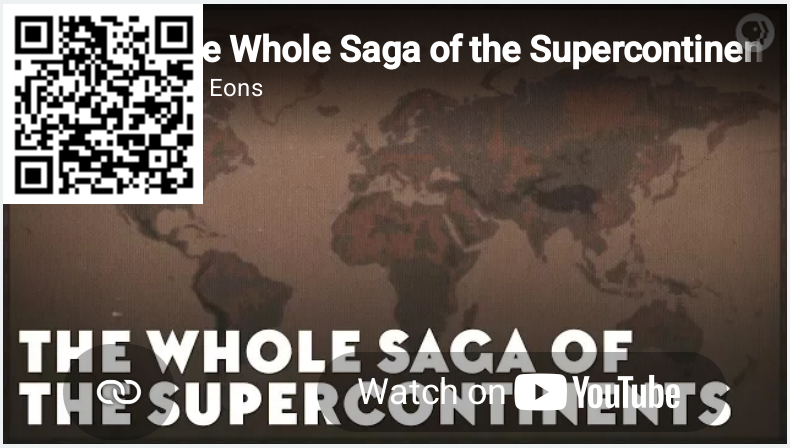
Geology

- In both mineral content and age, the rocks in a region on the east coast of Brazil match precisely those found in Ghana on the west coast of Africa.
- The low mountain ranges and rock types in eastern Canada and the New England region of the United States appear to be continued in parts of Great Britain, France, and Scandinavia.
- India and the southern part of Africa both show evidence of periodic glaciation during Paleozoic times (even though both are now close to the equator). The pattern of glacial deposits in the two regions match each other and glacial deposits found in South America, Australia, and Antarctica.

Fossils

- Fossil reptile species found in South Africa are also found in Brazil and Argentina.
- Fossil amphibians and reptiles found in Antarctica are also found in South Africa, India, and China.
- Most of the marsupials alive today are confined to South America and Australia. If these two continents were connected by Antarctica in the Mesozoic, as the theory suggests, one might expect to find fossil marsupials there. In March 1982, this prediction was fulfilled with the discovery in Antarctica of the remains of *Polydolops*, a 2.7 meter marsupial.

Video



This 9-minute video discusses supercontinents and how their formation and breakup shaped life.
Question after watching: What type of fossils might you expect to find in Kenorland? Why (what is the rationale?)
What about Rodinia? What kinds of fossils might be found in Labrador?

Meteors: The Impact Hypotheses

The Cretaceous period, the last period of the Mesozoic, marked the end of the Age of Reptiles. It was followed by the Cenozoic era, the Age of Mammals. Although extinctions have occurred throughout the history of life, many of them occurred in a relatively brief period at the end of the Cretaceous. Why?

The Alvarez Hypothesis

In the 1980s, Louis Alvarez, his son Walter, and their colleagues proposed that a giant asteroid or comet striking the Earth some 66 million years ago caused the massive die-off at the end of the Cretaceous Period. The impact is hypothesized to have generated so much dust and gases that skies were darkened all over the Earth, photosynthesis declined, and global temperatures dropped. As many as 75% of all species, including most dinosaurs, became extinct.

The key piece of evidence for the **Alvarez Hypothesis** was the finding of thin deposits of clay containing the element iridium at the interface between the rocks of the Cretaceous and those of the Paleogene Epoch (called the K-Pg boundary after the German word for Cretaceous). Iridium is a rare element on Earth but occurs in certain meteorites at concentrations thousands of times greater than in the Earth's crust.

In the 1990s, the Alvarez Hypothesis gained strong support from the discovery of the remains of a huge (180 km in diameter) crater in the Yucatan Peninsula of Mexico that dated to 65 million years ago.

The abundance of sulfate-containing rock in the region suggests that the impact generated enormous amounts of sulfur dioxide (SO_2), which later returned to Earth as long-lasting showers of acid rain. A smaller crater in Iowa, formed at the same time, indicates another impact may have contributed to the devastation. Perhaps during this period, the Earth passed through the tail of a comet, or a swarm of asteroids. These repeated impacts would have made the Earth uninhabitable for many creatures of the Mesozoic Era.

Video





This entertaining video provides an overview of the evidence that led researchers to conclude that an asteroid impact caused the demise of the dinosaurs.

Question after watching:

One researcher, in tongue-in-cheek fashion, claims that we still live in the age of the dinosaurs. How do you think that the ages are named (i.e., why is this called the age of the mammals)? Dinosaurs are often thought to be ectotherms ("cold-blooded") like reptiles. However, birds are endothermic ("warm-blooded"). Based on this observation, do you think that dinosaurs were ectothermic or endothermic? Explain your reasoning.

Other Impacts

Mass extinctions have occurred at other times in Earth's history. There was another large extinction of non-dinosaur reptiles that occurred earlier, at the end of the Triassic. It was followed by a great expansion in the diversity of dinosaurs. The recent discovery of a layer enriched in iridium in rocks formed at the boundary between the Triassic and Jurassic suggests that impact from an asteroid or comet may have been responsible then, just as it was at the K-Pg boundary.

Attributions

- Hendricks, J.R. Geologic Time Scale. https://www.digitalatlasofancientlife.org/learn/ CC-BY-SA 4.0

This page titled 5.1.1: Deep Time is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.12: Geologic Eras** by John W. Kimball is licensed CC BY 3.0. Original source: https://www.biology-pages.info/.

Origins of Life

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain the different problems to solve, and scientific hypotheses, on the origins of life

Introduction

The Origins of Life - A Mystery to Solve

To account for the origin of life on our Earth requires solving several problems:

1. How did the organic molecules that define life, e.g., amino acids, nucleotides, originate?
2. How were macromolecules assembled, e.g., proteins and nucleic acids, - a process requiring catalysts?
3. How were macromolecules able to reproduce themselves?
4. How were these macromolecules assembled into a system separate from their surroundings (i.e., a cell)?

Several hypotheses address each of these problems.

Video





This 13-minute video provides an overview of the origins of life, exploring along the way "what is life"? Question after watching: "Life is what living things do" (in contrast to what living things have). What does this mean? Do you agree with this statement based on what you know so far from this course?

Problem 1: How did the organic molecules that define life, e.g., amino acids, nucleotides, originate?

For the first problem, four hypotheses have been proposed:

- Hypothesis 1: Organic molecules were synthesized from inorganic compounds in the atmosphere,
- Hypothesis 2: Organic molecules rained down on the Earth from outer space,
- Hypothesis 3: Organic molecules were synthesized at hydrothermal vents on the ocean floor, and/or
- Hypothesis 4: Organic molecules were synthesized when comets or asteroids struck the early Earth.

Hypothesis 1: Organic molecules were synthesized from inorganic compounds in the atmosphere

In the fall of 1951, **Stanley Miller** was a graduate student looking for a research project. He attended a lecture by Nobel Laureate Harold C. Urey. Urey described how the Earth's atmosphere was thought to be in its early formation and how it might have led, through chemical reactions, to the formation of the first organic molecules. Miller decided to test this idea. He created an apparatus that mimicked the Earth's early conditions and atmosphere (or at least, what was thought, in 1951, to be the Earth's early conditions). The apparatus is shown in Figure 5.1.2.1. He filled it with water (H_2O), methane (CH_4), ammonia (NH_3), and

hydrogen (H2) but no oxygen since before life existed no oxygen had been released in the atmosphere by photosynthesis. The mixture circulated in the system by continuously boiling and then condensing/cooling the water. The gases passed through a chamber containing two electrodes with a spark passing between them, simulating lightening.

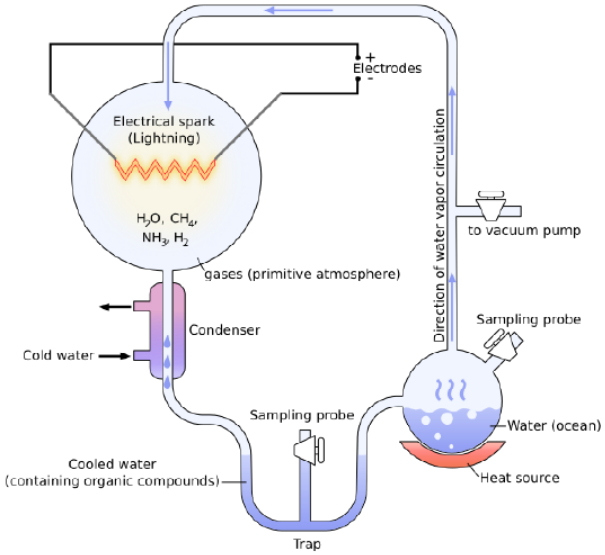


Figure 5.1.2.1: Miller experiment. (CC BY-SA; Yassine Mrabet).

At the end of the week-long experiment, Miller used paper chromatography to analyze the chemicals found in the flask. He discovered it now contained several amino acids (glycine, alanine, and aspartic acid) as well as other organic molecules, such as gamma-amino butyric acid or GABA (a chemical now used by many animals as a neurotransmitter).

It is now thought that the atmosphere of the early Earth was different than Miller supposed. However, in the years since Miller's work, many variants of his procedure have been tried with different mixtures of gases as our understanding of the early Earth's composition has changed. In nearly all versions of the experiment, organic molecules have almost always been formed, including the following results:

- 17 of the 20 amino acids used in protein synthesis, and all the purines and pyrimidines used in nucleic acid synthesis can be created in experiments similar to Miller's. They are easy to create by chemical reactions outside of living organisms.
- The synthesis of ribose, and thus of nucleotides, has been much more difficult outside of living organisms. However, success in synthesizing pyrimidine ribonucleotides under conditions that might have existed in the early Earth was reported in the 14 May 2009 issue of the scientific journal Nature. Thus, the synthesis of these molecules outside of a living organism is possible.
- In 2015, chemists in Cambridge, England led by John Sutherland reported that they had synthesized precursors for 12 of the 20 amino acids used in protein synthesis, two (of the four) ribonucleotides used to make RNA, and a precursor of lipids - all from a non-living system. In fact, they created these molecules using only hydrogen cyanide (HCN) and hydrogen sulfide (H_2S) irradiated with ultraviolet light in the presence of mineral catalysts.

Hypothesis 2: Organic molecules rained down on the Earth from outer space

Video





This 4 min video provides an overview of the hypothesis that the molecules of life may have been brought to Earth from outer space.

Question after watching: What is the evidence for the hypothesis of Panspermia?

Astronomers, using infrared spectroscopy, have identified a variety of organic molecules in interstellar gas clouds, including methane (CH_4), methanol (CH_3OH), formaldehyde (HCHO), cyanoacetylene (HC_3N) (which in Miller-type experiments is a precursor to the pyrimidine cytosine), polycyclic aromatic hydrocarbons (PAHs), as well as other important molecules such as carbon dioxide (CO_2), carbon monoxide (CO), ammonia (NH_3), hydrogen sulfide (H_2S), and hydrogen cyanide (HCN). There are organic molecules in space. These could have found their way to Earth and provided the building blocks of life.

Several laboratories have reported producing amino acids and other organic molecules by taking a mixture of molecules known to be present in interstellar space such as ammonia (NH_3), carbon monoxide (CO), methanol (CH_3OH), water (H_2O), and hydrogen cyanide (HCN) and exposing it to temperatures close to that of space (near absolute zero) and intense ultraviolet (UV) radiation. In other words, there is nothing special about creating organic molecules – they arise in the universe through the conditions found in space. They do not require living systems to create them. Whether or not the molecules that formed terrestrial life arrived here from space, there is little doubt that organic matter continuously rains down on the Earth (estimated at 30 tons per day). These could have served as the building blocks for the first living organism.

Alternatively, organic molecules can be transported to Earth via meteorites as demonstrated by the Murchison Meteorite that fell near Murchison, Australia on 28 September 1969 (Figure 5.1.2.2). This meteorite contains many organic molecules including purines and pyrimidines and 12 different amino acids. The relative proportion of each amino acid in the meteorite mirrored those found as a result of Miller's experiments. This suggests that abiotic chemical reactions produce these organic molecules easily and reliably, and whether they were formed on the early Earth or in space, they could have served to construct the first living organism.

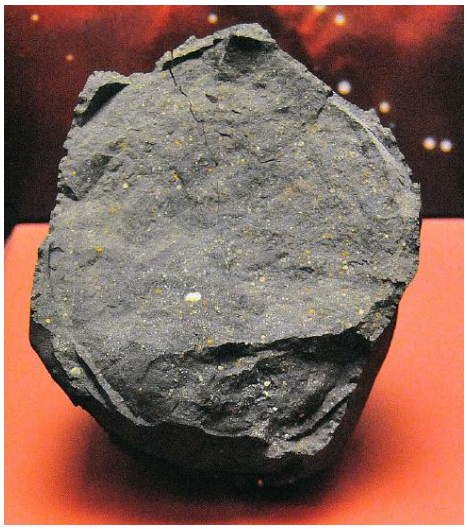
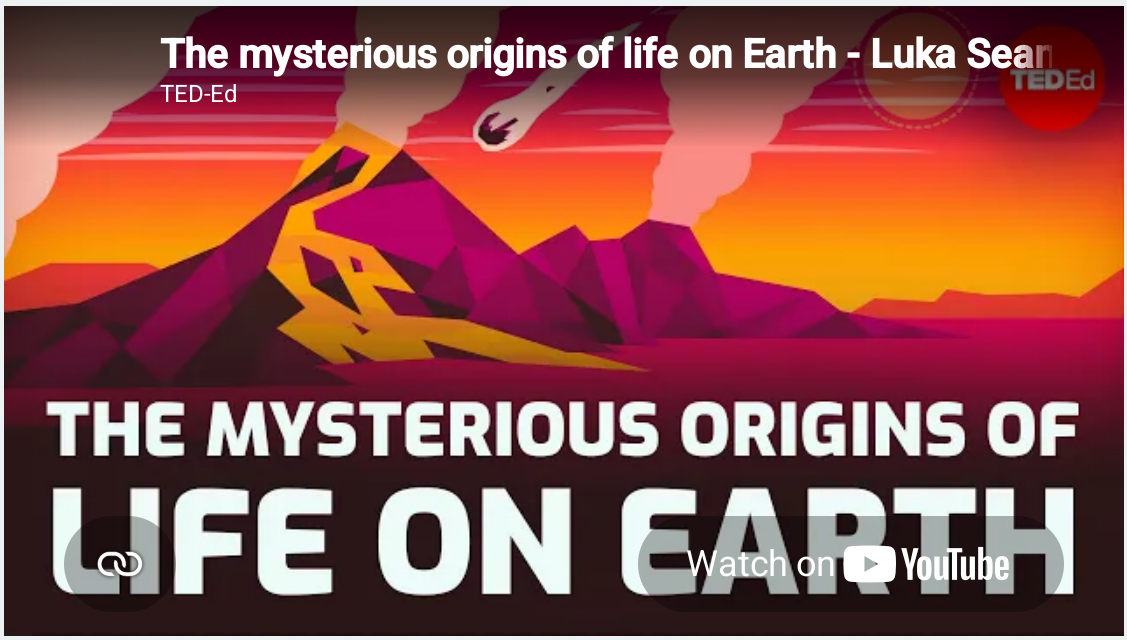


Figure 5.1.2.2: Murchison meteorite at The National Museum of Natural History (Washington). (CC SA-BY 3.0; Basilicofresco)

Hypothesis 3: Organic molecules were synthesized at hydrothermal vents on the ocean floor

Another location suspected of serving as a cradle for life are deep-sea hydrothermal vents. These vents would have provided a relatively stable environment for life to begin while the early planet was bombarded by meteorites. Some deep-sea hydrothermal vents discharge copious amounts of hydrogen, hydrogen sulfide, and carbon dioxide at temperatures around 100°C. The gases bubble up through chambers rich in iron sulfides (FeS, FeS_2). The iron sulfide surfaces can facilitate chemical reactions (i.e., serve as catalysts) that lead to the formation of simple organic molecules like acetate. Note also that life today depends on enzymes that have Fe and S atoms in their active (catalytic) site, so these iron sulfide minerals could have been a precursor for today's living system enzymes.

Video





This 5-minute video provides an overview of the hypothesis that life began at hydrothermal vents.
Question after watching: What are some characteristics of LUCA? How do we know that this organism had these characteristics?

Hypothesis 4: Organic molecules were synthesized when comets or asteroids struck the early Earth

The ingredients for the creation of organic molecules include basic inorganic chemicals like carbon dioxide (CO_2) or hydrogen cyanide (HCN), but the rearrangement of their atoms into organic molecules also requires an infusion of energy. In the hypotheses we have investigated thus far, the energy came from lighting, chemical gradients, or UV light. In this hypothesis, the energy comes from the impact of meteorites with the early Earth.

Researchers in the Czech Republic reported in 2014 that they had succeeded in the abiotic synthesis of adenine (A), guanine (G), cytosine (C), and uracil (U) — the four bases found in RNA and three of the four found in DNA. They achieved this by bombarding a mixture of formamide and clay with powerful laser pulses that mimicked the temperature and pressure expected when a large meteorite strikes the Earth. Formamide is a simple substance, CH_3NO, thought to have been abundant on the early Earth and containing the four elements fundamental to all life. It could serve as a basis for the creation of many of the organic molecules used by living systems today. Thus, the meteorite impact may have sparked life on Earth.

Problem 2: How were macromolecules assembled?

Once the organic molecules of life are created (monomers), the next step in the creation of life is to assemble them into large macromolecules (polymers). For example, nucleotides need to be assembled into RNA or DNA; and amino acids need to assemble into proteins.

Researchers who study this problem think that early polymers were assembled on solid, mineral surfaces These surfaces worked like catalysts, holding the monomers in the right orientation to facilitate their assembly into larger polymers, and once formed the mineral surface held on to the polymer and in so doing, protected them from degradation. In the laboratory, polypeptides and polynucleotides (RNA molecules) containing about ~50 monomers linked together have been synthesized on mineral (e.g., clay) surfaces.

Today, all living organisms have metabolism to create more of themselves from simpler building blocks and this activity depends on enzymes. Until recently, every enzyme science knew off was a protein. But proteins are synthesized from information encoded in DNA and translated into mRNA. So here is a chicken-and-egg dilemma. The synthesis of DNA and RNA requires proteins. So proteins cannot be made without nucleic acids and nucleic acids cannot be made without proteins.

The discovery that certain RNA molecules have enzymatic activity on their own provides a possible solution. These RNA molecules, called **ribozymes**, incorporate both the features required of life: storage of information and the ability to act as catalysts. This leads to what is known as the **RNA World Hypothesis**.

Video



This 3-minute video describes the RNA World Hypothesis.

Question after watching: In your notes, write a short description of the RNA world hypothesis and the argument for it. How could natural selection operate on the molecular level (as demonstrated in the RNA World Hypothesis)?

While no ribozyme in nature has yet been found that can replicate itself, ribozymes have been synthesized in the laboratory (using artificial selection) that can catalyze the assembly of short oligonucleotides into exact complements of themselves. The ribozyme serves as both the *template* on which short lengths of RNA ("oligonucleotides" are assembled following the rules of base pairing and the *catalyst* for covalently linking these oligonucleotides.

In principle, life might have begun as a self-replicating RNA. Only later did proteins take over the catalytic machinery of metabolism and DNA take over as the repository of the genetic code. Several other bits of evidence support the RNA World Hypothesis:

- Many of the enzyme cofactors important for life today are based on a ribose nucleotide; for example:
  - ATP
  - NAD
  - FAD
  - coenzyme A

  - cyclic AMP
  - GTP
- In the cell, all deoxyribonucleotides are synthesized from ribonucleotide precursors.
- Many organisms control the transcription and/or translation of certain genes with RNA molecules, not protein molecules.

Problem 3: How were macromolecules able to reproduce themselves?

Once macromolecules were created, the next problem we must try to understand is how they were able to generate more of themselves, identical in composition and structure. Without this reproductive ability, life would change each generation and there would be no continuity.

The advantage of the RNA World Hypothesis is that it proposes a way in which the creation of the first macromolecule (an RNA with the ability to encode information and replicate itself) and of creating progeny with similar properties. It would explain this step, and provide a mechanism for natural selection to work on this population of "organisms" (RNA ribozymes) to change, with the best replicators emerging from the pool in greater numbers at each succeeding generation.

For the other hypotheses about the creation of life, the mechanism for the reproduction of macromolecules is less understood.

Problem 4: How were these macromolecules assembled into a system separate from their surroundings (i.e., a cell)?

To function, the machinery of life must be separated from its surroundings so that the building blocks are held in greater concentration to facilitate chemical reactions and so that the products do not float away. The chemicals of life need to be separated from the extracellular fluid (ECF). Today, this function is provided by the plasma membrane.

The plasma membranes of all currently living organisms are made of a double layer of phospholipids. They are only permeable to small, uncharged molecules like H_2O, CO_2, and O_2. Specialized transmembrane transporters are needed for ions, hydrophilic, and charged organic molecules (e.g., amino acids and nucleotides) to pass into and out of the cell.

Researchers in this field, including Jack Szostak and colleagues from Harvard University, have confirmed that fatty acids, fatty alcohols, and monoglycerides, all molecules that can be synthesized under prebiotic conditions, can also form lipid bilayers and these can spontaneously assemble into enclosed vesicles.

Unlike phospholipid vesicles, these

- admit charged molecules like nucleotides
- admit hydrophilic molecules like ribose
- grow by self-assembly
- are impermeable to, and thus retain, polymers like oligonucleotides.

Here, then, is a simple system that is a plausible model for the creation of the first cells from the primeval "soup" of organic molecules.

Other hypotheses have been proposed, like the formation of an iron sulfide cell as a precursor of cells in deep-sea hydrothermal vents. The advantage of these enclosures is that they would have served as catalysts as well as to keep the chemicals created by the early life from floating away. In time, lipids may have come to coat the surface of these metal cells and bud away, seeding life in the ocean.

This page titled 5.1.2: Origins of Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **18.9: The Origin of Life** by John W. Kimball is licensed CC BY 3.0. Original source: https://www.biology-pages.info/.

Evidence for Early Life

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Discuss the origins of prokaryotic organisms in terms of the geologic timeline
- Distinguish Bacteria from Archaea in terms of their origins
- Discuss the distinguishing features of extremophiles and the environments that produce biofilms

Introduction

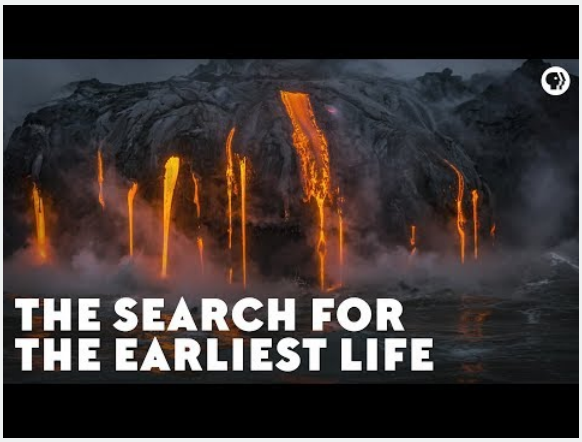
When and where did life begin? What were the conditions on Earth when life began? Prokaryotes were the first forms of life on Earth, existing for billions of years before plants and animals appeared. The Earth and its moon are about 4.54 Ga. This estimate is based on evidence from radiometric dating of meteorite material together with other substrate material from the Earth and the moon.

Early Earth had a very different atmosphere than it does today, for example, it contained less molecular oxygen since photosynthesis had not yet evolved to produce it as a by-product. It was also subjected to strong radiation from outer space since the composition of the early atmosphere did not protect the surface as it does today. Thus, the first organisms would have flourished where they were more protected, such as in ocean depths or beneath the surface of the Earth. Also at this time, strong volcanic activity was common on Earth. It is probable that these first organisms, the first prokaryotes, were adapted to very high temperatures. The early Earth was prone to geological upheaval, volcanic eruptions, and bombardment by mutagenic radiation from the sun. The first organisms were prokaryotes that could withstand these harsh conditions. **Prokaryotes** are single-celled organisms without a nucleus or membrane-bound organelles.

Although prokaryotic cell fossils date to almost 3.5 billion years ago, most prokaryotes do not have distinctive morphologies; fossil shapes cannot be used to distinguish them between Archaea and Bacteria. Instead, chemical fossils of unique lipids are more informative because such compounds do not occur in other organisms. Some publications suggest that archaean or eukaryotic lipid remains are present in rock formations dating from 2.7 billion years ago in Precambrian formations. The oldest such traces come from Greenland, in Earth's oldest sediments, which formed 3.8 billion years ago.

Video





This 5.5-minute video describes the search for the earliest evidence of life on Earth.
Question after watching: Evidence for life on Earth is that it happened relatively quickly after the formation of the planet. What are the implications of this hypothesis?

Optional Activity 5.1.3.1

Why do scientists believe that the first organisms on Earth were extremophiles?

Answer

Because the environmental conditions on early Earth were extreme by current standards: high temperatures, lack of oxygen, high radiation, etc.

Current Model: Prokaryotes, the First Inhabitants of Earth

The first, living organisms were likely prokaryotes, which may have evolved from one or more of the circumstances in Unit 5.1.2. The evidence strongly suggests that eukaryotes evolved much later in the history of life. They are discussed in Unit 5.1.4.

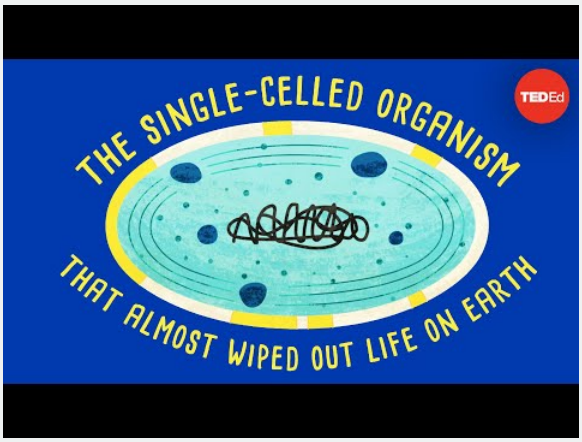
Evolution of Prokaryotes

In the recent past, scientists grouped living things into five kingdoms (animals, plants, fungi, protists, and prokaryotes) based on several criteria such as: the absence or presence of a nucleus and other membrane-bound organelles, the absence or presence of cell walls, multicellularity, etc. In the late 20th century, the pioneering work of Carl Woese and others compared sequences of the small-subunit ribosomal RNA (SSU rRNA), which are found in every living organism. This resulted in insights into the evolution of living organisms, their relationships, and a more fundamental way to group organisms on Earth. Based on differences in the structure of cell membranes and in the sequences of their rRNA, Woese and his colleagues proposed that all life on Earth evolved along three domains. The **Domain Bacteria** comprises all eubacteria (a type of prokaryote), the **Domain Archaea** comprises the archaeans (also a type of prokaryote), and the **Domain Eukarya** comprises all eukaryotes, including organisms in the kingdoms Animalia, Plantae, Fungi, and Protista.

Two of the three domains, Bacteria and Archaea, are prokaryotic. Based on fossil and molecular evidence, prokaryotes were the first inhabitants on Earth, appearing 3.5-3.8 billion years ago during the Precambrian Period. These organisms are abundant and ubiquitous; that is, they are present everywhere on Earth today. In addition to inhabiting moderate environments, they are found in extreme conditions: from boiling hot springs to permanently frozen environments such as tundra and sea ice; from salty environments like the Dead Sea to environments under tremendous pressure, such as the depths of the ocean; and from areas without oxygen, such as a waste management plant, to radioactively-contaminated regions, such as Chernobyl in Ukraine. Prokaryotes reside in the human digestive system and on human skin, are responsible for some illnesses, and serve an important role in the preparation of many foods.

Video





This 4-minute video explains how bacteria almost extinguished life on Earth early in life's history. Question after watching: Why was the creation of oxygen by photosynthesis problematic?

Prokaryotic Life

Microbial Mats

Microbial mats**,** or large **biofilms**, may represent the earliest forms of life on Earth; there is fossil evidence of their presence starting about 3.5 billion years ago. A microbial mat is a multi-layered sheet of prokaryotes that includes mostly bacteria, but also archaea (Figure 5.1.3.1). Microbial mats are a few centimeters thick, typically growing where different types of materials interface, mostly on moist surfaces. The different species of prokaryotes that comprise the mats use different metabolic pathways, which is the reason for their varied colors. Prokaryotes in a microbial mat are held together by a glue-like sticky substance that they secrete called **extracellular matrix**.

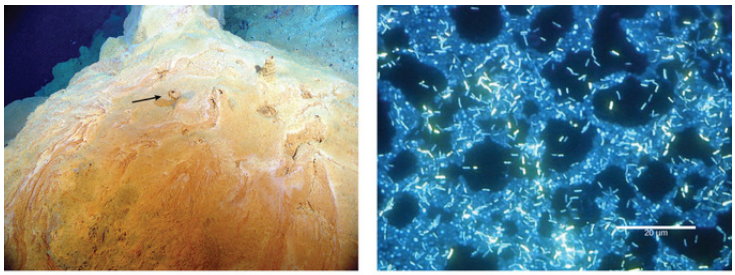


Figure 5.1.3.1: (a) This microbial mat, about one meter in diameter, grows over a hydrothermal vent in the Pacific Ocean in a region known as the "Pacific Ring of Fire." The mat helps retain microbial nutrients. Chimneys, such as the one indicated by the arrow, allow gases to escape. (b) In this micrograph, individual bacteria in a microbial mat are visualized using fluorescence microscopy.

The organisms in the first biofilms likely obtained their energy from chemicals found near **hydrothermal vents**. A hydrothermal vent is a fissure in the Earth's surface that releases geothermally-heated water and chemicals leached from rocks in the Earth's interior. With the evolution of photosynthesis about 3 billion years ago, some prokaryotes in microbial mats came to use a more widely available energy source, sunlight, whereas others were still dependent on chemicals from hydrothermal vents for energy and food.

? Optional Activity 5.1.3.2

Microbial mats _____.

A. are the earliest forms of life on Earth
B. obtain their energy and food from hydrothermal vents
C. are multi-layered sheets of prokaryotes including mostly Bacteria but also Archaea
D. all of the above

Answer

D. All of the above

The Ecology of Biofilms

Until a couple of decades ago, microbiologists used to think of prokaryotes as isolated entities living apart. This model, however, does not reflect the now better-understood ecology of prokaryotes, most of which prefer to live in communities where they can interact. A biofilm is a microbial community held together in a gummy-textured matrix that consists primarily of polysaccharides secreted by the organisms, together with some proteins and nucleic acids (Figure 5.1.3.2). Biofilms grow attached to surfaces to secure them in place. Some of the best-studied biofilms are composed of prokaryotes, although fungal biofilms have also been described, as well as some composed of a mixture of fungi and bacteria.

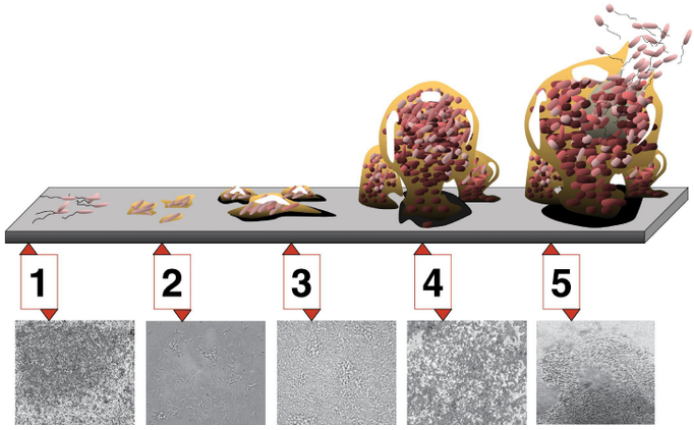


Figure 5.1.3.2: Micrographs of a *Pseudomonas aeruginosa* biofilm in each of the stages of development. Biofilm development occurs in five stages as shown. During stage 1, initial attachment, prokaryotes adhere to a solid surface. During stage 2, irreversible attachment, hairlike appendages called pili permanently anchor the prokaryotes to the surface. During stage 3, maturation I, the biofilm grows through cell division and recruitment of other prokaryotes. An extracellular matrix composed primarily of polysaccharides holds the biofilm together. During stage 4, maturation II, the biofilm continues to grow and takes on a more complex shape. During stage 5, dispersal, the biofilm matrix is partly broken down, allowing some prokaryotes to escape and colonize another surface.

Biofilms are present almost everywhere: they are visible on the surface of some lakes and can cause the clogging of pipes. They also colonize household surfaces, such as kitchen counters, cutting boards, sinks, and toilets, as well as places on the human body, such as the surfaces of our teeth (plaque). They also play a major role in food contamination.

Interactions among the organisms that populate a biofilm, together with their protective extracellular matrix, make these communities more robust than free-living prokaryotes. The sticky substance that holds bacteria together also excludes most antibiotics and disinfectants, making biofilm bacteria hardier than their free-living counterparts. Overall, biofilms are very difficult to destroy because they are resistant to many common forms of sterilization.

Stromatolites

Fossilized microbial mats represent the earliest record of life on Earth. A **stromatolite** is a sedimentary structure formed when minerals are precipitated out of water by prokaryotes in a microbial mat (Figure 5.1.3.3). Stromatolites form layered rocks made of carbonate or silicate. Although most stromatolites are artifacts from the past, there are places on Earth where stromatolites are still forming. For example, growing stromatolites have been found in the Anza-Borrego Desert State Park in San Diego County, California.



Figure 5.1.3.3: Stromatolites: (a) These living stromatolites are located in Shark Bay, Australia. (b) These fossilized stromatolites, found in Glacier National Park, Montana, are nearly 1.5 billion years old.

In addition, the US's National Aeronautic and Space Administration (NASA) is studying Pavilion Lake, north of Whistler BC, for its microbialite populations (Figure 5.1.3.4). These bacteria colonies live at the bottom of the lake and precipitate minerals that form coral-like structures. These structures formed 10,000 years ago when the glaciers retreated from the area.

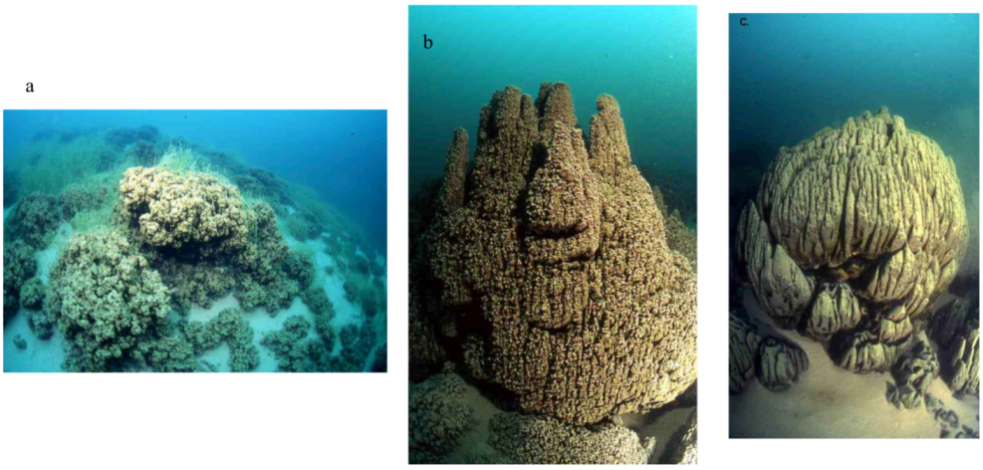


Figure 5.1.3.4: Examples of microbialite morphologies in Pavillion Lake (CC-BY-SA; Schulze-Makuch, D. et al. https://www.mdpi.com/2075-1729/3/1/21#)

Video





This 2-minute video describes what stromatolites are.

Question after watching: Why are stromatolites relevant to the study of the origin and early evolution of life?

Microbes Are Adaptable: Life in Moderate and Extreme Environments

Some organisms have developed strategies that allow them to survive harsh conditions. Prokaryotes thrive in a vast array of environments; some grow in conditions that would seem very normal to us, whereas others are able to thrive and grow under conditions that would kill a plant or animal. Almost all prokaryotes have a cell wall: a protective structure that allows them to survive in both hyper- and hypo-osmotic conditions. Some soil bacteria can form endospores that resist heat and drought, thereby allowing the organism to survive until favorable conditions recur. These adaptations, along with others, have made bacteria the most abundant life form in all terrestrial and aquatic ecosystems today.

Other bacteria and archaea are adapted to grow under extreme conditions and are called **extremophiles**, meaning "lovers of extremes". Extremophiles have been found in all kinds of environments: the depth of the oceans, hot springs, the Arctic and the Antarctic, in very dry places, deep inside the Earth, in harsh chemical environments, and in high radiation environments, just to mention a few (Figure 5.1.3.5).



Figure 5.1.3.5: Certain prokaryotes can live in extreme environments such as the Morning Glory pool, a hot spring in Yellowstone National Park, Wyoming, USA. The spring's vivid blue color is from prokaryotes that thrive in its hot waters.

These organisms give us a better understanding of prokaryotic diversity and help us understand the range of environmental conditions that life can tolerate. This allows us to understand where life may have originated, and where we may find it in the future (including on other planets and moons in the solar system). In addition, the unique enzymes and chemical pathways that extremophiles develop to adapt to their environment raise the possibility of finding new therapeutic drugs or industrial applications.

Because they have specialized adaptations that allow them to live in extreme conditions, many extremophiles cannot survive in moderate environments. There are many different groups of extremophiles. They are identified based on the conditions in which they grow best. For example, organisms that live in acidic (low pH) conditions are called **acidophiles**. Those that live in hot environments are called **thermophiles**. Some habitats are extreme in multiple ways. For example, a soda lake is both salty and alkaline, so organisms that live in a soda lake must be both **alkaliphiles** and **halophiles**.

Other extremophiles, like radioresistant organisms, do not prefer an extreme environment (in this case, one with high levels of radiation), but have adapted to survive in it (Figure 5.1.3.6).

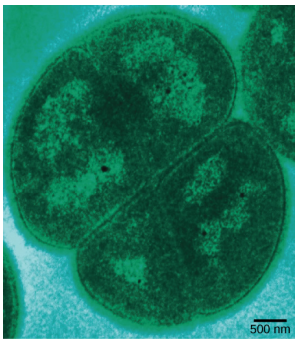


Figure 5.1.3.6: Deinococcus radiodurans, visualized in this false-color transmission electron micrograph, is a prokaryote that can tolerate very high doses of ionizing radiation. It has evolved DNA repair mechanisms, refined from existing ones found in other organisms, but specialized for its environment, that allow it to reconstruct its chromosome even if it has been broken into hundreds of pieces by radiation or heat.

Prokaryotes in the Dead Sea

One example of a harsh environment is the Dead Sea, a hypersaline basin that is located between Jordan and Israel. **Hypersaline** environments are concentrated seawater. In the Dead Sea, the sodium concentration is 10 times higher than in seawater. The water also contains high levels of magnesium (about 40 times higher than seawater) that are toxic to most living things. Iron, calcium, and magnesium, elements that form divalent ions (Fe^{2+}, Ca^{2+}, and Mg^{2+}), produce what is commonly referred to as “hard” water. Taken together, the high concentration of divalent cations, the acidic pH (6.0), and the intense solar radiation flux make the Dead Sea a unique, and hostile, ecosystem.



Figure 5.1.3.6: (a) The Dead Sea is hypersaline. Nevertheless, salt-tolerant bacteria thrive in this sea. (b) These halobacteria cells can form salt-tolerant bacterial mats.

Career Connection: Paleontologist

Natural history museums display the fossil casts of extinct animals and information about how these animals evolved, lived, and died. Paleontologists are scientists who study past life. They use fossils to observe and explain how life evolved on Earth and how species interacted with each other and the environment. A paleontologist must be knowledgeable in biology, ecology, chemistry, geology, and other scientific disciplines. A paleontologist’s work may involve field studies: searching for and studying fossils. In addition to digging for and finding fossils, paleontologists also prepare fossils for further study and analysis. Although dinosaurs are probably the first animals that come to mind when thinking about paleontology, paleontologists study everything from plant life, fungi, and fish to sea animals and birds.

An undergraduate degree in Earth science or biology is a good place to start toward the career path of becoming a paleontologist. Most often, a graduate degree is necessary. Additionally, work experience in a museum or in a paleontology lab is useful.

This page titled 5.1.3: Evidence for Early Life is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **22.1: Prokaryotic Diversity** by OpenStax is licensed CC BY 4.0.
- **22.0: Prelude to Prokaryotes** by OpenStax is licensed CC BY 4.0.
- **27.4: The Evolutionary History of the Animal Kingdom** by OpenStax is licensed CC BY 4.0.

Unit 3.3.4 - Eukaryotic Origins

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- Bolded terms are located at the end of the unit in the Glossary. There is also a Unit Summary at the end of the Unit.
- To navigate to Unit 3.4, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

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

Introduction

Living things fall into three large Domains: Archaea, Bacteria, and Eukarya. The first two have prokaryotic cells, and the third contains all eukaryotes. A relatively sparse fossil record is available to help discern what the first members of each of these lineages looked like, so it is possible that all the events that led to the last common ancestor of extant eukaryotes will remain unknown. However, the comparative biology of extant organisms and the limited fossil record provide some insight into the history of Eukarya.

The earliest fossils of living organisms appear to be Bacteria, most likely cyanobacteria. They are about 3.5 billion years old and are recognizable because of their relatively complex structure and, for prokaryotes, relatively large cells. Most other prokaryotes have small cells, 1 or 2 μm in size, and would be difficult to pick out as fossils. Most living eukaryotes have cells measuring 10 μm or greater. Structures this size, which might be fossils, appear in the geological record about 2.1 billion years ago.

Characteristics of Eukaryotes

Data from these fossils have led comparative biologists to the conclusion 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 must have been present in the last common ancestor.

These characteristics that are common to nearly all eukaryotes include:

1. Cells with nuclei that are 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 currently living eukaryotes have cells with nuclei.
2. Mitochondria. An organelle that processes glucose using oxygen to produce ATP. Some extant eukaryotes have very reduced remnants of mitochondria in their cells, whereas other members of their lineages have “typical” mitochondria.
3. A cytoskeleton containing 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 there is molecular evidence that they are descended from ancestors that possessed them.
5. Chromosomes, each consisting 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 based on information contained in their DNA.
6. Mitosis, which is a process of cellular division wherein replicated chromosomes are divided and separated into two new cells using elements of the cytoskeleton. Mitosis is universally present in eukaryotes.
7. Sexual reproduction and meiosis, a process of cell division and genetic recombination unique to eukaryotes.

Endosymbiosis and the Evolution of Eukaryotes

To understand eukaryotic organisms, it is necessary to understand that all **extant** (currently living) eukaryotes are descendants of an 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. 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 such as plants. Before explaining this further, it is necessary to consider metabolism in prokaryotes.

Prokaryotic Metabolism

Prokaryotes are much more metabolically diverse than eukaryotes. This makes sense when considering that the evolution of eukaryotes represents only one branch of the tree of life, and a relatively recent one at that.

Many important metabolic processes such as nitrogen fixation (see Unit 3.4.2), are never found in eukaryotes. One that is not unique to eukaryotes (i.e., some prokaryotes can do it), but that is present in all eukaryotes is the process of **aerobic respiration** (cellular respiration in the presence of oxygen) and it happens in the mitochondria. This suggests that the ability to respire came from a type of prokaryote that could do aerobic respiration; they eventually became the eukaryotic cell's mitochondria. This is discussed in more detail below.

The Problem with Oxygen

While today's atmosphere is about one-fifth molecular oxygen (O_2), geological evidence shows that the atmosphere originally lacked O_2. Without oxygen, aerobic respiration would not be possible, and prokaryotes would have relied on fermentation as a means of transforming the energy in their food into something that they use for their cells. At some point around 3.5 billion years ago, some prokaryotes began using energy from sunlight to power the formation of organic compounds. That is, they evolved the ability to do **photosynthesis**. The group of Gram-negative bacteria that gave rise to cyanobacteria used water as the hydrogen source and released O_2 as a waste product. They used chemical gradients across their cell membrane to do it.

Eventually, the amount of photosynthetic oxygen built up in some environments to levels that were toxic to the organisms living at that time. Oxygen is reactive (it is a strong electron acceptor) and can damage many organic compounds. Metabolic processes evolved to protect organisms from oxygen. Aerobic respiration, one of these processes, utilized the newly available chemical, and its properties as an electron acceptor, to extract energy out of reduced chemicals (a reduced chemical is one that contains many electrons). As energy was extracted from these reduced chemicals, the cell captured the energy to make ATP, a chemical it could readily use to power its processes. This ability to use oxygen to process reduced chemicals (i.e., aerobic respiration) became widely present among prokaryotes, including in a group we now call alpha-proteobacteria (described below).

Organisms that did not evolve aerobic respiration continued to exist, but the were restricted to living in oxygen-free environments. Originally, oxygen-rich environments were likely localized around places where cyanobacteria were active. By about 2 billion years ago, however, geological evidence shows that oxygen built up to higher concentrations in the atmosphere. This is known as the **Great Oxygenation Event (GOE)** (Figure 5.1.4.1). Even though levels were rising, oxygen amounts similar to today's only arose within the last 600 Ma just before the beginning of the Cambrian Period.

Recall that the first fossils that we believe to be eukaryotes date to about 2 Ga, so they appeared during the GOE. Also, recall that all extant eukaryotes descended from an ancestor with mitochondria. These organelles were first observed by scientists in the late 1800s, where they were described as somewhat worm-shaped structures that moved 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.

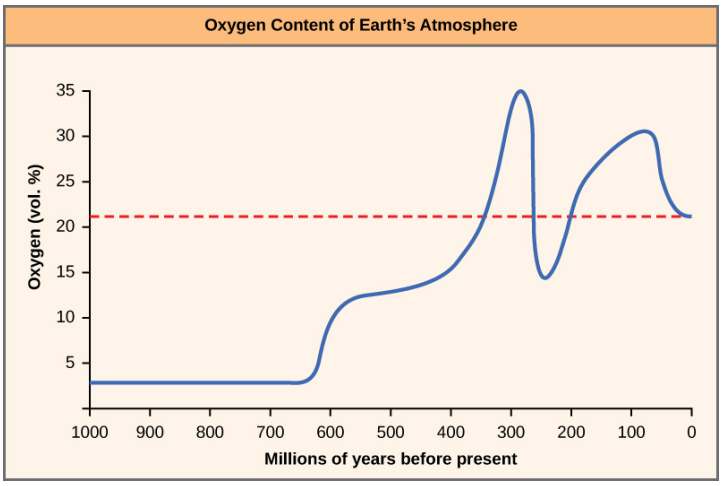


Figure 5.1.4.1: The oxygen concentration in Earth's atmosphere rose sharply around 300 million years ago. The red dotted line indicates current levels of oxygen in the atmosphere for reference.

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 the 1960s, biologist Lynn Margulis proposed the **endosymbiotic theory**, suggesting that eukaryotes were the product of one cell engulfing another. In the proposed model, once engulfed, the two cells continued to live together and evolved co-dependence so that they could no longer live independently of one another. Although Margulis' work initially was met with resistance, 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.

Broadly, it has become clear that many of the nuclear genes and the molecular machinery responsible for replication and the expression of those genes appear closely related to those in Archaea. On the other hand, the metabolic organelles and genes responsible for many energy-harvesting processes had their origins in bacteria.

Much remains to be clarified about how this relationship occurred; this continues to be an exciting field of 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 all eukaryotes. Over many generations, a symbiotic relationship can result if the two organisms depend on each other so completely that neither could survive on its own.

Video





This 8-minute video provides an overview of the steps in the evolution of eukaryotes from prokaryotes. Question after watching: Which organelle do you think evolved first: chloroplasts that photosynthesize or mitochondria that extract energy from reduced chemicals using oxygen? What is your rationale?

Evidence for Endosymbiosis: Mitochondria

One of the major features distinguishing prokaryotes from eukaryotes is the presence of **mitochondria**. Eukaryotic cells may contain anywhere from one to several thousand mitochondria, depending on the cell's level of energy consumption. Each mitochondrion measures 1 to 10 or greater micrometers (μm) in length and exists in the cell as an organelle that can be ovoid, worm-shaped, or intricately branched (Figure 5.1.4.2).

Mitochondria arise from the division of existing mitochondria; they may fuse together; and they may be moved around inside the cell by interactions with the cytoskeleton. However, mitochondria cannot survive outside the cell. As the atmosphere was oxygenated by photosynthesis, and as successful aerobic prokaryotes evolved, evidence suggests that an ancestral cell with some membrane compartmentalization engulfed a free-living aerobic prokaryote, specifically an alpha-proteobacterium, thereby giving the host cell the ability to use oxygen to release energy stored in nutrients.

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. Several lines of evidence support that mitochondria are

derived from this endosymbiotic event. Most mitochondria are shaped like alpha-proteobacteria and are surrounded by two membranes, which would result when one membrane-bound organism was engulfed into a vacuole by another membrane-bound organism. The mitochondrial inner membrane is extensive and involves substantial infoldings called cristae that resemble the textured, outer surface of alpha-proteobacteria. The matrix and inner membrane are rich with the enzymes necessary for aerobic respiration.

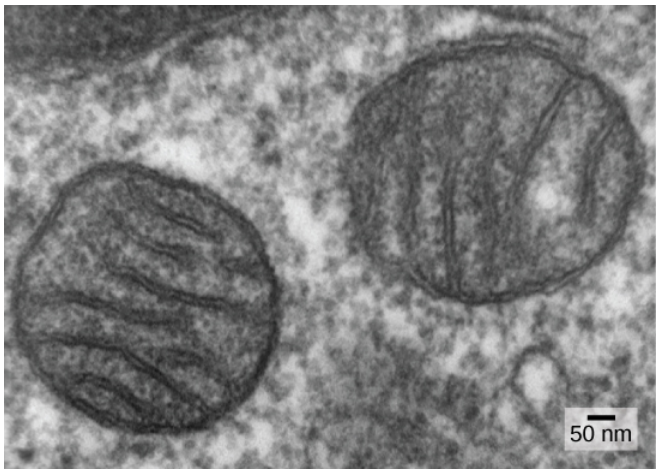


Figure 5.1.4.2: In this transmission electron micrograph of mitochondria in a mammalian lung cell, the cristae, infoldings of the mitochondrial inner membrane, can be seen in cross-section. (credit: Louise Howard)

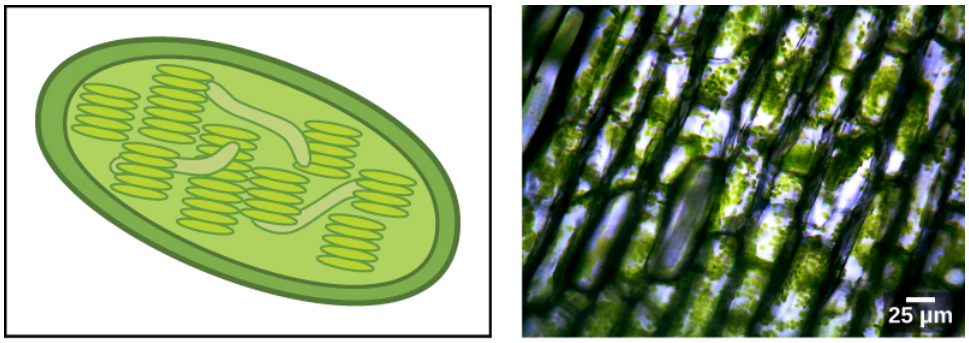
Mitochondria divide independently by a process that resembles binary fission in prokaryotes. Specifically, mitochondria are not formed from scratch (de novo) by the eukaryotic cell; they reproduce within it and are distributed with the cytoplasm when a cell divides or two cells fuse. Therefore, although these organelles are highly integrated into the eukaryotic cell, they still reproduce as if they are independent organisms within the cell. However, their reproduction is synchronized with the activity and division of the cell. Mitochondria have their own (usually) circular DNA chromosome that is stabilized by attachments to the inner membrane and carries genes like genes expressed by alpha-proteobacteria. Mitochondria also have special ribosomes and transfer RNAs that resemble these components in prokaryotes. These features all support that mitochondria were once free-living prokaryotes.

Mitochondria that carry out aerobic respiration have their own genomes, with genes similar to those in alpha-proteobacteria. However, many of the genes for respiratory proteins are located in the nucleus. When these genes are compared to those of other organisms, they appear to be of alpha-proteobacterial origin. Additionally, in some eukaryotic groups, such genes are found in the mitochondria, whereas in other groups, they are found in the nucleus. This has been interpreted as evidence that genes have been transferred from the endosymbiont chromosome to the host genome. This loss of genes by the endosymbiont is probably one explanation why mitochondria cannot live without a host.

Some living eukaryotes are anaerobic and cannot survive in the presence of oxygen. Some appear to lack organelles that could be recognized as mitochondria. In the 1970s to 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. However, later findings suggest that reduced organelles are found in most, if not all, anaerobic eukaryotes, and that 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. Therefore, most biologists now accept that the LCA of eukaryotes had mitochondria.

Evidence of Endosymbiosis: 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 5.1.4.3).



(a) (b)

Figure 5.1.4.3: (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. (credit b: modification of work by Brandon Zierer; scale-bar data from Matt Russell)

Like mitochondria, plastids appear to have an endosymbiotic origin. This hypothesis was also championed by Lynn Margulis. Plastids are derived from cyanobacteria that lived inside the cells of an ancestral, aerobic, heterotrophic eukaryote. This is called primary endosymbiosis, and plastids of primary origin are surrounded by two membranes. This likely happened twice in the history of eukaryotes.

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 (Figure 5.1.4.4). Cyanobacteria also have the peptidoglycan wall and lipopolysaccharide layer associated with Gram-negative bacteria.

Chloroplasts of primary origin have thylakoids, a circular DNA chromosome, and ribosomes like those of cyanobacteria. Each chloroplast is surrounded by two membranes. The outer membrane surrounding the plastid is thought to be derived from the vacuole in the host, and the inner membrane is thought to be derived from the plasma membrane of the symbiont.

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 engulfing of the chloroplast ancestor occurred 1 to 1.5 billion years ago, at least 500 million years after the fossil record suggests that eukaryotes were present.

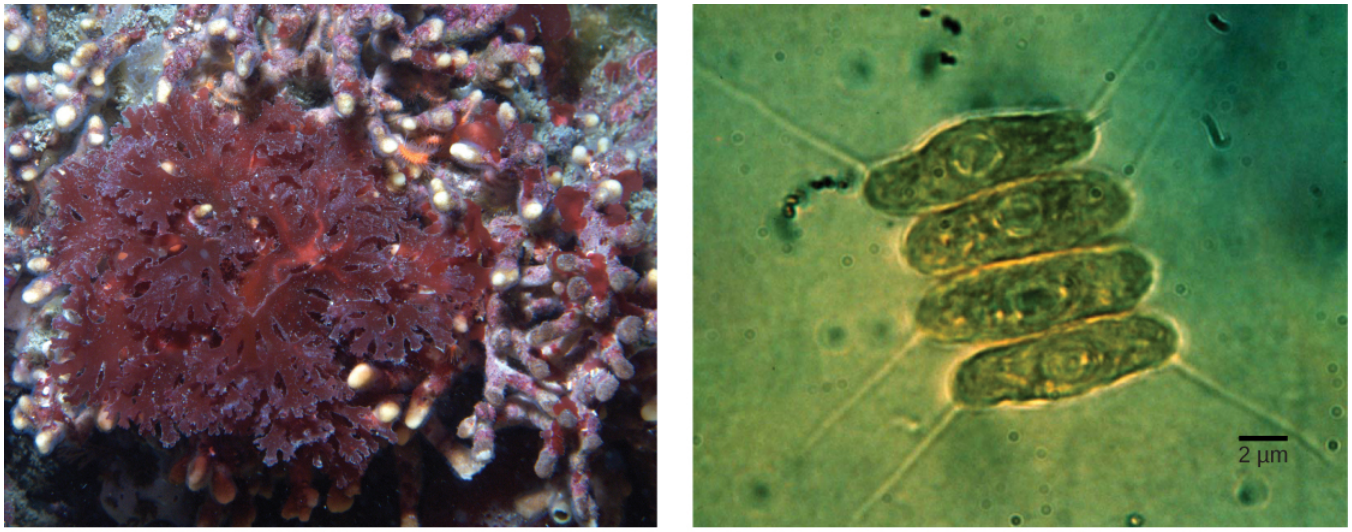


Figure 5.1.4.4: (a) Red algae and (b) green algae (visualized by light microscopy) share similar DNA sequences with photosynthetic cyanobacteria. Scientists speculate that, in a process called endosymbiosis, an ancestral prokaryote engulfed a photosynthetic cyanobacterium that evolved into modern-day chloroplasts. (credit a: modification of work by Ed Bierman; credit b: modification of work by G. Fahnenstiel, NOAA; scale-bar data from Matt Russell)

Optional Activity 5.1.4.1

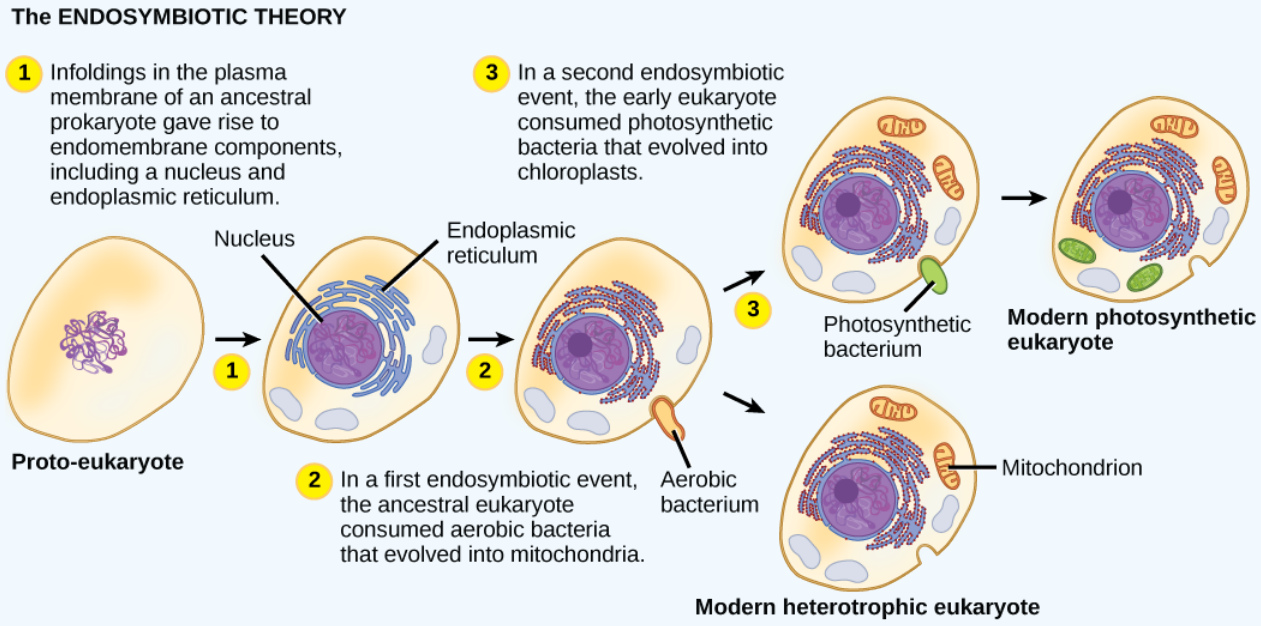


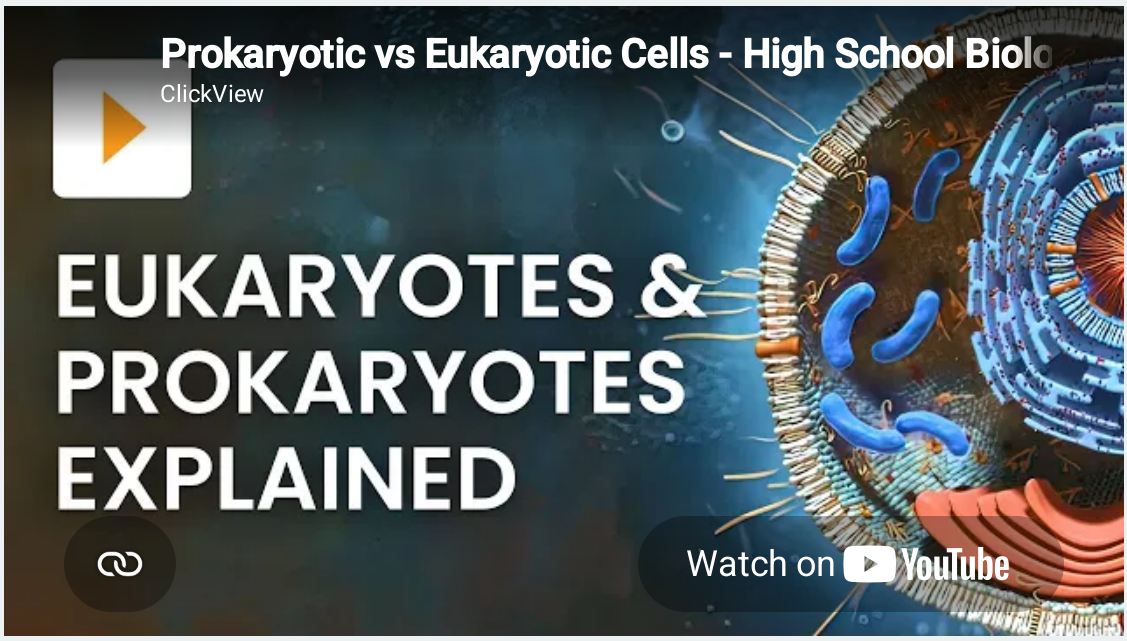
Figure 5.1.4.5: The first eukaryote may have originated from an ancestral prokaryote that had undergone membrane proliferation, compartmentalization of cellular function (into a nucleus, lysosomes, and an endoplasmic reticulum), and the establishment of endosymbiotic relationships with an aerobic prokaryote, and, in some cases, a photosynthetic prokaryote, to form mitochondria and chloroplasts, respectively.

What evidence is there that mitochondria were incorporated into the ancestral eukaryotic cell before chloroplasts?

Answer

All eukaryotic cells have mitochondria, but not all eukaryotic cells have chloroplasts.

Video





This 4.5-minute video provides a quick overview of the differences between prokaryotes and eukaryotes. Question after watching: What do the characteristics contained in both prokaryotes and eukaryotes tell you about the evolution of life on Earth?

This page titled 5.1.4: Eukaryotic Origins is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **23.1: Eukaryotic Origins** by OpenStax is licensed CC BY 4.0.

5.2: Acellular Entities - Viruses, Prions, and Viroids

Acellular Entities: Viruses, Prions, and Viroids

- Please read and watch the following Mandatory Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe how viruses were first discovered and how they are detected
- Identify three hypotheses about how viruses evolved
- Explain the Baltimore classification systems for viruses
- Describe prions and their basic properties
- Define viroids and their targets of infection

Introduction - Viruses

No one knows exactly when viruses emerged or from where they came, since viruses do not leave physical footprints such as fossils. Modern viruses are thought to be a mosaic of bits and pieces of nucleic acids picked up from past hosts along their evolutionary paths.

Viruses exist in a netherworld between a living organism and a nonliving entity. Living things grow, metabolize, reproduce, and evolve. Viruses exhibit some of these abilities but cannot do any of them on their own. They must infect a host cell and hijack the host's replication machinery to produce (nearly) identical progeny virus particles. Since their reproduction is not perfect, they can evolve through natural selection. They do not have their own metabolism and are entirely dependent on their host cells to replicate. They do not metabolize or grow but rather are assembled into their mature form by the host cell.

Viruses are acellular parasitic entities that are not classified within any domain or kingdom. Viruses are diverse entities. They vary in their structure, their replication methods, and in their target hosts. Nearly all forms of life—from bacteria and archaea to eukaryotes such as plants, animals, and fungi—have viruses that infect them. While most biological diversity can be understood through evolutionary history such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown.

Video





In this 4-minute video, viruses are described as the most common biological unit on Earth, outnumbering all other types combined.

Question after watching: Why do scientists talk about "types" of viruses rather than "species" of viruses?

Video





This 11-minute video points out, viruses are all around us, they evolve, grow, and can be killed. Question after watching: What hypotheses are offered to reconsider viruses as being alive? Are you convinced? Why or why not?

Virus Discovery and Detection

Viruses were first discovered after the development of a porcelain filter, called the Chamberland-Pasteur filter, which could remove all bacteria visible in the microscope from any liquid sample. In 1886, Adolph Meyer demonstrated that a disease of tobacco plants, tobacco mosaic disease, could be transferred from a diseased plant to a healthy one via liquid plant extracts. In 1892, Dmitri Ivanowski showed that this disease could be transmitted in this way even after the Chamberland-Pasteur filter had removed all viable bacteria from the extract. Still, it was many years before it was proven that these "filterable" infectious agents were not simply very small bacteria but were a new type of very small, disease-causing particle.

Virions, single virus particles outside of the cell, are very small, about 20–250 nanometers in diameter. These individual virus particles are the infectious form of a virus outside the host cell. Unlike bacteria (which are about 100x larger), we cannot see viruses with a light microscope (except for some large virions of the poxvirus family). It was not until the development of the electron microscope in the late 1930s that scientists got their first look of the structure of the tobacco mosaic virus (TMV) (Figure 5.2.1) and other viruses (Figure 5.2.2). The surface structure of virions can be observed by both scanning and transmission electron microscopy, whereas the internal structures of the virus can only be observed in images from a transmission electron microscope. The use of these technologies has allowed for the discovery of many viruses from all types of living organisms. They were initially grouped by shared morphology. Later, groups of viruses were classified by the type of nucleic acid they contained, DNA or RNA, and whether their nucleic acid was single- or double-stranded. More recently, molecular analysis of viral replicative cycles has further refined their classification.

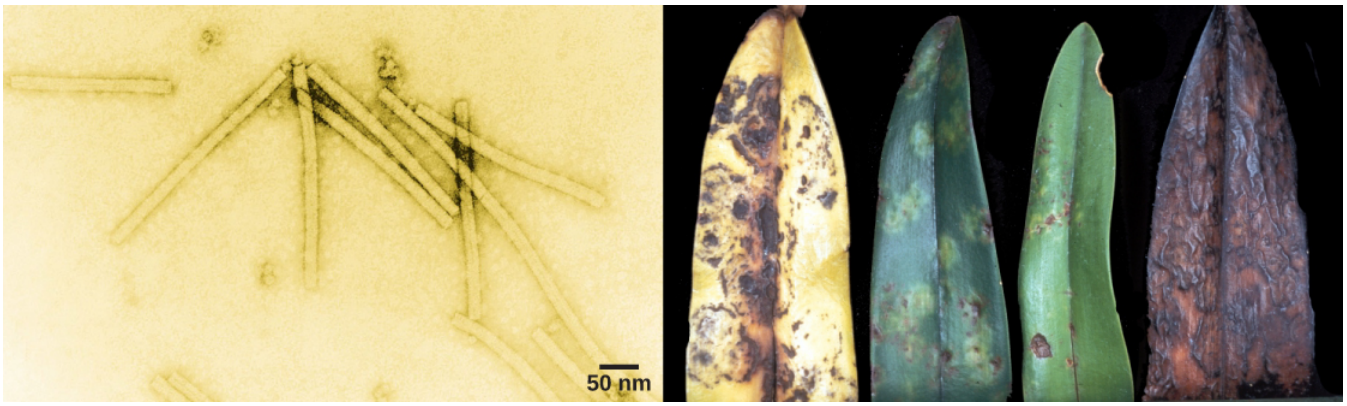
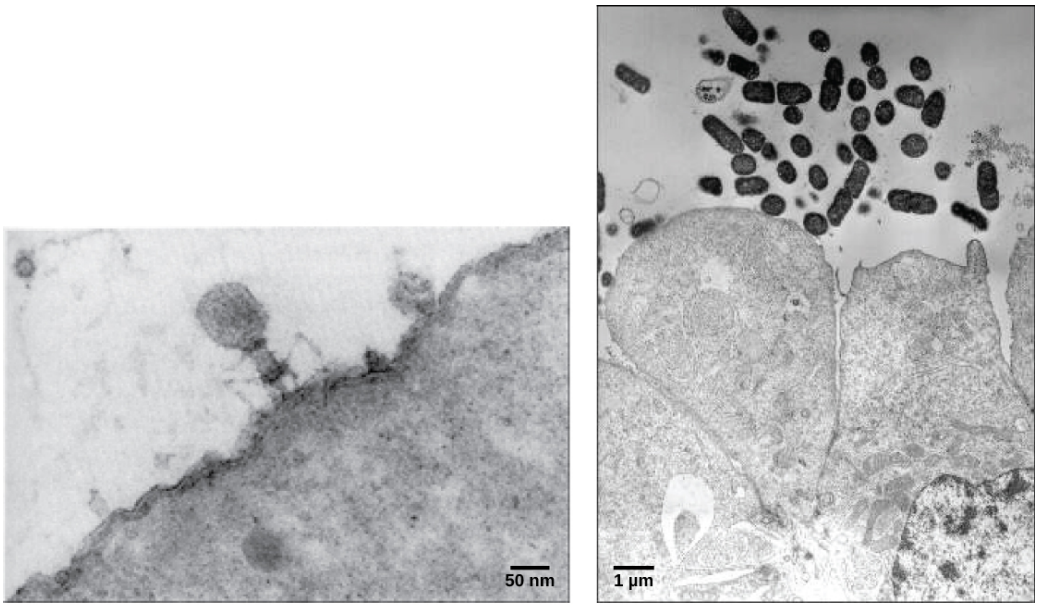


Figure 5.2.1: The tobacco mosaic virus (left), seen here by transmission electron microscopy, was the first virus to be discovered. The virus causes disease in tobacco and other plants, such as the orchid (right). (credit a: USDA ARS; credit b: modification of work by USDA Forest Service, Department of Plant Pathology Archive North Carolina State University; scale-bar data from Matt Russell)



(a) (b)

Figure 5.2.2: In these transmission electron micrographs, (a) a virus (which looks like a moon lander) is dwarfed by the bacterial cell it infects (only a portion of which fills the bottom right of the image). For size comparison, (b) bacterial *E. coli* cells (dark oval shapes) are dwarfed by cultured colon cells (the light grey larger blobs in the middle and bottom of the image). (credit a: modification of work by U.S. Dept. of Energy, Office of Science, LBL, PBD; credit b: modification of work by J.P. Nataro and S. Sears, unpub. data, CDC; scale-bar data from Matt Russell)

Evolution of Viruses

Although biologists have accumulated a significant amount of knowledge about how present-day viruses evolve, much less is known about how viruses originated in the first place. When exploring the evolutionary history of most organisms, scientists can look at fossil records and similar physical evidence. However, viruses do not fossilize, so researchers must conjecture by investigating how today's viruses evolve and by using biochemical and genetic information to create speculative virus histories.

While most findings agree that viruses do not have a single common ancestor, scholars have yet to agree on a hypothesis about the origins of viruses. One such hypothesis, called devolution or the **regressive hypothesis**, proposes that viruses evolved from free-living cells that progressively lost the ability to reproduce and metabolize on their own. A second hypothesis (called escapist or the **progressive hypothesis**) suggests that viruses originated from RNA and DNA molecules that escaped from a host cell. This theory accounts for viruses having either an RNA or a DNA genome. A third hypothesis posits a system of self-replication similar to that of other self-replicating molecules, likely evolving alongside the cells they rely on as hosts. Studies of some plant pathogens support this hypothesis.

As technology advances, scientists may develop and refine further hypotheses to explain the origin of viruses. The emerging field called **virus molecular systematics** attempts to do that through comparisons of sequenced genetic material. Researchers in this field hope their work could someday lead to advances in the treatments for the ailments of viral diseases.

Video





This 2-minute video describes the speed at which viruses evolve through mutations.
Questions after watching: Why do some evolutionary scientists focus on viruses? Why is it important to humans?

Video



The SARS-CoV-2 (Covid-19) pandemic has altered life throughout the world. This 1.5-minute video describes how SARS-CoV-2 infects humans and reproduces.

Question after watching: What are three things you learned from this video that you did not know prior to watching?

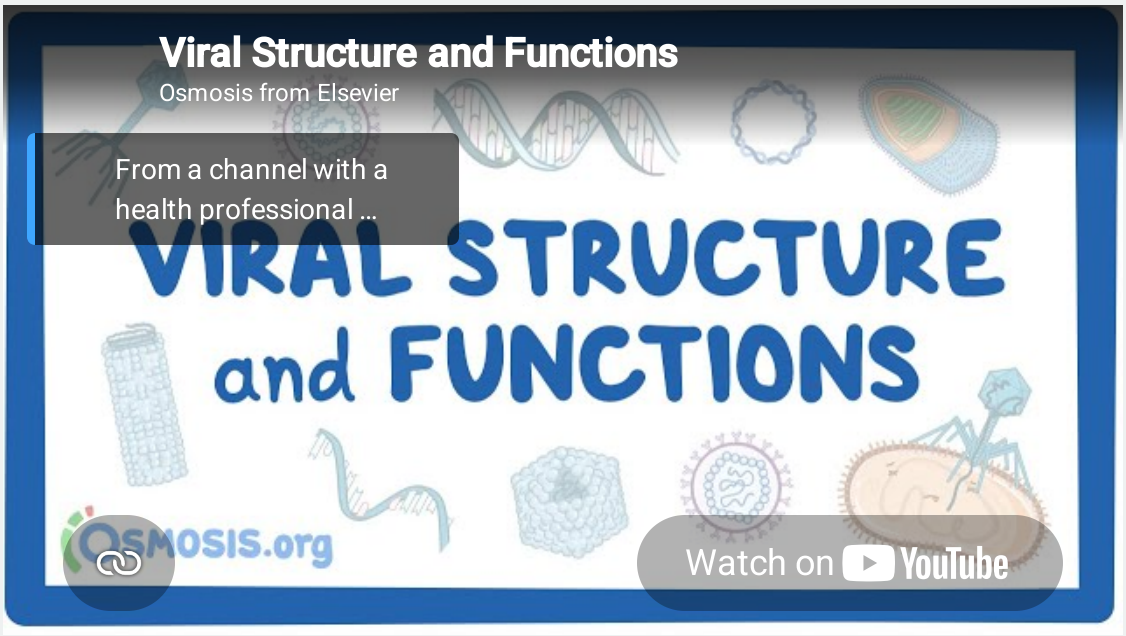
Viral Structure and Function

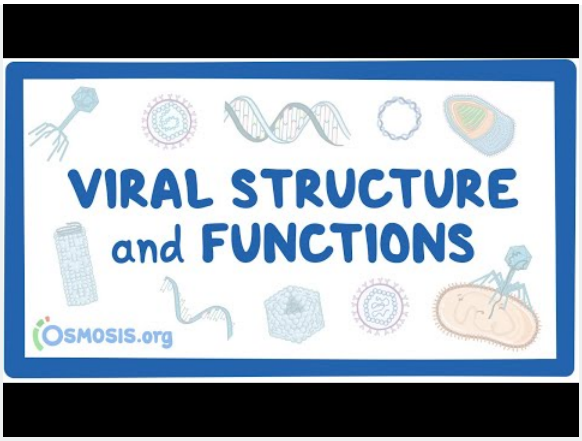
Viruses are **acellular**, meaning they are biological entities that do not have a cellular structure. Therefore, they lack most of the components of cells, such as organelles, ribosomes, and the plasma membrane. A virion consists of a nucleic acid core, an outer protein coating or capsid, and sometimes (notably among viruses that infect animal cells) an outer envelope made of protein and phospholipid membranes derived from the host cell. Viruses may also contain additional proteins, such as enzymes. The most obvious difference between members of viral families is their morphology, which is quite diverse. An interesting feature of viral complexity is that the complexity of the host does not correlate with the complexity of the virion. Some of the most complex virion structures are observed in **bacteriophages**, viruses that infect the simplest living organisms, bacteria.

Viruses come in many shapes and sizes, but these are consistent and distinct for each viral family. All virions have a nucleic acid genome covered by a protective layer of proteins, called a **capsid**. The capsid is made up of protein subunits called capsomeres. Some viral capsids are simple polyhedral "spheres," whereas others are quite complex in structure.

Unlike nearly all living organisms that use DNA as their genetic material, viruses may use either DNA or RNA to encode their information. Some viruses are composed of single-stranded RNA, double-stranded RNA, single-stranded DNA, or double-stranded DNA. It may be linear or circular. While most viruses contain a single nucleic acid, others have genomes that have several, which are called **segments** (analogous to chromosomes). The **virus core** contains the genome or total genetic content of the virus. Viral genomes tend to be small, containing only those genes that encode proteins that the virus cannot get from the host cell.

Video





In this 7-minute video, discover the wide variety of viral shapes and types.
Question after watching: Why are viruses dependent on other organisms for their reproduction?

Virus Classification

To understand the features shared among different groups of viruses, a classification scheme is necessary. Biologists have used several classification systems in the past, based on the morphology and genetics of different viruses. However, these earlier classification methods grouped viruses differently, based on which features of the virus they were using to classify them. The most commonly used classification method today is called the Baltimore classification scheme and is based on how messenger RNA (mRNA) is generated in each type of virus.

Baltimore Classification

The most commonly used system of virus classification was developed by Nobel Prize-winning biologist David Baltimore in the early 1970s. In addition to the differences in morphology and genetics mentioned above, the **Baltimore classification** scheme groups viruses according to how the mRNA is produced during the replicative cycle of the virus. The characteristics of each group in the Baltimore classification are summarized in Table 5.2.1 with examples of each group.

Table 5.2.1: Baltimore Classification

Group	Characteristics	Mode of mRNA Production	Example
I	Double-stranded DNA	mRNA is transcribed directly from the DNA template	Herpes simplex (herpesvirus)
II	Single-stranded DNA	DNA is converted to double-stranded form before RNA is transcribed	Canine parvovirus (parvovirus)
III	Double-stranded RNA	mRNA is transcribed from the RNA genome	Childhood gastroenteritis (rotavirus)
IV	Single stranded RNA (+)	Genome functions as mRNA	Common cold (pircornavirus)
V	Single stranded RNA (-)	mRNA is transcribed from the RNA genome	Rabies (rhabdovirus)
VI	Single stranded RNA viruses with reverse transcriptase	Reverse transcriptase makes DNA from the RNA genome; DNA is then incorporated in the host genome; mRNA is transcribed from the incorporated DNA	Human immunodeficiency virus (HIV)
VII	Double stranded DNA viruses with reverse transcriptase	The viral genome is double-stranded DNA, but viral DNA is replicated through an RNA intermediate; the RNA may serve directly as mRNA or as a template to make mRNA	Hepatitis B virus (hepadnavirus)

Virus Replication

Viral replication within a living cell always produces changes in the cell, sometimes resulting in cell death and sometimes slowly killing the infected cells. There are six basic stages in the virus replication cycle: attachment, penetration, uncoating, replication, assembly, and release. A viral infection may be productive, resulting in new virions, or nonproductive, which means that the virus remains inside the cell without producing new virions. Bacteriophages are viruses that infect bacteria. They have two different modes of replication: the lytic cycle, where the virus replicates and bursts out of the bacteria, and the lysogenic cycle, which involves the incorporation of the viral genome into the bacterial host genome (Figure 5.2.3).

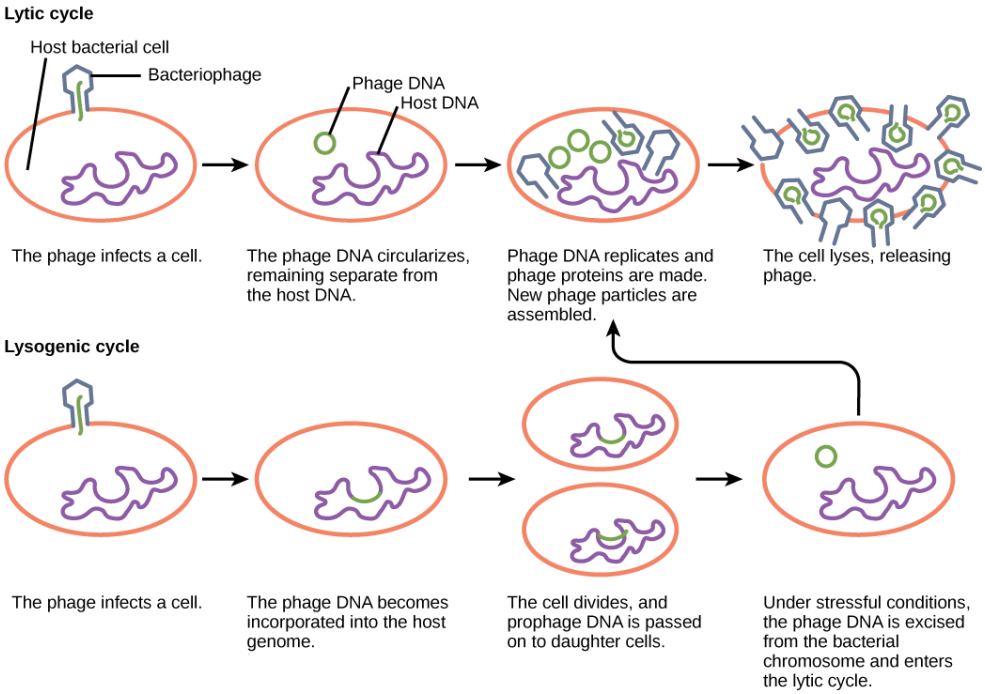
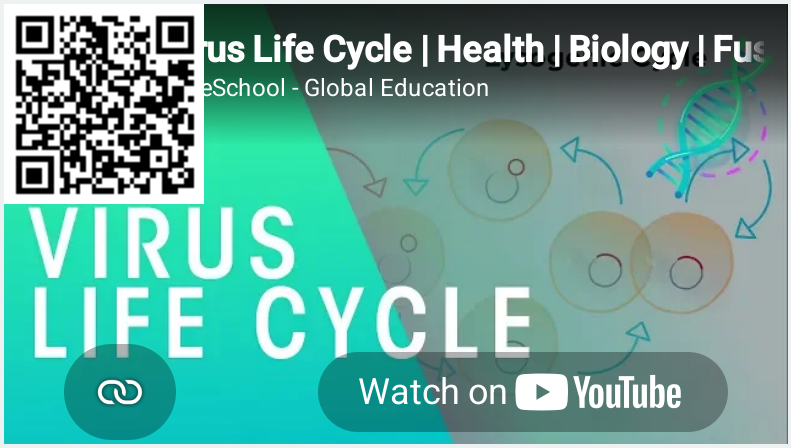


Figure 5.2.3: A temperate bacteriophage has both lytic and lysogenic cycles. In the lytic cycle, the phage replicates and lyses the host cell. In the lysogenic cycle, phage DNA is incorporated into the host genome, where it is passed on to subsequent generations. Environmental stressors such as starvation or exposure to toxic chemicals may cause the prophage to excise and enter the lytic cycle.

Video



Note that the narrator misspeaks when she says that viruses are 'microorgansms'. Viruses are often very specific as to which hosts and which cells within the host they will infect.

Viruses can be seen as obligate, intracellular parasites. A virus must attach to a living cell's surface, be taken inside, manufacture its proteins and copy its genome, and find a way to escape the cell so that the virus can infect other cells. Viruses can infect only certain species and only certain cells within that host. Cells that a virus may use to replicate are called **permissive**. For most viruses, the molecular basis for this specificity is that a particular surface molecule known as the **viral receptor** must be found on the host cell surface for the virus to attach. Also, metabolic and host cell immune response differences seen in different cell types based on differential gene expression are a likely factor in the type of cells a virus may target. The permissive cell must make the substances that the virus needs or the virus will not be able to replicate there.

A virus must use cell processes to replicate. The viral replication cycle can produce dramatic biochemical and structural changes in the host cell, which may cause cell damage. These changes, called **cytopathic** (causing cell damage) effects, can change cell

functions or even destroy the cell. Some infected cells, such as those infected by the common cold virus known as rhinovirus, die through **lysis** (bursting) or **apoptosis** (programmed cell death or "cell suicide"), releasing all progeny virions at once. The symptoms of viral diseases result from the immune response to the virus, which attempts to control and eliminate the virus from the body, and from cell damage caused by the virus. Many animal viruses, such as HIV (human immunodeficiency virus), leave the infected cells of the immune system by a process known as **budding**, where virions leave the cell individually. During the budding process, the cell does not undergo lysis and is not immediately killed. However, the damage to the cells that the virus infects may make it impossible for the cells to function normally, even though the cells remain alive for a period of time.

? Optional Activity 5.2.1

Influenza virus is packaged in a viral envelope that fuses with the plasma membrane. This way, the virus can exit the host cell without killing it. What advantage does the virus gain by keeping the host cell alive?

Answer

The host cell can continue to make new virus particles.

Career Connection: Virologist

Virology is the study of viruses, and a virologist is an individual trained in this discipline. Training in virology can lead to many different career paths. Virologists are actively involved in academic research and teaching in colleges and medical schools. Some virologists treat patients or are involved in the development and/or production of vaccines. They might participate in epidemiologic studies (Figure 5.2.3) or become science writers, to name just a few possible careers.

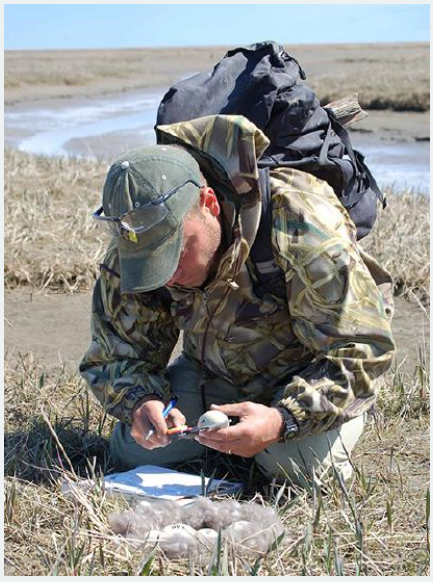


Figure 5.2.4: This virologist is engaged in fieldwork, sampling eggs from this nest for avian influenza. (credit: Don Becker, USGS EROS, U.S. Fish and Wildlife Service)

If you think you may be interested in a career in virology, find a mentor in the field. Many large medical centers have departments of virology, and smaller hospitals usually have virology labs within their microbiology departments. Volunteer in a virology lab for a semester or work in one over the summer. Discussing the profession and getting a first-hand look at the work will help you decide whether a career in virology is right for you.

Viral Infections

Note



Most human disease-causing pathogens (60%+) come from animals. This transference of a disease from an animal to a human being is called zoonoses, and all such diseases collectively are called zoonotic diseases.
Question after watching: What are the different ways that zoonotics are transmitted are transmitted from animals to humans and back to animals?

Viruses cause a variety of diseases in animals, including humans, ranging from the common cold to potentially fatal illnesses like meningitis (Figure 5.2.5). These diseases can be treated by antiviral drugs or by vaccines, but some viruses, such as HIV, are capable of both avoiding the immune response and mutating to become resistant to antiviral drugs. On the other hand, viruses may have also had large influences in evolution, leading to new species, and even help by keeping bacterial populations in check.

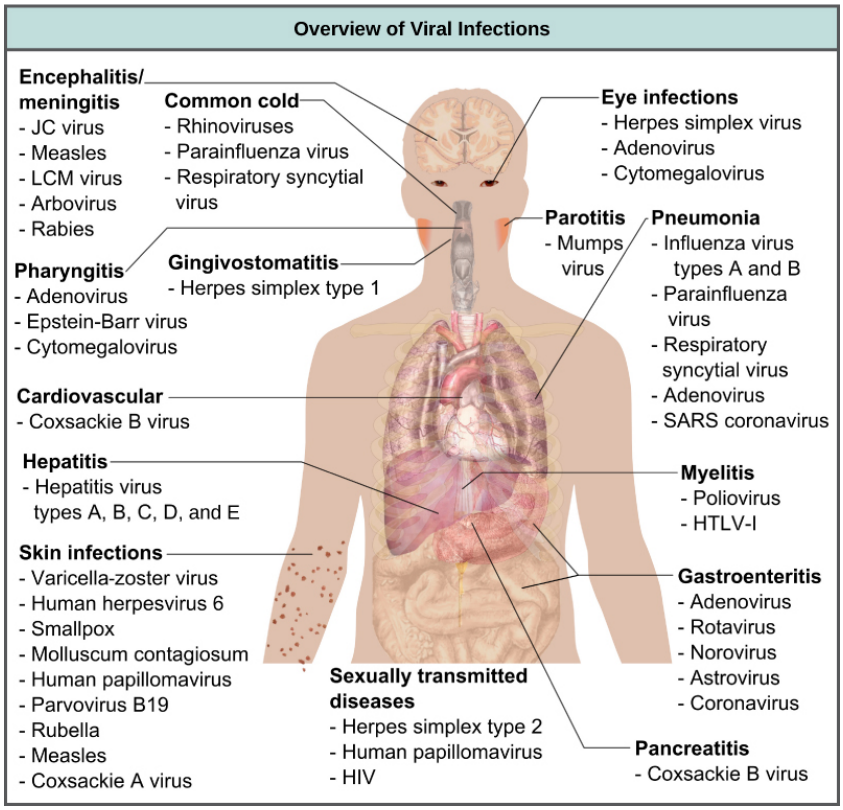


Figure 5.2.5: Viruses can cause dozens of ailments in humans, ranging from mild illnesses to serious diseases. These are just some of the viral infections humans can get. (credit: modification of work by Mikael Häggström)

Vaccines for Prevention

While we do have limited numbers of effective antiviral drugs, such as those used to treat HIV and influenza, the primary method of controlling viral disease is by vaccination, which is intended to prevent outbreaks by building immunity to a virus or virus family. Vaccines may be prepared using live viruses, killed viruses, or molecular subunits of the virus. The killed viral vaccines and subunit viruses are both incapable of causing disease.

Live viral vaccines are designed in the laboratory to cause few symptoms in recipients while giving them protective immunity against future infections. Polio was one disease that represented a milestone in the use of vaccines. Mass immunization campaigns in the 1950s (killed vaccine) and 1960s (live vaccine) significantly reduced the incidence of the disease, which caused muscle paralysis in children and generated a great amount of fear in the general population when regional epidemics occurred. The success of the polio vaccine paved the way for the routine dispensation of childhood vaccines against measles, mumps, rubella, chickenpox, and other diseases.

Some vaccines are in continuous development because certain viruses, such as influenza and HIV, have a high mutation rate compared to other viruses and normal host cells. With influenza, mutations in the surface molecules of the virus help the organism evade the protective immunity that may have been obtained in a previous influenza season, making it necessary for individuals to get vaccinated every year. Other viruses, such as those that cause the childhood diseases measles, mumps, and rubella, mutate so infrequently that the same vaccine is used year after year.

Note



Learn the science behind how vaccines trigger an immune response and teach our bodies to recognize dangerous pathogens.

Question after watching: Why is it that vaccines not only protect those who get vaccinated, but others as well.

Vaccines and Anti-viral Drugs for Treatment

In some cases, vaccines can be used to treat an active viral infection. The concept behind this is that by giving the vaccine, immunity is boosted without adding more disease-causing virus. In the case of rabies, a fatal neurological disease transmitted via the saliva of rabies virus-infected animals, the progression of the disease from the time of the animal bite to the time it enters the central nervous system may be 2 weeks or longer. This is enough time to vaccinate an individual who suspects that they have been bitten by a rabid animal, and their boosted immune response is sufficient to prevent the virus from entering nervous tissue.

Another way of treating viral infections is the use of antiviral drugs. These drugs often have limited success in curing viral disease, but in many cases, they have been used to control and reduce symptoms for a wide variety of viral diseases. For most viruses, these drugs can inhibit the virus by blocking the actions of one or more of its proteins. It is important that the targeted proteins be encoded by viral genes and that these molecules are not present in a healthy host cell. Antiviral drugs like Paxlovid have been critical in treating Covid-19, especially in vulnerable populations.

Other Acellular Entities: Prions and Viroids

Prions and viroids are **pathogens** (agents with the ability to cause disease) that have simpler structures than viruses but, in the case of prions, still can produce deadly diseases.

Prions

Prions, so-called because they are made of a protein, are infectious particles—smaller than viruses—that contain no nucleic acids (neither DNA nor RNA). Historically, the idea of an infectious agent that did not use nucleic acids was considered impossible, but pioneering work by Nobel Prize-winning biologist Stanley Prusiner has convinced most biologists that such agents exist.

Fatal neurodegenerative diseases, such as kuru in humans and bovine spongiform encephalopathy (BSE) in cattle (commonly called “mad cow disease”) were shown to be transmitted by prions. The disease was spread by the consumption of meat, nervous tissue, or internal organs. Individuals with kuru and BSE show symptoms of loss of motor control and unusual behaviors, such as uncontrolled bursts of laughter with kuru, followed by death.

BSE was initially thought to only affect cattle. Cattle dying of the disease were shown to have developed lesions or “holes” in the brain, causing the brain tissue to resemble a sponge. Later, however, it was shown that a similar encephalopathy in humans known as Creutzfeldt-Jakob disease (CJD) could be acquired from eating meet from animals with BSE (Figure 5.2.4). This led to bans by several countries on the importation of British beef and causing considerable economic damage to the British cattle industry. BSE still exists in some areas of the world, and although a rare disease, CJD is difficult to detect and to treat. The disease can be spread from human to human by blood, so many countries have banned blood donation from regions associated with BSE.

The cause of spongiform encephalopathies, such as kuru and BSE, is an infectious structural variant of a normal cellular protein called PrP (prion protein). It is this variant that constitutes the prion particle. PrP exists in two forms, PrP^{c}, the normal form of the protein, and PrP^{sc}, the infectious form. Once introduced into the body, the PrP^{sc} prion binds to normal PrP^{c} protein and converts it to PrP^{sc}. This leads to an exponential increase of PrP^{sc} proteins, which aggregate. PrP^{sc} is folded abnormally, and the resulting conformation (shape) is directly responsible for the lesions seen in the brains of infected cattle with BSE and humans with CJD. Thus, the prion seems to be an entirely new form of infectious agent, the first one found whose transmission is not reliant upon genes made of DNA or RNA.

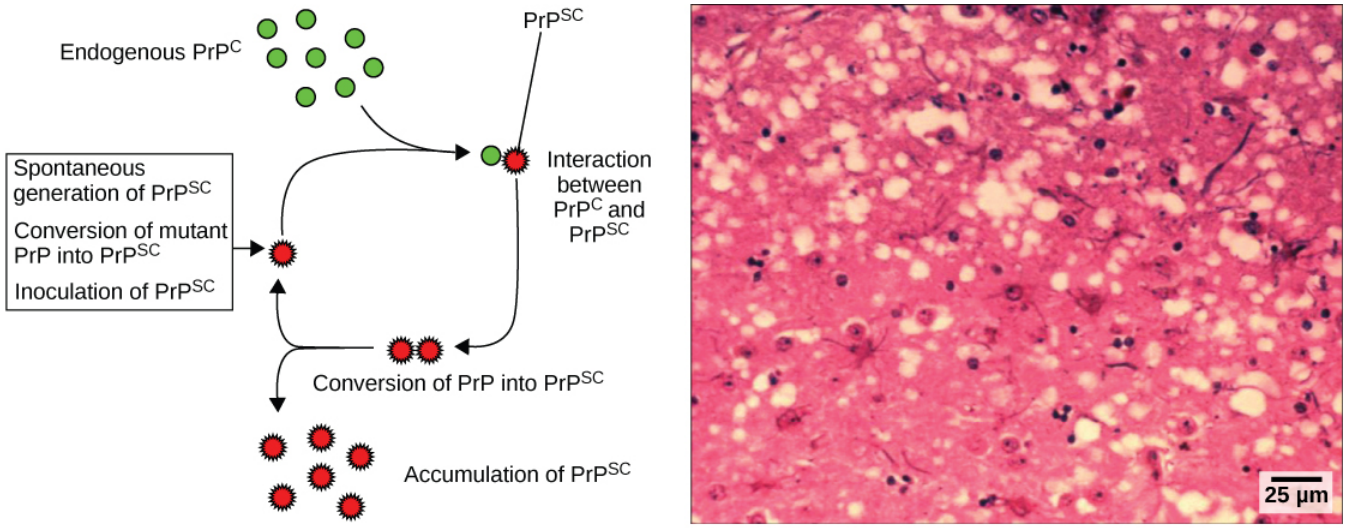


Figure 5.2.5: (a) Endogenous normal prion protein (PrP^{c}) is converted into the disease-causing form (PrP^{sc}) when it encounters this variant form of the protein. PrP^{sc} may arise spontaneously in brain tissue, especially if a mutant form of the protein is present, or it may occur via the spread of misfolded prions consumed in food. (b) This prion-infected brain tissue, visualized using light microscopy, shows the vacuoles that give it a spongy texture (the light-colored holes), typical of transmissible spongiform encephalopathies. (credit b: modification of work by Dr. Al Jenny, USDA APHIS; scale-bar data from Matt Russell)

Video





In this 5-minute video, Hank describes prions - misfolded proteins that are responsible for destroying brain cells and infect new hosts by eating an abnormal prion protein.

Question after watching: Why were some women and children more at risk to Kuru than men? Why were some resistant to Kuru?

Optional Activity 5.2.1

Which of the following is not associated with prions?

A. replicating shapes
B. mad cow disease
C. DNA
D. mutations in the gene for a protein

Answer

C

Viroids

Viroids are plant pathogens: small, single-stranded, circular RNA particles that are much simpler than a virus. They do not have a capsid or outer envelope, but like viruses can reproduce only within a host cell. Viroids do not, however, manufacture any proteins, and they only produce a single, specific RNA molecule. Human diseases caused by viroids have yet to be identified.

Viroids are known to infect plants (Figure 5.2.5) and are responsible for crop failures and the loss of millions of dollars in agricultural revenue each year. Some of the plants they infect include potatoes, cucumbers, tomatoes, chrysanthemums, avocados, and coconut palms.



Figure 5.2.6: These potatoes have been infected by the potato spindle tuber viroid (PSTV), which is typically spread when infected knives are used to cut healthy potatoes, which are then planted. (credit: Pamela Roberts, University of Florida Institute of Food and Agricultural Sciences, USDA ARS)

Video





This 4-minute video describes the discovery of viroids: infectious, replicating bits of RNA. Question after watching: How are viroids helping biologists investigate the origin of life?

? Optional Activity 5.2.2

Which statement is true of viroids?

A. They are single-stranded RNA particles.
B. They reproduce only outside of the cell.
C. They produce proteins.
D. They affect both plants and animals.

Answer

A. They are single-stranded RNA particles.

This page titled 5.2: Acellular Entities - Viruses, Prions, and Viroids is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **21.0: Prelude to Viruses** by OpenStax is licensed CC BY 4.0.
- **21.1: Viral Evolution, Morphology, and Classification** by OpenStax is licensed CC BY 4.0.
- **21.2: Virus Infections and Hosts** by OpenStax is licensed CC BY 4.0.
- **21.4: Other Acellular Entities - Prions and Viroids** by OpenStax is licensed CC BY 4.0.
- **21.3: Prevention and Treatment of Viral Infections** by OpenStax is licensed CC BY 4.0.
- **21.E: Viruses (Exercises)** is licensed CC BY 4.0.

5.2.E: Viruses (Exercises)

Viral Evolution, Morphology, and Classification

Viruses are diverse entities. They vary in their structure, their replication methods, and in their target hosts. Nearly all forms of life—from bacteria and archaea to eukaryotes such as plants, animals, and fungi—have viruses that infect them. While most biological diversity can be understood through evolutionary history, such as how species have adapted to conditions and environments, much about virus origins and evolution remains unknown.

Review Questions

Which statement is true?

A. A virion contains DNA and RNA.
B. Viruses are acellular.
C. Viruses replicate outside of the cell.
D. Most viruses are easily visualized with a light microscope.

Answer

B

The viral _____ plays a role in attaching a virion to the host cell.

A. core
B. capsid
C. envelope
D. both b and c

Answer

D

Viruses_____.

A. all have a round shape
B. cannot have a long shape
C. do not maintain any shape
D. vary in shape

Answer

D

Free Response

The first electron micrograph of a virus (tobacco mosaic virus) was produced in 1939. Before that time, how did scientists know that viruses existed if they could not see them? (Hint: Early scientists called viruses “filterable agents.”)

Answer

Viruses pass through filters that eliminated all bacteria that were visible in the light microscopes at the time. As the bacteria-free filtrate could still cause infections when given to a healthy organism, this observation demonstrated the existence of very small infectious agents. These agents were later shown to be unrelated to bacteria and were classified as viruses.

Virus Infections and Hosts

Viruses can be seen as obligate, intracellular parasites. A virus must attach to a living cell, be taken inside, manufacture its proteins and copy its genome, and find a way to escape the cell so that the virus can infect other cells. Viruses can infect only certain species of hosts and only certain cells within that host. Cells that a virus may use to replicate are called permissive.

Review Questions

Which statement is *not* true of viral replication?

A. A lysogenic cycle kills the host cell.
B. There are six basic steps in the viral replication cycle.
C. Viral replication does not affect host cell function.
D. Newly released virions can infect adjacent cells.

Answer

D

Which statement is true of viral replication?

A. In the process of apoptosis, the cell survives.
B. During attachment, the virus attaches at specific sites on the cell surface.
C. The viral capsid helps the host cell produce more copies of the viral genome.
D. mRNA works outside of the host cell to produce enzymes and proteins.

Answer

B

Which statement is true of reverse transcriptase?

A. It is a nucleic acid.
B. It infects cells.
C. It transcribes RNA to make DNA.
D. It is a lipid.

Answer

C

Oncogenic virus cores can be_____.

A. RNA
B. DNA
C. neither RNA nor DNA
D. either RNA or DNA

Answer

D

Which is true of DNA viruses?

A. They use the host cell’s machinery to produce new copies of their genome.
B. They all have envelopes.
C. They are the only kind of viruses that can cause cancer.

D. They are not important plant pathogens.

Answer

A

A bacteriophage can infect _____.

A. the lungs
B. viruses
C. prions
D. bacteria

Answer

D

Free Response

Why can't dogs catch the measles?

Answer

The virus can't attach to dog cells, because dog cells do not express the receptors for the virus and/or there is no cell within the dog that is permissive for viral replication.

One of the first and most important targets for drugs to fight infection with HIV (a retrovirus) is the reverse transcriptase enzyme. Why?

Answer

Reverse transcriptase is needed to make more HIV-1 viruses, so targeting the reverse transcriptase enzyme may be a way to inhibit the replication of the virus. Importantly, by targeting reverse transcriptase, we do little harm to the host cell, since host cells do not make reverse transcriptase. Thus, we can specifically attack the virus and not the host cell when we use reverse transcriptase inhibitors.

In this section, you were introduced to different types of viruses and viral diseases. Briefly discuss the most interesting or surprising thing you learned about viruses.

Answer

Answer is open and will vary.

Although plant viruses cannot infect humans, what are some of the ways in which they affect humans?

Answer

Plant viruses infect crops, causing crop damage and failure, and considerable economic losses.

Prevention and Treatment of Viral Infections

Viruses cause a variety of diseases in animals, including humans, ranging from the common cold to potentially fatal illnesses like meningitis . These diseases can be treated by antiviral drugs or by vaccines, but some viruses, such as HIV, are capable of both avoiding the immune response and mutating to become resistant to antiviral drugs.

Review Questions

Which of the following is NOT used to treat active viral disease?

A. vaccines
B. antiviral drugs
C. antibiotics
D. phage therapy

Answer

C

Vaccines_____.

A. are similar to viroids
B. are only needed once
C. kill viruses
D. stimulate an immune response

Answer

D

Free Response

Why is immunization after being bitten by a rabid animal so effective and why aren't people vaccinated for rabies like dogs and cats are?

Answer

Rabies vaccine works after a bite because it takes week for the virus to travel from the site of the bite to the central nervous system, where the most severe symptoms of the disease occur. Adults are not routinely vaccinated for rabies for two reasons: first, because the routine vaccination of domestic animals makes it unlikely that humans will contract rabies from an animal bite; second, if one is bitten by a wild animal or a domestic animal that one cannot confirm has been immunized, there is still time to give the vaccine and avoid the often fatal consequences of the disease.

Other Acellular Entities - Prions and Viroids

Prions and viroids are pathogens (agents with the ability to cause disease) that have simpler structures than viruses but, in the case of prions, still can produce deadly diseases.

Review Questions

Which of the following is not associated with prions?

A. replicating shapes
B. mad cow disease
C. DNA
D. toxic proteins

Answer

C

Which statement is true of viroids?

A. They are single-stranded RNA particles.

B. They reproduce only outside of the cell.
C. They produce proteins.
D. They affect both plants and animals.

Answer

A

Free Response

Prions are responsible for variant Creutzfeldt-Jakob Disease, which has resulted in over 100 human deaths in Great Britain during the last 10 years. How do humans obtain this disease?

Answer

This prion-based disease is transmitted through human consumption of infected meat.

How are viroids like viruses?

Answer

They both replicate in a cell, and they both contain nucleic acid.

This page titled 5.2.E: Viruses (Exercises) is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **21.E: Viruses (Exercises)** is licensed CC BY 4.0.

SECTION OVERVIEW

6: Unit VI- Ecology

Ecology is the study of the interactions of living organisms with their environment. One core goal of ecology is to understand the distribution and abundance of living things in the physical environment. Attainment of this goal requires the integration of scientific disciplines inside and outside of biology, such as biochemistry, physiology, evolution, biodiversity, molecular biology, geology, and climatology. Some ecological research also applies aspects of chemistry and physics, and it frequently uses mathematical models. In Unit 8, ecological concepts are broadly covered in this unit, with features highlighting localized, real-world issues of conservation and biodiversity.

6.1: Ecosystems and the Biosphere

6.1.1: Ecology of Ecosystems
6.1.2: Energy Flow through Ecosystems
6.1.3: Terrestrial Biomes
6.1.4: Aquatic Biomes
6.1.5: Biogeochemical Cycles
6.1.6: Biogeography
6.1.S: Chapter Resources

6.2: Biodiversity and HIPPPOC

6.2.1: Introduction to Biodiversity
6.2.2: Importance of Biodiversity
6.2.3: The Biodiversity Crisis - HIPPPOC
6.2.4: Preserving Biodiversity
6.2.S: Chapter Resources

6.3: Climate Change

6.3.1: Introduction to Climate Change
6.3.2: Anthropogenic Climate Change
6.3.3: Current and Future Climate Change Impacts
6.3.4: Climate Strategies

Contributors and Attributions

Connie Rye (East Mississippi Community College), Robert Wise (University of Wisconsin, Oshkosh), Vladimir Jurukovski (Suffolk County Community College), Jean DeSaix (University of North Carolina at Chapel Hill), Jung Choi (Georgia Institute of Technology), Yael Avissar (Rhode Island College) among other contributing authors. Original content by OpenStax (CC BY 4.0; Download for free at http://cnx.org/contents/185cbf87-c72...f21b5eabd@9.87).

This page titled 6: Unit VI- Ecology is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

CHAPTER OVERVIEW

6.1: Ecosystems and the Biosphere

Learning Objectives

- Discuss how life and the planet exist as a system
- Outline the flow of energy through an ecosystem using trophic dynamics theory
- Describe the basic ecosystem types
- Explain the methods that ecologists use to study ecosystem structure and dynamics
- Identify the different methods of ecosystem modeling

Video



In this 10-minute video, Hank will provide an overview of ecosystem ecology and its various subfields.
Question after watching: After watching this video, make a list of questions that you have about ecosystems.

6.1.1: Ecology of Ecosystems
6.1.2: Energy Flow through Ecosystems
6.1.3: Terrestrial Biomes
6.1.4: Aquatic Biomes
6.1.5: Biogeochemical Cycles
6.1.6: Biogeography
6.1.S: Chapter Resources

This page titled 6.1: Ecosystems and the Biosphere is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg via source content that was edited to the style and standards of the LibreTexts platform.

6.1.1: Ecology of Ecosystems

Ecology of Ecosystems

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 30 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe the basic types of ecosystems on Earth
- Explain the methods that ecologists use to study ecosystem structure and dynamics
- Identify the different methods of ecosystem modeling
- Differentiate between food chains and food webs and recognize the importance of each

Introduction to Ecosystems

Video



Learn about feedback loops in this 5-minute TED-Ed video.
Question after watching: Describe at least one other example of positive feedback, and one example of negative feedback in the world (not necessarily in ecology).

Life in an ecosystem is often about competition for limited resources, a characteristic of the theory of natural selection. Competition in communities (all living things within specific habitats) is observed both within species and among different species. The resources for which organisms compete include organic material from living or previously living organisms, sunlight, and mineral nutrients, which provide the energy for living processes and the matter to make up organisms' physical structures. Other critical factors influencing community dynamics are the components of its physical and geographic environment: a habitat's latitude, amount of rainfall, topography (elevation), and available species. These are all important environmental variables that determine which organisms can exist within a particular area.

As was defined in Unit 4.2, 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 (such as on the coast of British Columbia), or large, such as the Amazon Rainforest in Brazil (Figure 6.1.1.1).



(a) (b)

Figure 6.1.1.1: A (a) tidal pool ecosystem in Matinicus Island in Maine, USA is a small ecosystem, while the (b) Amazon Rainforest in Brazil is a large ecosystem. (credit a: modification of work by “takomabibelot”/Flickr; credit b: modification of work by Ivan Mlinaric)

There are three broad categories of ecosystems based on their general environment: freshwater, marine (ocean), and terrestrial. Within these broad categories are individual ecosystem types based on the organisms present and the type of environmental habitat.

Ocean ecosystems are the most common, comprising 75 percent of the Earth's surface and consisting of three basic types: shallow ocean, open ocean surface water, and deep ocean (the low-depth areas of the deep oceans). The shallow ocean ecosystems include extremely biodiverse coral reef ecosystems, and the open ocean surface is known for its large numbers of plankton and krill (small crustaceans) that support it. These two environments are especially important to producers worldwide as the phytoplankton that live there (protist and bacterial producers) are responsible for 40 percent of all photosynthesis on Earth. Although not as diverse as the other two, deep ocean ecosystems contain a wide variety of marine organisms. Ecosystems exist even at the bottom of the ocean where light is unable to penetrate through the water such as sponge reefs in the Georgia Strait and deep-sea hydrothermal vents in the Juan de Fuca Ridge.

Freshwater ecosystems are the rarest, occurring on only 1.8 percent of the Earth's surface. These are made of lakes, rivers, streams, and springs; they are quite diverse and support a variety of fish, amphibians, reptiles, insects, phytoplankton, fungi, and bacteria.

Terrestrial ecosystems, also known for their diversity, are grouped into large categories, such as tropical rain forests, savannas, deserts, coniferous forests, deciduous forests, and tundra. Grouping these ecosystems into just a few categories obscures the great diversity of the individual ecosystems within them. For example, there is great variation in desert vegetation: the saguaro cacti and other plant life in the Sonoran Desert, in the United States, are relatively abundant compared to the desolate rocky desert of Boa Vista, an island off the coast of Western Africa (Figure 6.1.1.2).



(a)



(b)

Figure 6.1.1.2: Desert ecosystems, like all ecosystems, can vary greatly. The desert in (a) Saguaro National Park, Arizona, has abundant plant life, while the rocky desert of (b) Boa Vista island, Cape Verde, Africa, is devoid of most plant life. (credit a: modification of work by Jay Galvin; credit b: modification of work by Ingo Wölbern)

Ecosystems are complex with many interacting parts. They are routinely exposed to various disturbances, or changes, in the environment that may affect their compositions. For example, yearly variations in rainfall and temperature and the slow processes of plant regrowth in response. Many of these disturbances are a result of natural processes. For example, when lightning causes a forest fire and destroys part of a forest ecosystem, the ground is eventually populated by grasses, then by bushes and shrubs, and later by mature trees, restoring the forest to its former state. The impact of environmental disturbances caused by human activities is as important as the changes wrought by natural processes. Human agricultural practices, air pollution, acid rain, global deforestation, overfishing, eutrophication, oil spills, and illegal dumping on land and into the ocean are all issues of concern to conservationists (Unit 5.2.3).

Equilibrium is the steady state of an ecosystem where all organisms are in balance with their environment and with each other. In ecology, two parameters are used to measure changes in ecosystems: resistance and resilience. The ability of an ecosystem to remain at equilibrium in spite of disturbances is called **resistance**. The speed at which an ecosystem recovers equilibrium after being disturbed is called its **resilience**. Ecosystem resistance and resilience are especially important when considering the impacts of humans. The nature of an ecosystem may change to such a degree that it can lose its resilience entirely. This process can lead to the complete destruction or irreversible altering of the ecosystem.

Evolution Connection: Three-spined Stickleback

It is well established by the theory of natural selection that changes in the environment play a major role in the evolution of species within an ecosystem. However, little is known about how the evolution of species within an ecosystem can alter the ecosystem environment. In 2009, Dr. Luke Harmon, from the University of Idaho in Moscow, published a paper that, for the first time, showed that the evolution of organisms into subspecies can have direct effects on their ecosystem environment.[1]

The three-spined stickleback (*Gasterosteus aculeatus*) is a freshwater fish that evolved from a saltwater fish to live in freshwater lakes about 10,000 years ago, which is considered a recent development in evolutionary time (Figure 6.1.1.3). Over the last 10,000 years, these freshwater fish then became isolated from each other in different lakes. Depending on which lake population was studied, findings showed that these sticklebacks either remained as one species or evolved into two species. The divergence of species was made possible by their use of different areas of the pond for feeding called micro niches.

Dr. Harmon and his team created artificial pond microcosms in 250-gallon tanks and added muck from freshwater ponds as a source of zooplankton and other invertebrates to sustain the fish. In different experimental tanks, they introduced one species of stickleback from either a single-species or double-species lake.

Over time, the team observed that some of the tanks bloomed with algae while others did not. This puzzled the scientists, and they decided to measure the water's dissolved organic carbon (DOC), which consists of mostly large molecules of decaying

organic matter that gives pond water its slightly brownish color. It turned out that the water from the tanks with two-species fish contained larger particles of DOC (and hence darker water) than water with single-species fish. This increase in DOC blocked the sunlight and prevented algal blooming. Conversely, the water from the single-species tank contained smaller DOC particles, allowing more sunlight penetration to fuel the algal blooms.

This change in the environment, which is due to the different feeding habits of the stickleback species in each lake type, probably greatly impacts the survival of other species in these ecosystems, especially other photosynthetic organisms. Stickleback species are, therefore, acting as foundational species. Thus, the study shows that, at least in these ecosystems, the environment and the evolution of populations have reciprocal effects that may now be factored into simulation models.



Figure 6.1.1.3: The three-spined stickleback evolved from a saltwater fish to freshwater fish. (credit: Barrett Paul, USFWS)

Ecosystem Research: Experimentation and Modeling

The study of the changes in ecosystem structure caused by changes in the environment (disturbances) or by internal forces is called **ecosystem dynamics**. Ecosystems are characterized using a variety of research methodologies. Some ecologists study ecosystems using controlled experimental systems, while some study entire ecosystems in their natural state, and others use both approaches.

Holistic Model and Experimentation

A **holistic ecosystem model** attempts to quantify the composition, interaction, and dynamics of entire ecosystems; it is a model of the most representative ecosystem in its natural state. A food web (Unit 4.4.2) is an example of a holistic ecosystem model. However, this type of study is limited by time and expense, as well as the fact that it is neither feasible nor ethical to do experiments on large natural ecosystems. To quantify all different species in an ecosystem and the dynamics in their habitat is difficult, especially when studying large habitats such as the Amazon Rainforest, which covers 1.4 billion acres (5.5 million km^2) of the Earth's surface.

For these reasons, scientists study ecosystems under more controlled conditions. Experimental systems usually involve either partitioning a part of a natural ecosystem that can be used for experiments, termed a **mesocosm**, or re-creating an ecosystem entirely in an indoor or outdoor laboratory environment, which is referred to as a **microcosm**. A major limitation to these approaches is that removing individual organisms from their natural ecosystem or altering a natural ecosystem through partitioning may change the dynamics of the ecosystem. These changes are often due to differences in species numbers and diversity and also to environmental alterations caused by partitioning (mesocosm) or re-creating (microcosm) the natural habitat. Thus, these types of experiments are not totally predictive of changes that would occur in the ecosystem from which they were gathered.

As both of these approaches have their limitations, some ecologists suggest that results from these experimental systems should be used only in conjunction with holistic ecosystem studies to obtain the most representative data about ecosystem structure, function, and dynamics.

Scientists use the data generated by these experimental studies to develop ecosystem models that demonstrate the structure and dynamics of ecosystems. Three basic types of ecosystem modeling are routinely used in research and ecosystem management: a conceptual model, an analytical model, and a simulation model. A conceptual model describes ecosystem structure and dynamics and shows how environmental disturbances affect the ecosystem; however, its ability to predict the effects of these disturbances is limited. Analytical and simulation models, in contrast, are mathematical methods of describing ecosystems that are indeed capable

of predicting the effects of potential environmental changes without direct experimentation, although with some limitations as to accuracy.

Conceptual Models

Conceptual models are ecosystem models that consist of flow charts to show interactions of different compartments of the living and nonliving components of the ecosystem. Conceptual models are useful for describing ecosystem structure and dynamics and for demonstrating the relationships between different organisms in a community and their environment. The organisms and their resources are grouped into specific compartments with arrows showing the relationship and transfer of energy or nutrients between them. Thus, these diagrams are sometimes called compartment models.

To model the cycling of mineral nutrients, organic and inorganic nutrients are subdivided into those that are bioavailable (ready to be incorporated into biological macromolecules) and those that are not (Unit 4.4.5). For example, in a terrestrial ecosystem near a deposit of coal, carbon will be available to the plants of this ecosystem as carbon dioxide gas in a short-term period, not from the carbon-rich coal itself. However, over a longer period, microorganisms capable of digesting coal will incorporate its carbon or release it as natural gas (methane, CH_4), changing this unavailable organic source into an available one. This conversion is greatly accelerated by the combustion of fossil fuels by humans, which releases large amounts of carbon dioxide into the atmosphere. This is thought to be a major factor in the rise of atmospheric carbon dioxide levels in the industrial age. The carbon dioxide released from burning fossil fuels is produced faster than photosynthetic organisms can use it. This process is intensified by the reduction of photosynthetic trees because of worldwide deforestation. Most scientists agree that high atmospheric carbon dioxide is a major cause of global climate change.

Conceptual models are also used to show the flow of energy through particular ecosystems. Figure 6.1.1.4 is based on Howard T. Odum's classical study of the Silver Springs, Florida, holistic ecosystem in the mid-twentieth century.[2] This study shows the energy content and transfer between various ecosystem compartments.

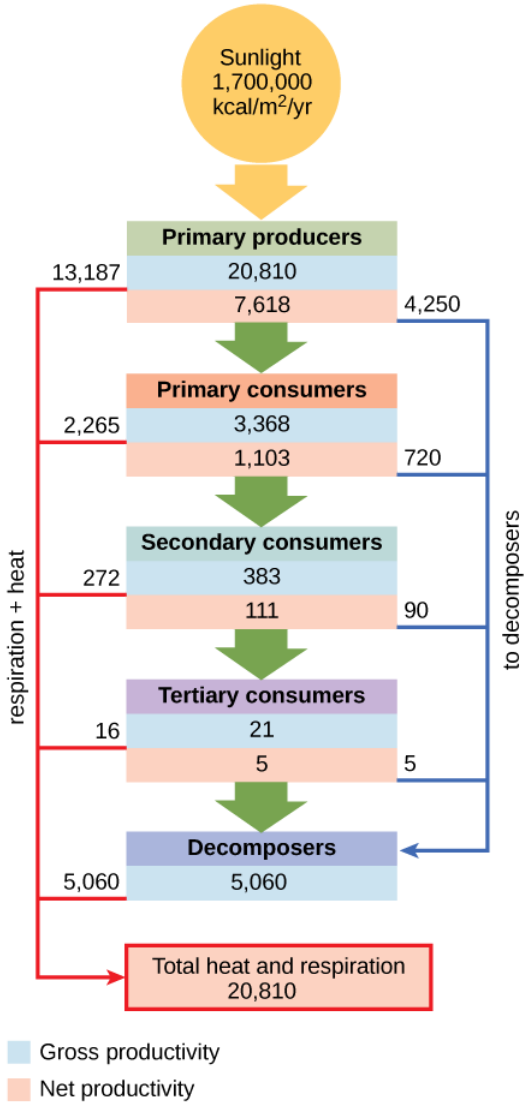


Figure 6.1.1.4: This conceptual model shows the flow of energy through a spring ecosystem in Silver Springs, Florida. Notice that the energy decreases with each increase in trophic level.

Analytical and Simulation Models

An **analytical model** is an ecosystem model that is created using simple mathematical formulas to predict the effects of environmental disturbances on ecosystem structure and dynamics. Analytical models often use simple, linear components of ecosystems, such as food chains, and are known to be complex mathematically; therefore, they require a significant amount of mathematical knowledge and expertise. An example would be a model that predicts the effects of primary production (g C/m^2) on a wetland on decomposition and consumption rates (g C/m^2/y). Although analytical models have great potential, their simplification of complex ecosystems is thought to limit their accuracy. Simulation models that use computer programs can better deal with the complexities of ecosystem structure.

A **simulation model** is an ecosystem model that is created using complex computer algorithms to holistically model ecosystems and predict the effects of environmental disturbances on ecosystem structure and dynamics. Ideally, these models are accurate enough to determine which components of the ecosystem are particularly sensitive to disturbances, and they can serve as a guide to ecosystem managers (such as conservation ecologists or fisheries biologists) in the practical maintenance of ecosystem health. Climate models are simulation models. A recent development in simulation modeling uses supercomputers to create and run individual-based simulations, which account for the behavior of individual organisms and their effects on the ecosystem as a whole. These simulations are considered to be the most accurate and predictive of the complex responses of ecosystems to disturbances.

Footnotes

1. 1 *Nature* (Vol. 458, April 1, 2009)
2. 2 Howard T. Odum, “Trophic Structure and Productivity of Silver Springs, Florida,” *Ecological Monographs* 27, no. 1 (1957): 47–112.

This page titled 6.1.1: Ecology of Ecosystems is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **46.1: Ecology of Ecosystems** by OpenStax is licensed CC BY 4.0.

Energy Flow through Ecosystems

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 90 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Describe how organisms acquire energy in a food web and in 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

Introduction

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

It is important to understand how organisms acquire energy and how that energy is passed from one organism to another through food webs and their constituent food chains. Food webs illustrate how energy flows directionally through ecosystems, including how efficiently organisms acquire it, use it, and how much remains for use by other organisms of the food web.

Food Chains and Food Webs

The term “food chain” is sometimes used metaphorically to describe human social situations. In this sense, food chains are thought of as a competition for survival, such as “who eats whom?” Someone eats and someone is eaten. Therefore, it is not surprising that in our competitive society, individuals who are considered successful are seen as being at the top of the food chain, consuming all others for their benefit, whereas the less successful are seen as being at the bottom.

The scientific understanding of a food chain is more precise than in its everyday usage. In ecology, a **food chain** is a linear sequence of organisms through which nutrients and energy pass: primary producers, primary consumers, and higher-level consumers are used to describe ecosystem structure and dynamics. There is a single path through the chain. 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 tropic levels, and so on, up to the organisms at the top of the food chain: the **apex consumers**. In the Lake Ontario food chain shown in Figure 6.1.2.1, the Chinook salmon is the apex consumer at the top of this food chain.

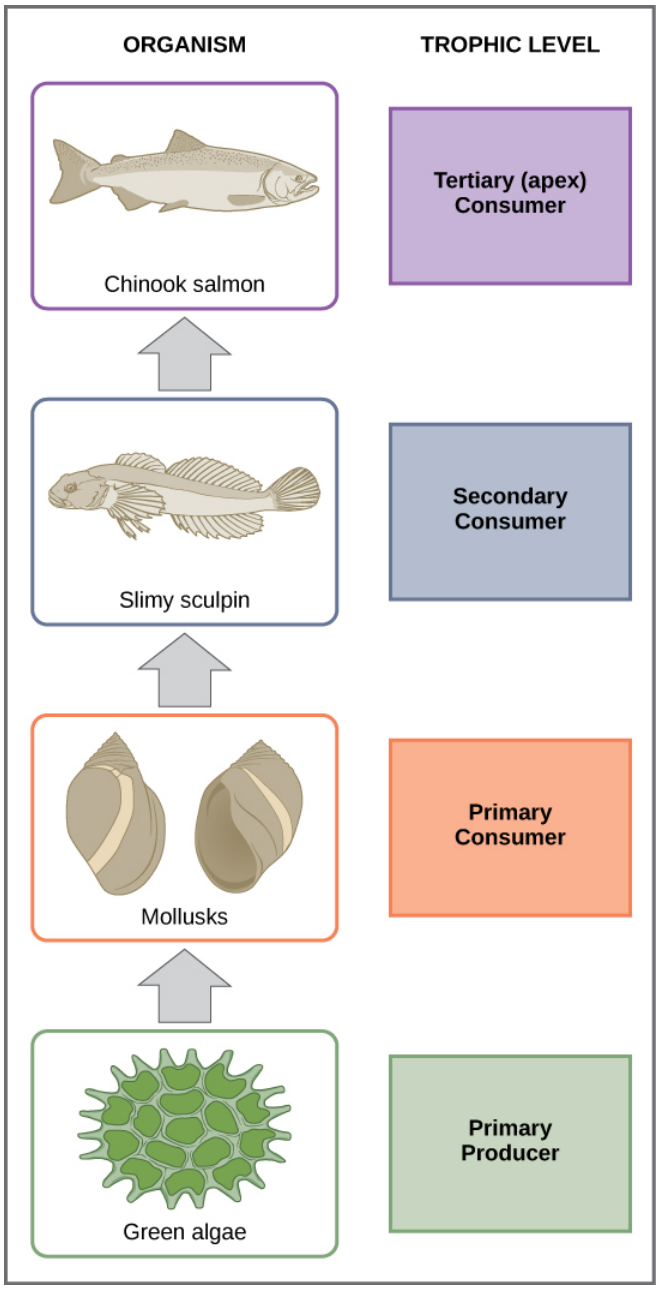


Figure 6.1.2.1: These are the trophic levels of a food chain in Lake Ontario at the border with the United States. Energy and nutrients flow from photosynthetic green algae at the bottom to the top of the food chain: the Chinook salmon.

One major factor that limits the length of food chains is energy. An average of 90% of energy is lost as heat between each trophic level due to the second law of thermodynamics. Thus, after a limited number of trophic energy transfers, the amount of energy remaining in the food chain may not be great enough to support viable populations at yet a higher trophic level. When one organism eats another, most of the energy is dissipated as heat and is not used to make more of the consumer. For example, when someone eats a potato, most of the energy available in the chemical bonds of the potato does not become energy to make new molecules in the individual. Only about 10% of the potato's energy is available to be assimilated into the individual eating the potato.

The loss of energy between trophic levels is illustrated by the pioneering studies of Howard T. Odum in the Silver Springs, Florida, ecosystem in the 1940s (Figure 6.1.2.2). The primary producers generated 20,819 kcal/m^2/yr (kilocalories per square meter per year), the primary consumers generated 3368 kcal/m^2/yr, the secondary consumers generated 383 kcal/m^2/yr, and the tertiary consumers only generated 21 kcal/m^2/yr. Thus, there is little energy remaining for another level of consumers in this ecosystem.

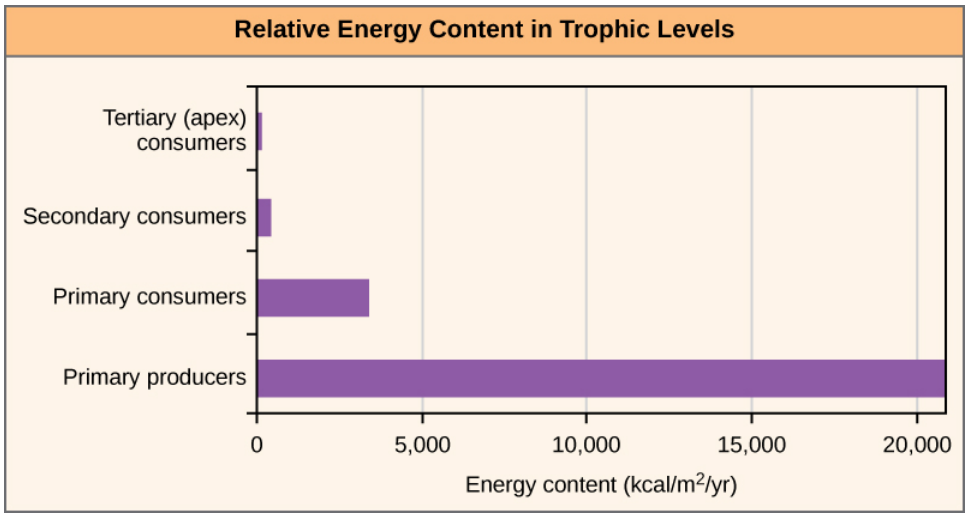


Figure 6.1.2.2: The relative energy in trophic levels in a Silver Springs, Florida, ecosystem is shown. Each trophic level has less energy available and supports fewer organisms at the next level.

There is a BIG problem when using food chains to accurately describe most ecosystems. Even when all organisms are grouped into appropriate trophic levels, many of these organisms can feed on species from more than one trophic level; likewise, some of these organisms can be eaten by species from multiple trophic levels. In other words, the linear model of ecosystems, the food chain, is not very descriptive of ecosystem structure, is not appropriate to truly understand ecosystem relationships, and is not generally used in ecosystem studies.

A holistic model—which accounts for all the interactions between different species and their complex interconnected relationships with each other and with the environment—is more accurate and descriptive for ecosystems. A **food web** is a graphic representation of a holistic, non-linear web of primary producers, primary consumers, and higher-level consumers used to describe ecosystem structure and dynamics (Figure 6.1.2.3).

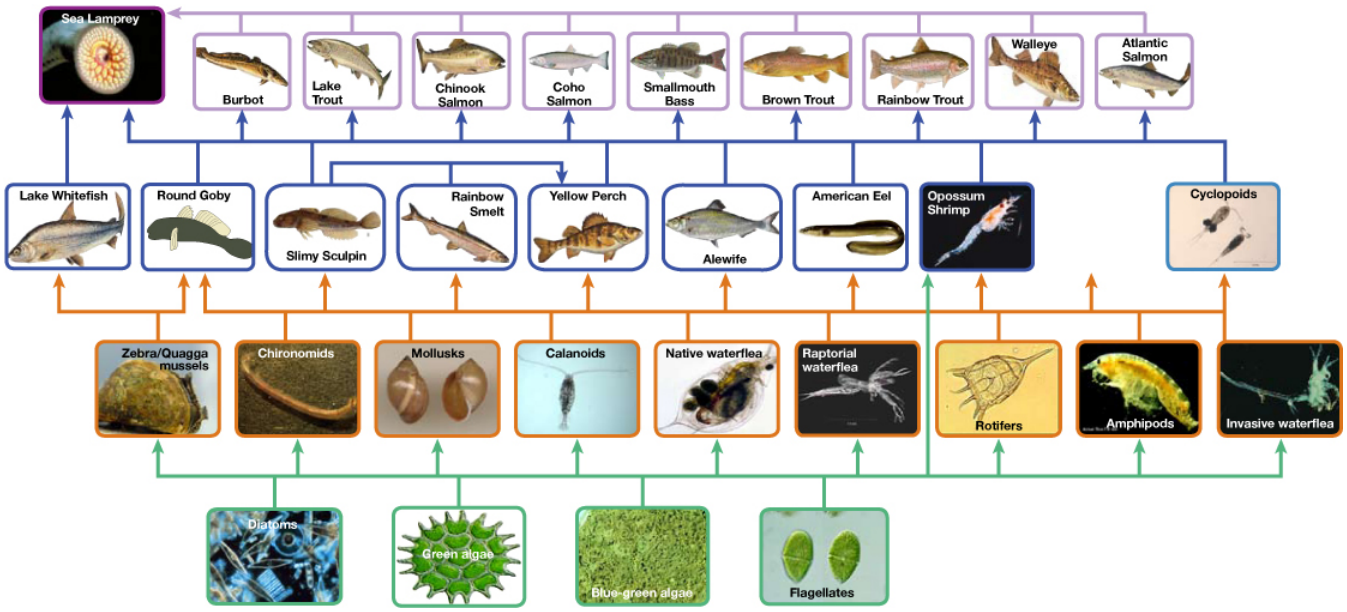


Figure 6.1.2.3: This food web shows the interactions between organisms across trophic levels in the Lake Ontario ecosystem. Primary producers are outlined in green, primary consumers in orange, secondary consumers in blue, and tertiary (apex) consumers in purple. Arrows point from an organism that is consumed to the organism that consumes it. Notice how some lines point to more than one trophic level. For example, the opossum shrimp eats both primary producers and primary consumers. (credit: NOAA, GLERL)

A comparison of the two types of structural ecosystem models shows strength in both. Food chains are more flexible for analytical modeling, are easier to follow, and are easier to learn from, whereas food web models more accurately represent ecosystem

structure and dynamics, and data can be directly used as input for simulation modeling.

Two general types of food webs are often shown interacting within a single ecosystem. A **grazing food web** (such as the Lake Ontario food web in Figure 6.1.2.3) has plants or other photosynthetic organisms at its base, followed by herbivores and various carnivores. As all ecosystems require a method to recycle material from dead organisms, most grazing food webs have an associated detrital food web. A **detrital food web** consists of a base of organisms that feed on decaying organic matter (dead organisms); these can be either decomposers or detritivores. **Decomposers** are bacteria or fungi that recycle organic material back into the ecosystem as they themselves are consumed by other organisms. **Detritivores** break larger materials such as leaves, dung, hides, etc., into material for decomposers.

Both grazing and detrital food webs exist in the same ecosystem at the same time. For example, in a meadow ecosystem, plants may support a grazing food web of different organisms, primary and other levels of consumers, while at the same time supporting a detrital food web of bacteria, fungi, and detrivorous invertebrates feeding off dead plants and animals.

How Organisms Acquire Energy in a Food Web

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 by 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 6.1.2.4). Many chemoautotrophs at hydrothermal vents use hydrogen sulfide (H_2S), a source of chemical energy released from the vents. 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.

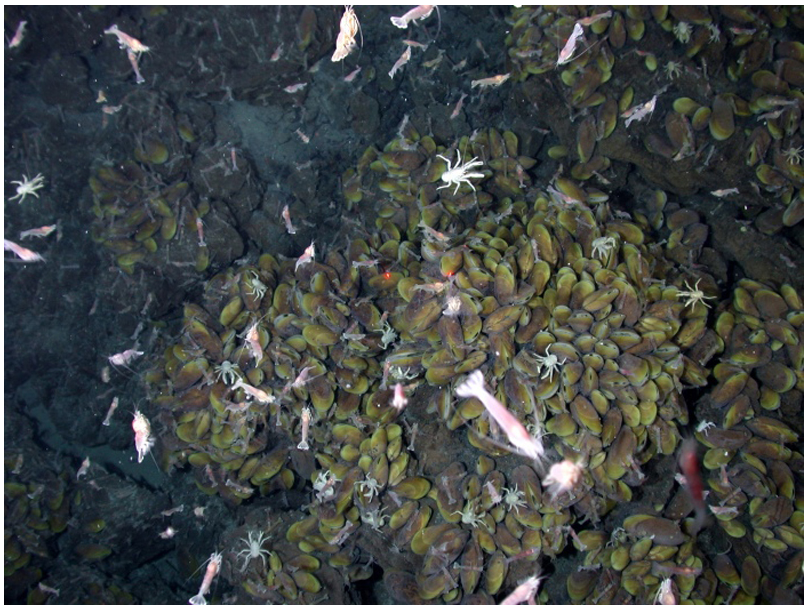


Figure 6.1.2.4: Swimming shrimp, a few squat lobsters, and hundreds of vent mussels are seen at a hydrothermal vent at the bottom of the ocean. As no sunlight penetrates to this depth, the ecosystem is supported by chemoautotrophic bacteria and organic material that sinks from the ocean's surface. This 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.

Productivity within Trophic Levels

Productivity within an ecosystem can be defined as the percentage of energy entering the ecosystem incorporated into biomass in a particular trophic level. **Biomass** is the total mass, in a unit area at the time of measurement, of living or previously living organisms within a trophic level. Ecosystems have characteristic amounts of biomass at each trophic level. For example, in the English Channel ecosystem the primary producers account for biomass of 4 g/m^2 (grams per meter squared), while the primary consumers exhibit biomass of 21 g/m^2.

The productivity of the primary producers is especially important in any ecosystem because these organisms bring energy to other living organisms by photoautotrophy or chemoautotrophy. The rate at which photosynthetic primary producers incorporate energy from the sun is called **gross primary productivity**. An example of gross primary productivity is shown in the pyramid of energy within the Silver Springs aquatic ecosystem as shown (Figure 6.1.2.5)C. In this ecosystem, gross primary productivity was shown to be 20,810 $kcal/m^2/yr$.

Because all organisms need to use some of this energy for their own functions (like respiration and resulting metabolic heat loss) scientists often refer to the net primary productivity of an ecosystem. **Net primary productivity** is the energy that remains in the primary producers after accounting for the organisms' respiration and heat loss. In terrestrial environments, net primary productivity is estimated by measuring the **aboveground biomass** per unit area, which is the total mass of living plants, excluding roots. This means that a large percentage of underground plant biomass is not included in this measurement. Net productivity is available to the primary consumers at the next trophic level. In our Silver Spring example, 13,187 of the 20,810 $kcal/m^2/yr$ were used for respiration or were lost as heat, leaving 7,632 $kcal/m^2/yr$ of energy for use by the primary consumers.

Modeling Ecosystems Energy Flow: Ecological Pyramids

The structure of ecosystems can be visualized with ecological pyramids, which were first described by the pioneering studies of Charles Elton in the 1920s. Ecological pyramids show the relative amounts of various parameters (such as number of organisms, energy, and biomass) across trophic levels.

Pyramids of numbers can be either upright or inverted, depending on the ecosystem. As shown in Figure 6.1.2.5B, typical grassland during the summer has a base of many plants and the number of organisms decreases at each trophic level. However, during the summer in a temperate forest, the base of the pyramid consists of few trees compared with the number of primary consumers, mostly insects. Because trees are large, they have great photosynthetic capability, and dominate other plants in this

ecosystem to obtain sunlight. Even in smaller numbers, primary producers in forests are still capable of supporting other trophic levels.

Another way to visualize ecosystem structure is with **pyramids of biomass**. This pyramid measures the amount of energy converted into living tissue at the different trophic levels. Using the Silver Springs ecosystem example, this data exhibits an upright biomass pyramid (Figure 6.1.2.5)A, whereas the pyramid from the English Channel example is inverted. The plants (primary producers) of the Silver Springs ecosystem make up a large percentage of the biomass found there. However, the phytoplankton in the English Channel example make up less biomass than the primary consumers, the zooplankton. As with inverted pyramids of numbers, this inverted pyramid is not due to a lack of productivity from the primary producers, but results from the high turnover rate of the phytoplankton. The phytoplankton are consumed rapidly by the primary consumers, thus, minimizing their biomass at any particular point in time. However, phytoplankton reproduce quickly, thus they are able to support the rest of the ecosystem.

Pyramid ecosystem modeling can also be used to show energy flow through the trophic levels in **pyramids of energy** (Figure 6.1.2.5)C. Notice that these numbers are the same as those used in the energy flow compartment diagram in Unit 4.4.1. Pyramids of energy are always upright, and an ecosystem without sufficient primary productivity cannot be supported. All types of ecological pyramids are useful for characterizing ecosystem structure. However, in the study of energy flow through the ecosystem, pyramids of energy are the most consistent and representative models of ecosystem structure.

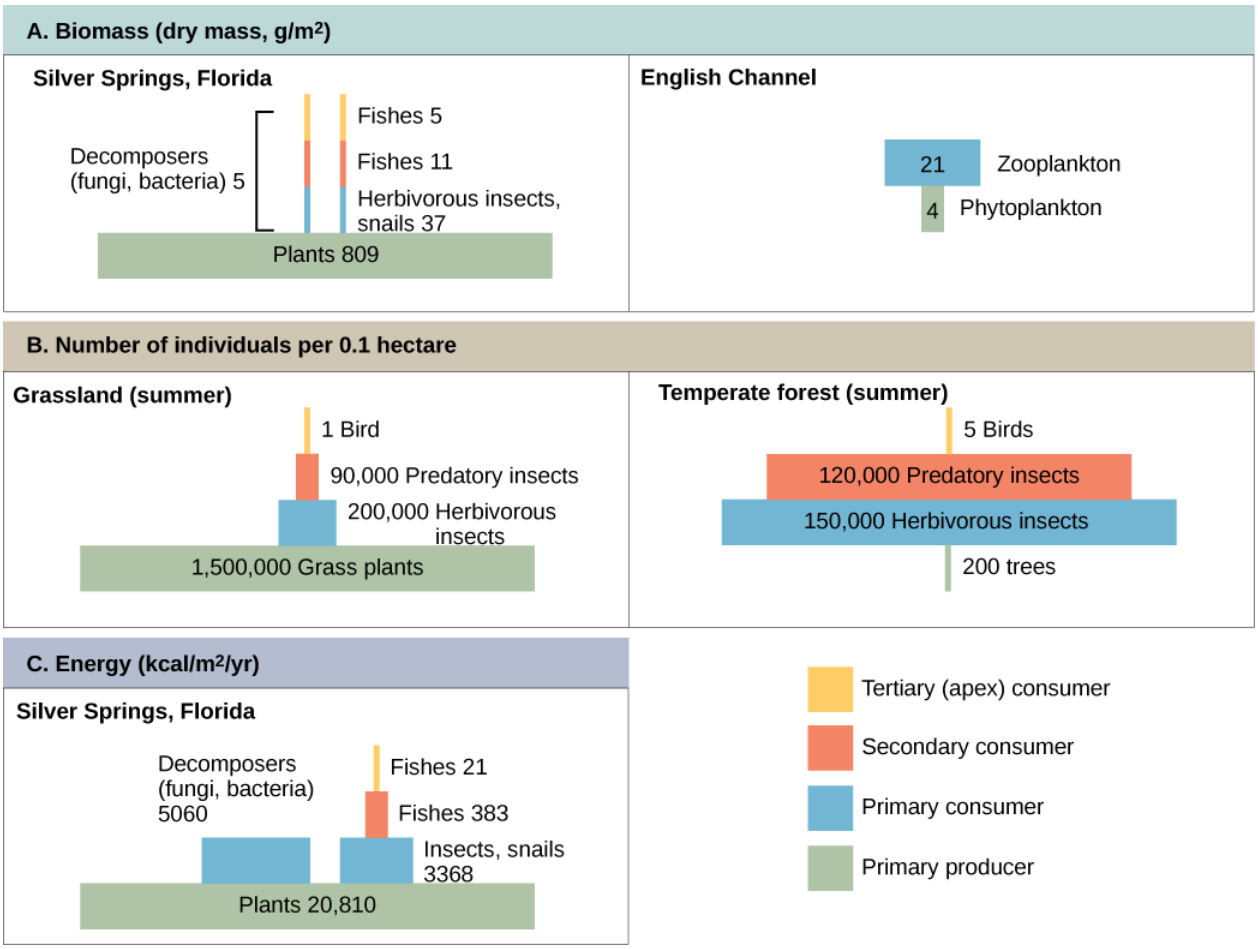


Figure 6.1.2.5: Ecological pyramids depict the (a) biomass, (b) number of organisms, and (c) energy in each trophic level. Note that in aquatic environments (English Channel) the biomass pyramids are often inverted due to the high turnover in populations of producers. The temperate forest number of organisms pyramid is inverted due to the presence of few, very large trees supporting production for the higher trophic levels versus many individual grasses in the grassland.

Ecological Efficiency: The Transfer of Energy between Trophic Levels

As illustrated in Figure 6.1.2.5C, large amounts of energy are lost from the ecosystem from one trophic level to the next level as energy flows from the primary producers through the various trophic levels of consumers and decomposers. The main reason for

this loss is the **second law of thermodynamics**, which states that whenever energy is converted from one form to another, there is a tendency toward disorder (entropy) in the system. In biological systems, this means a great deal of energy is lost as metabolic heat when the organisms from one trophic level consume the next level. In the Silver Springs ecosystem example (Figure 6.1.2.5C), we see that the primary consumers produced 1103 kcal/m^2/yr from the 7618 kcal/m^2/yr of energy available to them from the primary producers. The measurement of energy transfer efficiency between two successive trophic levels is termed the **trophic level transfer efficiency** (TLTE) and is defined by the formula:

$$\text{TLTE} = \frac{\text{production at present trophic level}}{\text{production at previous trophic level}} * 100$$

In Silver Springs, the TLTE between the first two trophic levels was approximately 14.8 percent. The low efficiency of energy transfer between trophic levels is usually the major factor that limits the length of food chains observed in a food web. The fact is, after four to six energy transfers, there is not enough energy left to support another trophic level's need to grow, survive, and reproduce.

Ecologists have many different methods of measuring energy transfers within ecosystems. Some transfers are easier or more difficult to measure depending on the complexity of the ecosystem and how much access scientists have to observe the ecosystem. In other words, some ecosystems are more difficult to study than others, and sometimes the quantification of energy transfers has to be estimated.

Another main parameter that is important in characterizing energy flow within an ecosystem is the net production efficiency. **Net production efficiency (NPE)** allows ecologists to quantify how efficiently organisms of a particular trophic level incorporate the energy they receive into biomass; it is calculated using the following formula:

$$\text{NPE} = \frac{\text{net consumer productivity}}{\text{assimilation}} * 100$$

Net consumer productivity is the energy content available to the organisms at the next trophic level. **Assimilation** is the biomass (energy content generated per unit area) of the present trophic level after accounting for the energy lost due to incomplete ingestion of food, energy used for respiration, and energy lost as waste. **Incomplete ingestion** refers to the fact that some consumers eat only a part of their food. For example, when a lion kills an antelope, it will eat everything except the hide and bones. The lion is missing the energy-rich bone marrow inside the bone, so the lion does not make use of all the calories its prey could provide.

Thus, NPE measures how efficiently each trophic level uses and incorporates the energy from its food into biomass to fuel the next trophic level. In general, organisms whose internal temperature is externally regulated (**ectotherms**), such as invertebrates, fish, amphibians, and reptiles, use less of the energy they obtain for respiration and heat than organisms that internally regulate their temperature (**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 NPE. Therefore, many endotherms have to eat more often than ectotherms to get the energy they need for survival. In general, NPE for ectotherms is an order of magnitude (10x) higher than for endotherms. For example, the NPE for a caterpillar eating leaves has been measured at 18 percent, whereas the NPE for a squirrel eating acorns may be as low as 1.6 percent.

The inefficiency of energy use by endotherms 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 NPE is low, much of the energy from animal feed is lost. For example, it costs about $0.01 to produce 1,000 dietary calories (kCcal) 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 1,000 Kcal. Much of this difference is due to the low NPE of cattle. Thus, there has been a growing movement worldwide to promote the consumption of non-meat and non-dairy foods so that less energy is wasted feeding animals for the meat industry.

? Optional Activity 6.1.2.1

Pyramids depicting the number of organisms or biomass may be inverted, upright, or even diamond-shaped. Energy pyramids, however, are always upright. Why?

Answer

Pyramids of numbers may be inverted or diamond-shaped because a large organism, such as a tree, can sustain many smaller organisms. Likewise, a low biomass of producers can sustain a larger biomass at the next trophic level because the producers may reproduce rapidly and thus supply continuous nourishment. Pyramids of energy, however, must always be upright because of the laws of thermodynamics. 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.

Consequences of Food Webs: Biological Magnification

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 classical studies with the pesticide **d**ichloro**d**iphenyl**t**richloroethane (DDT). The results of these observations and analyses were published in the 1960s bestseller, *Silent Spring*, by 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. The use of DDT was banned in the United States in the 1970s.

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 6.1.2.6), 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.

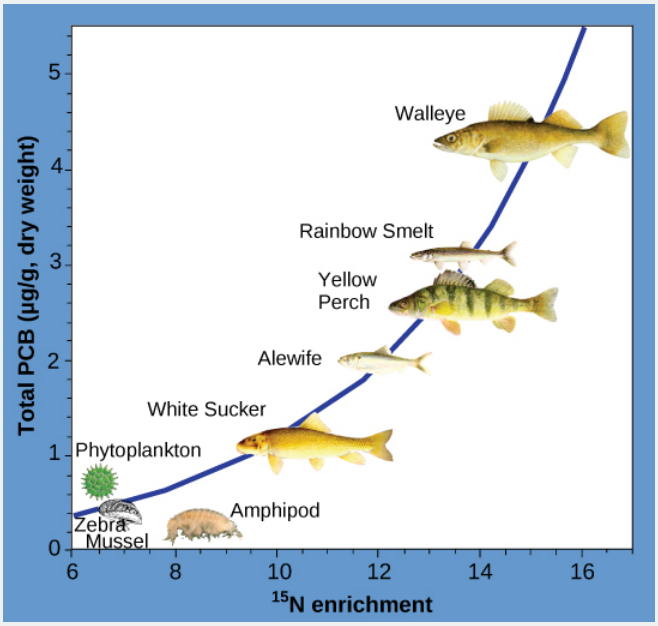


Figure 6.1.2.6: This chart shows the PCB concentrations found at the various trophic levels in the Saginaw Bay ecosystem of Lake Huron. Numbers on the x-axis reflect enrichment with heavy isotopes of nitrogen (^{15}N), which is a marker for increasing trophic level. Notice that the fish in the higher trophic levels accumulate more PCBs than those in lower trophic levels. (credit: Patricia Van Hoof, NOAA, GLERL)

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 women 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.

This page titled 6.1.2: Energy Flow through Ecosystems is shared under a not declared license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **46.2: Energy Flow through Ecosystems** by OpenStax is licensed CC BY 4.0.
- **46.1: Ecology of Ecosystems** by OpenStax is licensed CC BY 4.0.

6.1.3: Terrestrial Biomes

Terrestrial Biomes

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify the two major abiotic factors that determine terrestrial biomes
- Recognize distinguishing characteristics of each of the eight major terrestrial biomes

Introduction

A **biome** is an ecological community of organisms that are adapted to a characteristic set of environmental conditions. The Earth's biomes are categorized into two major groups: terrestrial and aquatic. Terrestrial biomes are based on land, while aquatic biomes include both ocean and freshwater biomes. The eight major terrestrial biomes on Earth are each distinguished by characteristic temperatures and amount of precipitation. Comparing the annual totals of precipitation and fluctuations in precipitation from one biome to another provides clues as to the importance of abiotic factors in the distribution of biomes. Temperature variation on a daily and seasonal basis is also important for predicting the geographic distribution of the biome and the vegetation type in the biome. The distribution of these biomes shows that the same biome can occur in geographically distinct areas with similar climates (Figure 6.1.3.1).

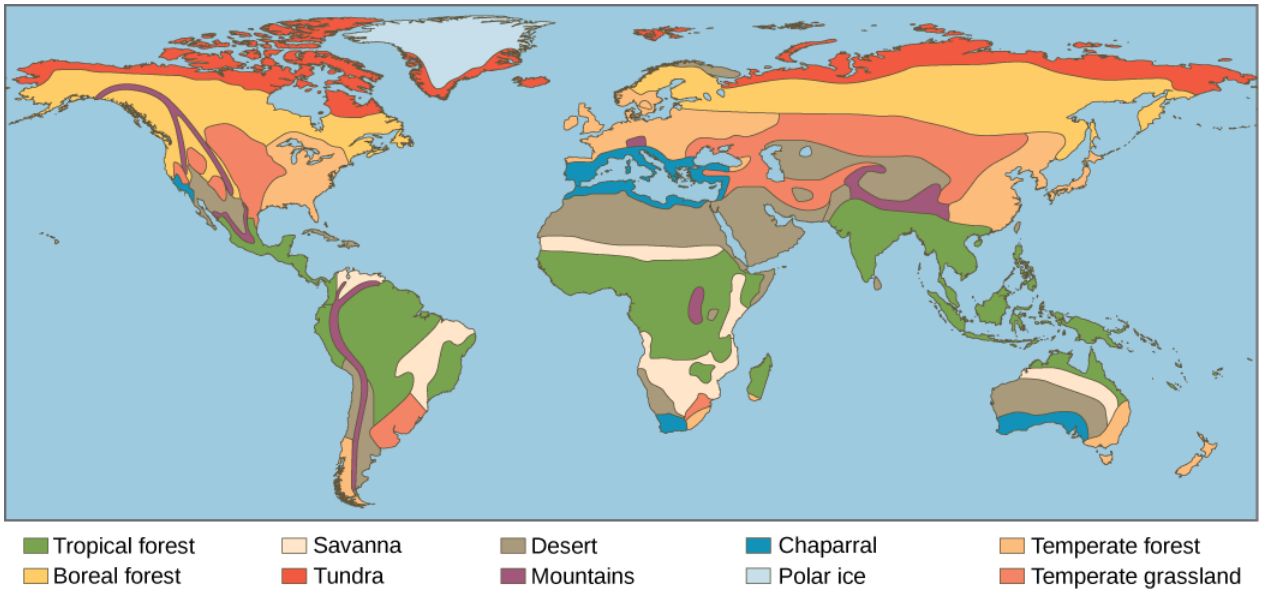
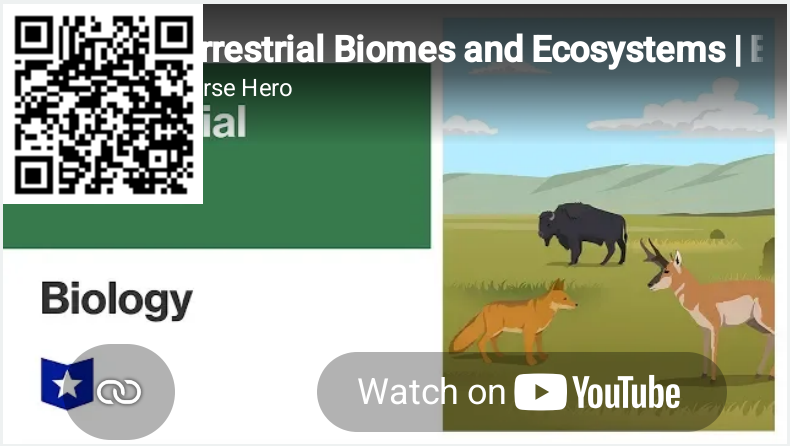


Figure 6.1.3.1: Each of the world's major biomes is distinguished by characteristic temperatures and amounts of precipitation. Polar ice and mountains are also shown.

Video



In this 7.5-minute video, you will review the characteristics of the eight terrestrial biomes.
Questions after watching: In which biome is your home located? Why do you think it is in this biome?

Tropical Wet Forest

Tropical wet forests are also referred to as tropical rainforests. This biome is found in equatorial regions (Figure 6.1.3.1). The vegetation is characterized by plants with broad leaves that fall off throughout the year. Unlike the trees of deciduous forests, the trees in this biome do not have a seasonal loss of leaves associated with variations in temperature and sunlight; these forests are "evergreen" year-round.

The temperature and sunlight profiles of tropical wet forests are very stable in comparison to that of other terrestrial biomes, with temperatures ranging from 20 °C to 34 °C. When one compares the annual temperature variation of tropical wet forests with that of other forest biomes, the lack of seasonal temperature variation in the tropical wet forest becomes apparent. This lack of seasonality leads to year-round plant growth, rather than the seasonal (spring, summer, and fall) growth seen in other biomes. In contrast to other ecosystems, tropical ecosystems do not have long days and short days during the yearly cycle. Instead, a constant daily amount of sunlight (11–12 hrs per day) provides more solar radiation, thereby, a longer period of time for plant growth.

The annual rainfall in tropical wet forests ranges from 125 to 660 cm with some monthly variation. While sunlight and temperature remain fairly consistent, annual rainfall is highly variable. Tropical wet forests have wet months in which there can be more than 30 cm of precipitation, as well as dry months in which there are fewer than 10 cm of rainfall. However, the driest month of a tropical wet forest still exceeds the *annual* rainfall of some other biomes, such as deserts.

Tropical wet forests have high net primary productivity because the annual temperatures and precipitation values in these areas are ideal for plant growth. Therefore, the extensive biomass present in the tropical wet forest leads to plant communities with very high species diversities (Figure 6.1.3.2). Tropical wet forests have more species of trees than any other biome; on average between 100 and 300 species of trees are present in a single hectare of South America. One way to visualize this is to compare the distinctive horizontal layers within the tropical wet forest biome. On the forest floor is a sparse layer of plants and decaying plant matter. Above that is an **understory** of short shrubby foliage. A layer of trees rises above this understory and is topped by a closed **upper canopy**—the uppermost overhead layer of branches and leaves. Some additional trees emerge through this closed upper canopy. These layers provide diverse and complex habitats for the variety of plants, fungi, animals, and other organisms within the tropical wet forests. For instance, **epiphytes** are plants that grow on other plants, which typically are not harmed. Epiphytes are found throughout tropical wet forest biomes. Many species of animals use the variety of plants and the complex structure of the tropical wet forests for food and shelter. Some organisms live several meters above ground and have adapted to this arboreal lifestyle.



Figure 6.1.3.2: Tropical wet forests, such as these forests of Madre de Dios, Peru, near the Amazon River, have high species diversity. (credit: Roosevelt Garcia)

Savannas

Savannas are grasslands with scattered trees, and they are located in Africa, South America, and northern Australia (Figure 6.1.3.3). Savannas are hot, tropical areas with temperatures averaging from 24 °C to 29 °C and an annual rainfall of 10–40 cm. Savannas have an extensive dry season; for this reason, forest trees do not grow as well as they do in tropical wet forests (or other forest biomes). As a result, within the grasses and **forbs** (herbaceous flowering plants) that dominate the savanna, there are relatively few trees (Figure 6.1.3.3). Since fire is an important source of disturbance in this biome, plants have evolved well-developed root systems that allow them to quickly re-sprout after a fire.



Figure 6.1.3.3: Savannas, like this one in Taita Hills Wildlife Sanctuary in Kenya, are dominated by grasses. (credit: Christopher T. Cooper)

Subtropical Deserts

Subtropical deserts exist between 15° and 30° north and south latitude and are centered on the Tropics of Cancer and Capricorn (Figure 6.1.3.4). This biome is very dry; in some years, evaporation exceeds precipitation. Subtropical hot deserts can have daytime soil surface temperatures above 60°C and nighttime temperatures approaching 0°C. In cold deserts, temperatures can be as high as 25°C and can drop below -30°C. Subtropical deserts are characterized by low annual precipitation of fewer than 30 cm with little monthly variation and a lack of predictability in rainfall. In some cases, the annual rainfall can be as low as 2 cm in subtropical deserts located in central Australia (“the Outback”) and northern Africa.

The vegetation and low animal diversity of this biome are closely related to this low and unpredictable precipitation. Very dry deserts lack perennial vegetation that lives from one year to the next; instead, many plants are annuals that grow quickly and reproduce when rainfall does occur, then they die. Many other plants in these areas are characterized by having a number of

adaptations that conserve water, such as deep roots, reduced foliage, and water-storing stems (Figure 6.1.3.4). Seed plants in the desert produce seeds that can be in dormancy for extended periods between rains. Adaptations in desert animals include **nocturnal** behavior (being awake at night) and burrowing.



Figure 6.1.3.4: To reduce water loss, many desert plants have tiny leaves or no leaves at all. The leaves of ocotillo (*Fouquieria splendens*), shown here in the Sonora Desert near Gila Bend, Arizona, appear only after rainfall, and then are shed.

Chaparral

The **chaparral** is also called the scrub forest and is found in California, along the Mediterranean Sea, and along the southern coast of Australia (Figure 6.1.3.5). The annual rainfall in this biome ranges from 65 cm to 75 cm, and the majority of the rain falls in the winter. Summers are very dry and many chaparral plants are dormant during the summertime. The chaparral vegetation, shown in Figure 6.1.3.5, is dominated by shrubs and is adapted to periodic fires, with some plants producing seeds that only germinate after a hot fire. The ashes left behind after a fire are rich in nutrients like nitrogen that fertilize the soil and promote plant regrowth.



Figure 6.1.3.5: The chaparral is dominated by shrubs. (credit: Miguel Vieira)

Temperate Grasslands

Temperate grasslands are found throughout central North America, where they are also known as prairies; they are also in Eurasia, where they are known as steppes (Figure 6.1.3.6). Temperate grasslands have pronounced annual fluctuations in temperature with hot summers and cold winters. The annual temperature variation produces specific growing seasons for plants. Plant growth is possible when temperatures are warm enough to sustain plant growth and when ample water is available, which occurs in the spring, summer, and fall. During much of the winter, temperatures are low, and water, which is stored in the form of ice, is not available for plant growth.

Annual precipitation ranges from 25-75 cm. Because of relatively lower annual precipitation in temperate grasslands, there are few trees except for those found growing along rivers or streams. The dominant vegetation tends to consist of grasses and some prairies sustain populations of grazing animals Figure 6.1.3.6. The vegetation is very dense and the soils are fertile because the subsurface of the soil is packed with the roots and rhizomes (underground stems) of these grasses. The roots and rhizomes act to anchor plants into the ground and replenish the organic material (**humus**) in the soil when they die and decay.



Figure 6.1.3.6: The prairies in Alberta.

Fires, mainly caused by lightning, are a natural disturbance in temperate grasslands. When fire is suppressed in temperate grasslands, the vegetation eventually converts to scrub and dense forests. Often, the restoration or management of temperate grasslands requires the use of controlled burns to suppress the growth of trees and maintain the grasses.

Temperate Forests

Temperate forests are the most common biome in eastern North America, Western Europe, Eastern Asia, Chile, and New Zealand (Figure 6.1.3.7). This biome is found throughout mid-latitude regions. Temperatures range between -30 °C and 30 °C and drop to below freezing on an annual basis. These temperatures mean that temperate forests have defined growing seasons during the spring, summer, and early fall. Precipitation is relatively constant throughout the year and ranges between 75 cm and 150 cm.

Because of the moderate annual rainfall and temperatures, deciduous trees are the dominant plant in this biome (Figure 6.1.3.7). Deciduous trees lose their leaves each fall and remain leafless in the winter. Thus, no photosynthesis occurs in deciduous trees during the dormant winter period. Each spring, new leaves appear as the temperature increases. Because of the dormant period, the net primary productivity of temperate forests is less than that of tropical wet forests. In addition, temperate forests show less diversity of tree species than tropical wet forest biomes.



Figure 6.1.3.7: Deciduous trees are the dominant plant in the temperate forest. (credit: Oliver Herold)

The trees of the temperate forests leaf out and shade much of the ground; however, this biome is more open than tropical wet forests because trees in temperate forests do not grow as tall as the trees in tropical wet forests. The soils of temperate forests are rich in inorganic and organic nutrients. This is due to the thick layer of leaf litter on forest floors. As this leaf litter decays, nutrients are returned to the soil. The leaf litter also protects soil from erosion, insulates the ground, and provides habitats for invertebrates (such as the pill bug or roly-poly, *Armadillidium vulgare*) and their predators, such as the red-backed salamander (*Plethodon cinereus*).

Boreal Forests

The **boreal forest**, also known as taiga or coniferous forest, is found south of the Arctic Circle and across most of Canada, Alaska, Russia, and northern Europe (Figure 6.1.3.8). This biome has cold, dry winters and short, cool, wet summers. The annual precipitation is from 40 cm to 100 cm and usually takes the form of snow. Little evaporation occurs because of the cold temperatures. In British Columbia, you can find them surrounding the towns of Fort St. John, Fort Nelson, and Telegraph Creek, at the northern and eastern tip of the province. It comprises 5% of Canada's boreal forest.

The long and cold winters in the boreal forest have led to the predominance of cold-tolerant cone-bearing plants. These are evergreen coniferous trees like pines, spruce, and fir, which retain their needle-shaped leaves year-round. Evergreen trees can photosynthesize earlier in the spring than deciduous trees because less energy from the sun is required to warm a needle-like leaf than a broad leaf. This benefits evergreen trees, which grow faster than deciduous trees in the boreal forest. In addition, soils in boreal forest regions tend to be acidic with little available nitrogen. Leaves are a nitrogen-rich structure and deciduous trees must produce a new set of these nitrogen-rich structures each year. Therefore, coniferous trees that retain nitrogen-rich needles may have a competitive advantage over broad-leafed deciduous trees.

The net primary productivity of boreal forests is lower than that of temperate forests and tropical wet forests. The aboveground biomass of boreal forests is high because these slow-growing tree species are long-lived and accumulate standing biomass over time. Plant species diversity is less than that seen in temperate forests and tropical wet forests. Boreal forests lack the pronounced elements of the layered forest structure seen in tropical wet forests. The structure of a boreal forest is often only a tree layer and a ground layer (Figure 6.1.3.8). When conifer needles are dropped, they decompose more slowly than broad leaves; therefore, fewer nutrients are returned to the soil to fuel plant growth.



Figure 6.1.3.8: The boreal forest (taiga) range in North America. Government of Canada - Boreal Forest

Arctic Tundra

The **Arctic tundra** lies north of the subarctic boreal forest and is located throughout the Arctic regions of the northern hemisphere (Figure 6.1.3.9). The average winter temperature is -34°C and the average summer temperature is from 3°C to 12°C. Plants in the arctic tundra have a very short growing season of approximately 10–12 weeks. However, during this time, there are almost 24 hours of daylight and plant growth is rapid. The annual precipitation of the Arctic tundra is very low with little annual variation in precipitation. And, as in the boreal forests, there is little evaporation due to the cold temperatures.

Plants in the Arctic tundra are generally low to the ground (Figure 6.1.3.9). There is little species diversity, low net primary productivity, and low aboveground biomass. The soils of the Arctic tundra may remain in a perennially frozen state referred to as **permafrost**. The permafrost makes it impossible for roots to penetrate deep into the soil and slows the decay of organic matter, which inhibits the release of nutrients from organic matter. During the growing season, the ground of the Arctic tundra can be completely covered with plants or lichens.



Figure 6.1.3.9**:** Low-growing plants dominate the tundra landscape. Alan877 CC BY-NC-ND 2.0.

Optional Activity 6.1.3.1

Figure 6.1.3.1: Which of the following statements about biomes is false?

A. Chaparral is dominated by shrubs.
B. Savannas and temperate grasslands are dominated by grasses.
C. Boreal forests are dominated by deciduous trees.
D. Lichens are common in the arctic tundra.

Answer

C. Boreal forests are not dominated by deciduous trees.

This page titled 6.1.3: Terrestrial Biomes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **44.3: Terrestrial Biomes** by OpenStax is licensed CC BY 4.0.

6.1.4: Aquatic Biomes

Aquatic Biomes

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

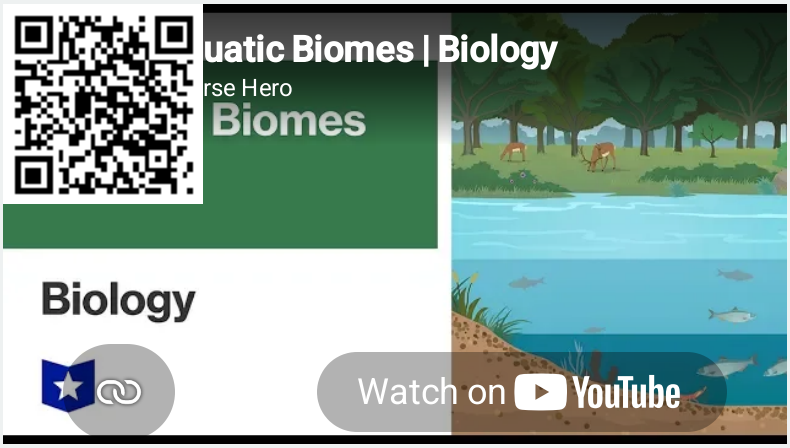
Learning Objectives

- Describe the effects of abiotic factors on the composition of plant and animal communities in aquatic biomes
- Compare and contrast the characteristics of the ocean zones
- Summarize the characteristics of standing water and flowing water freshwater biomes

Introduction

Like terrestrial biomes, aquatic biomes are influenced by a series of abiotic factors. The aquatic medium—water— has different physical and chemical properties than air. Even if the water in a pond or other body of water is perfectly clear (there are no suspended particles), water, on its own, absorbs light. As one descends into a deep body of water, there will eventually be a depth at which sunlight cannot reach. While there are some abiotic and biotic factors in a terrestrial ecosystem that might obscure light (like fog, dust, or insect swarms), usually these are not permanent features of the environment. The importance of light in aquatic biomes is central to the communities of organisms found in both freshwater and marine ecosystems. In freshwater systems, **stratification** due to differences in density is perhaps the most critical abiotic factor and is related to the energy aspects of light. The thermal properties of water (rates of heating and cooling) are significant to the function of marine systems and have major impacts on global climate and weather patterns. Marine systems are also influenced by large-scale physical water movements, such as currents; these are less important in most freshwater lakes.

Video



In this 6-minute video, review aquatic biomes which encompass the majority of the Earth.
Question after watching: The terrestrial biomes are distinguished by climate, whereas this is not the case for aquatic biomes. Why is this?

Marine Biomes

The ocean is the largest marine biome. It is a continuous body of salt water that is relatively uniform in chemical composition; it is a weak solution of mineral salts and decayed biological matter. Within the ocean, coral reefs are a second kind of marine biome.

Estuaries, coastal areas where salt water and fresh water mix, form a third unique marine biome.

Ocean

The ocean is categorized by several areas or zones (Figure 6.1.4.1). The physical diversity of the ocean is a significant influence on plants, animals, and other organisms. The ocean is categorized into different zones based on how far light reaches into the water. Each zone has a distinct group of species adapted to the biotic and abiotic conditions particular to that zone.

All of the ocean's open water is referred to as the **pelagic realm** (or zone). The **benthic realm** (or zone) extends along the ocean bottom from the shoreline to the deepest parts of the ocean floor. Within the pelagic realm is the **photic zone**, which is the portion of the ocean that light can penetrate (approximately 200 m). At depths greater than 200 m, light cannot penetrate; thus, this is referred to as the **aphotic zone**. The majority of the ocean is aphotic and lacks sufficient light for photosynthesis. The deepest part of the ocean, the Challenger Deep (in the Mariana Trench, located in the western Pacific Ocean), is about 11,000 m deep. To give some perspective on the depth of this trench, the ocean is, on average, 4,267 m deep. These realms and zones are relevant to freshwater lakes as well.

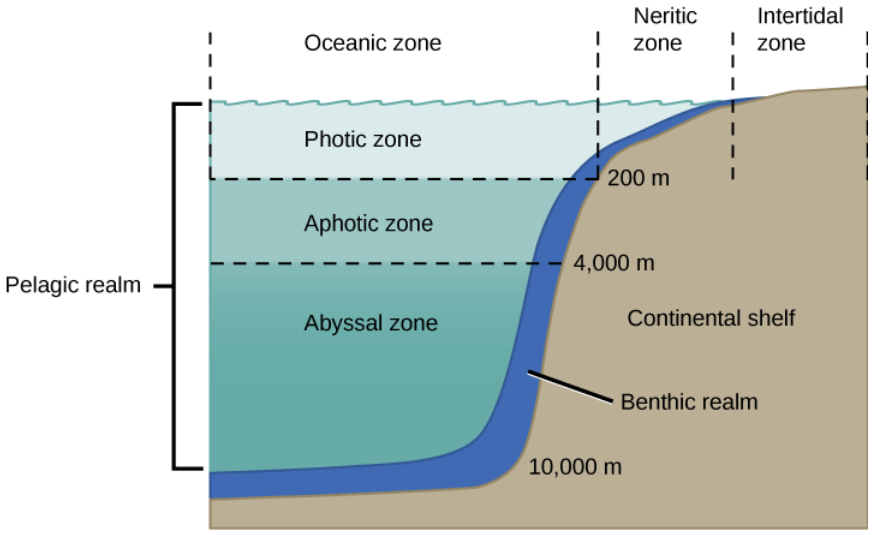


Figure 6.1.4.1: The ocean is divided into different zones based on water depth and distance from the shoreline.

Optional Activity 6.1.4.1

Figure 6.1.4.1: In which of the following regions would you expect to find photosynthetic organisms?

A. the aphotic zone, the neritic zone, the oceanic zone, and the benthic realm
B. the photic zone, the intertidal zone, the neritic zone, and the oceanic zone
C. the photic zone, the benthic zone, the neritic zone, and the oceanic zone
D. the pelagic realm, the aphotic zone, the neritic zone, and the oceanic zone

Answer

C. Photosynthetic organisms would be found in the photic, benthic, neritic, and oceanic zones.

The **intertidal zone**, which is the zone between high and low tide, is the oceanic region that is closest to land (Figure 6.1.4.1). Generally, most people think of this portion of the ocean as a sandy beach. In some cases, the intertidal zone is indeed a sandy beach, but it can also be rocky or muddy. The intertidal zone is an extremely variable environment because of tides. Organisms are exposed to air and sunlight at low tide and are underwater most of the time, especially during high tide. Therefore, living things that thrive in the intertidal zone are adapted to being dry for long periods of time. The shore of the intertidal zone is also repeatedly struck by waves, and the organisms found there are adapted to withstand damage from the pounding action of the waves (Figure 6.1.4.2). The exoskeletons of shoreline crustaceans (such as the shore crab, *Carcinus maenas*) are tough and protect them from

desiccation (drying out) and wave damage. Another consequence of the pounding waves is that few algae and plants establish themselves in the constantly moving rocks, sand, or mud.



Figure 6.1.4.2: Sea urchins, mussel shells, and leather and purple sea stars are often found in the intertidal zone of BC. This photo was takenin Kachemak Bay, Alaska, but it is representative of BC intertidal life. (credit: NOAA)

The **neritic zone** (Figure 6.1.4.1) extends from the intertidal zone to depths of about 200 m at the edge of the continental shelf. Since light can penetrate this depth, photosynthesis can occur in the neritic zone. The water here contains silt and is well-oxygenated, low in pressure, and stable in temperature. Phytoplankton and floating *Sargassum* (a type of free-floating marine seaweed) provide a habitat and food source for some sea life found in the neritic zone. Zooplankton, protists, small fishes, and shrimp are found in the neritic zone and are the base of the food chain for most of the world's fisheries.

Beyond the neritic zone is the open ocean area known as the **oceanic zone** (Figure 6.1.4.1). Within the oceanic zone there is thermal stratification where warm and cold waters mix because of ocean currents. Abundant plankton serve as the base of the food chain for larger animals such as whales and dolphins. Nutrients are scarce and this is a relatively less productive part of the marine biome. When photosynthetic organisms and the protists and animals that feed on them die, their bodies fall to the bottom of the ocean where they remain; unlike freshwater lakes, the open ocean lacks a process for bringing the organic nutrients back up to the surface. The majority of organisms in the aphotic zone include sea cucumbers (phylum Echinodermata) and other organisms that survive on the nutrients contained in the dead bodies of organisms in the photic zone.

Beneath the pelagic zone is the benthic realm, the deepwater region beyond the continental shelf (Figure 6.1.4.1). The bottom of the benthic realm is comprised of sand, silt, and dead organisms. Temperature decreases, remaining above freezing, as water depth increases. This is a nutrient-rich portion of the ocean because of the dead organisms that fall from the upper layers of the ocean. Because of this high level of nutrients, a diversity of fungi, sponges, sea anemones, marine worms, sea stars, fishes, and bacteria exist.

The deepest part of the ocean is the **abyssal zone**, which is at depths of 4,000 m or greater. The abyssal zone (Figure 6.1.4.1) is very cold and has very high pressure, high oxygen content due to stratification, and low nutrient content. There are a variety of invertebrates and fishes found in this zone, but the abyssal zone does not have plants because of the lack of light. Hydrothermal vents are found primarily in the abyssal zone; chemosynthetic bacteria utilize the hydrogen sulfide and other minerals emitted from the vents. These chemosynthetic bacteria use hydrogen sulfide as an energy source and serve as the base of the food chain found in the abyssal zone.

Coral Reefs

Coral reefs are ocean ridges formed by marine invertebrates living in warm shallow waters within the photic zone of the ocean. They are found within 30˚ north and south of the equator. The Great Barrier Reef is a well-known reef system located several miles off the northeastern coast of Australia. Other coral reef systems are fringing islands, which are directly adjacent to land, or atolls, which are circular reef systems surrounding a former landmass that is now underwater. The coral organisms (members of phylum Cnidaria) are colonies of saltwater polyps that secrete a calcium carbonate skeleton. These calcium-rich skeletons slowly accumulate, forming the underwater reef (Figure 6.1.4.3). Corals found in shallower waters (at a depth of approximately 60 m) have a mutualistic relationship with photosynthetic unicellular algae (dinoflagellates known as zooxanthellae). The relationship provides

corals with the majority of the nutrition and the energy they require. The waters in which these corals live are nutritionally poor and, without this mutualism, it would not be possible for large corals to grow. Some corals living in deeper and colder water do not have a mutualistic relationship with algae; these corals attain energy and nutrients using stinging cells on their tentacles to capture prey.

It is estimated that more than 4,000 fish species inhabit coral reefs. These fishes can feed on coral, the **cryptofauna** (invertebrates found within the calcium carbonate substrate of the coral reefs), or the seaweed and algae that are associated with the coral. In addition, some fish species inhabit the boundaries of a coral reef; these species include predators, herbivores, or **planktivores** (that eat plankton).

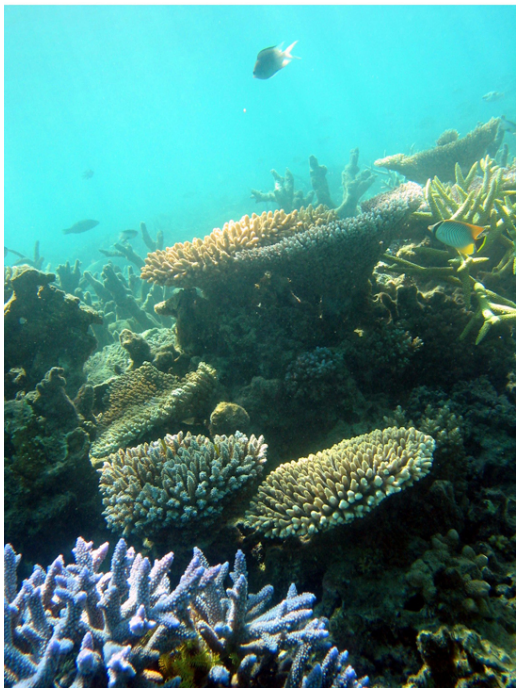


Figure 6.1.4.3: Coral reefs are formed by the calcium carbonate skeletons of coral organisms, which are marine invertebrates in the phylum Cnidaria. (credit: Terry Hughes)

Evolution Connection: Global Decline of Coral Reefs

It takes a long time to build a coral reef. The animals that create coral reefs have evolved over millions of years, continuing to slowly deposit the calcium carbonate that forms their characteristic ocean homes. Bathed in warm tropical waters, the coral animals and their symbiotic algal partners evolved to survive at the upper limit of ocean water temperature.

Together, climate change and human activity pose dual threats to the long-term survival of the world's coral reefs. Excessive sea surface temperatures due to climate change cause the reefs to expel their symbiotic, food-producing algae, resulting in a phenomenon known as **bleaching**. When bleaching occurs, the reefs lose much of their characteristic color as the algae and the coral animals die if loss of the symbiotic zooxanthellae is prolonged.

In addition, as CO_2 dissolves in ocean waters, it lowers the pH and increases ocean acidity. As acidity increases, it interferes with the calcification that normally occurs as coral animals build their calcium carbonate homes. When a coral reef begins to die, species diversity plummets as animals lose food and shelter. Coral reefs are also economically important tourist destinations, so the decline of coral reefs poses a serious threat to coastal economies.

Human population growth has damaged corals in other ways, too. As human coastal populations increase, the runoff of sediment and agricultural chemicals has increased causing some of the once-clear tropical waters to become cloudy. At the same time, overharvesting has allowed the predator species that eat corals to go unchecked.

Although a rise in global temperatures of 1–2˚C (a conservative projection) in the coming decades may not seem large, it is significant to this biome. When change occurs rapidly, species can become extinct before evolution leads to new adaptations. Many scientists believe that climate change, with its rapid (in terms of evolutionary time) and inexorable increases in temperature, is tipping the balance beyond the point at which many of the world's coral reefs can recover.

More is covered in (Unit 5.3)

Estuaries

Estuaries are biomes that occur where a source of fresh water, such as a river, meets the ocean. Therefore, both fresh water and salt water are found in the same vicinity; mixing results in a diluted (**brackish**) saltwater. Estuaries form protected areas where many of the young offspring of crustaceans, mollusks, and fish begin their lives. Salinity is a very important factor that influences the organisms and the adaptations of the organisms found in estuaries. The salinity of estuaries varies and is based on the rate of flow of its freshwater sources. Once or twice a day, high tides bring salt water into the estuary. Low tides occurring at the same frequency reverse the current of salt water.

The short-term and rapid variation in salinity due to the mixing of fresh water and salt water is a difficult physiological challenge for the plants and animals that inhabit estuaries. Many estuarine plant species are **halophytes**: plants that can tolerate salty conditions. Halophytic plants are adapted to deal with the salinity resulting from saltwater on their roots or from sea spray. In some halophytes, filters in the roots remove the salt from the water that the plant absorbs. Other plants are able to pump oxygen into their roots. Animals, such as mussels and clams (phylum Mollusca), have developed behavioral adaptations that expend a lot of energy to function in this rapidly changing environment. When these animals are exposed to low salinity, they stop feeding, close their shells, and switch from aerobic respiration (in which they use gills) to anaerobic respiration (a process that does not require oxygen). When high tide returns to the estuary, the salinity and oxygen content of the water increases, and these animals open their shells, begin feeding, and return to aerobic respiration.

Freshwater Biomes

Freshwater biomes include lakes and ponds (standing water) as well as rivers and streams (flowing water). They also include wetlands, which will be discussed below. Humans rely on freshwater biomes to provide aquatic resources for drinking water, crop irrigation, sanitation, and industry. These various roles and human benefits are referred to as ecosystem services. Lakes and ponds are found in terrestrial landscapes and are, therefore, connected with abiotic and biotic factors influencing these terrestrial biomes.

Lakes and Ponds

Lakes and ponds can range in area from a few square meters to thousands of square kilometers. Temperature is an important abiotic factor affecting living things found in lakes and ponds. In the summer, thermal stratification of lakes and ponds occurs when the upper layer of water is warmed by the sun and does not mix with deeper, cooler water. Light can penetrate within the photic zone of the lake or pond. Phytoplankton (algae and cyanobacteria) are found here and carry out photosynthesis, providing the base of the food web of lakes and ponds. Zooplankton, such as rotifers and small crustaceans, consume phytoplankton. At the bottom of lakes and ponds, bacteria in the aphotic zone break down dead organisms that sink to the bottom.

Nitrogen and phosphorus are important limiting nutrients in lakes and ponds. Because of this, they are density-dependent factors for phytoplankton growth in lakes and ponds. When there is a large input of nitrogen and phosphorus known as **eutrophication** (from sewage and runoff from fertilized lawns and farms, for example), the growth of algae skyrockets, resulting in a large accumulation of algae called an algal bloom. **Algal blooms** can become so extensive that they reduce light penetration in water (Figure 6.1.4.4). As a result, the lake or pond becomes aphotic and photosynthetic plants cannot survive. When the algae die and decompose, severe oxygen depletion of the water occurs. Fishes and other organisms that require oxygen are then more likely to die, and resulting dead zones are found across the globe (Unit 4.4.5). Lake Erie and the Gulf of Mexico represent freshwater and marine habitats where phosphorus control and stormwater runoff pose significant environmental challenges.



Figure 6.1.4.4: The uncontrolled growth of algae in this lake has resulted in an **algal bloom**. (credit: Jeremy Nettleton)

Rivers and Streams

Rivers and streams are continuously moving bodies of water that carry large amounts of water from the source, or headwater, to a lake or ocean. The largest rivers include the Nile River in Africa, the Amazon River in South America, and the Mackenzie River in the Northern Territories.

Abiotic features of rivers and streams vary along the length of the river or stream. Streams begin at a point of origin referred to as **source water**. The source water is usually cold, low in nutrients, and clear. The **channel** (the width of the river or stream) is narrower than at any other place along the length of the river or stream. Because of this, the current is often faster here than at any other point of the river or stream.

The fast-moving water results in minimal silt accumulation at the bottom of the river or stream; therefore, the water is clear. Photosynthesis here is mostly attributed to algae that are growing on rocks; the swift current inhibits the growth of phytoplankton. An additional input of energy can come from leaves or other organic material that falls into the river or stream from trees and other plants that border the water. When the leaves decompose, the organic material and nutrients in the leaves are returned to the water. Plants and animals have adapted to this fast-moving water. For instance, leeches (phylum Annelida) have elongated bodies and suckers on both ends. These suckers attach to the substrate, keeping the leech anchored in place. Freshwater trout species (phylum Chordata) are important predators in these fast-moving rivers and streams.

As the river or stream flows away from the source, the width of the channel gradually widens and the current slows. This slow-moving water, caused by the gradient decrease and the volume increase as tributaries unite, has more sedimentation. Phytoplankton can also be suspended in slow-moving water. Therefore, the water will not be as clear as it is near the source. The water is also warmer. Worms (phylum Annelida) and insects (phylum Arthropoda) can be found burrowing into the mud. The higher-order predator vertebrates (phylum Chordata) include waterfowl, frogs, and fishes. These predators must find food in these slow-moving, sometimes murky, waters, and, unlike the trout in the waters at the source, these vertebrates may not be able to use vision as their primary sense to find food. Instead, they are more likely to use taste or chemical cues to find prey.

Wetlands

Wetlands are environments in which the soil is either permanently or periodically saturated with water. Wetlands are different from lakes because wetlands are shallow bodies of water whereas lakes vary in depth. **Emergent vegetation** consists of wetland plants that are rooted in the soil but have portions of leaves, stems, and flowers extending above the water's surface. There are several types of wetlands including marshes, swamps, bogs, mudflats, and salt marshes (Figure 6.1.4.5). The three shared characteristics among these types—what makes them wetlands—are their hydrology, hydrophytic vegetation, and hydric soils.



Figure 6.1.4.5: Located in southern Florida, Everglades National Park is a vast array of wetland environments, including sawgrass marshes, cypress swamps, and estuarine mangrove forests. Here, a great egret walks among cypress trees. (credit: NPS)

Freshwater **marshes and swamps** are characterized by slow and steady water flow. **Bogs** develop in depressions where water flow is low or nonexistent. Bogs usually occur in areas where there is a clay bottom with poor percolation. **Percolation** is the movement of water through the pores in the soil or rocks. The water found in a bog is stagnant and oxygen depleted because the oxygen that is used during the decomposition of organic matter is not replaced. As the oxygen in the water is depleted, decomposition slows. This leads to organic acids and other acids building up and lowering the pH of the water. At a lower pH, nitrogen becomes unavailable to plants. This creates a challenge for plants because nitrogen is an important limiting resource. Some types of bog plants (such as sundews, pitcher plants, and Venus flytraps) capture insects and extract nitrogen from their bodies. Bogs have low net primary productivity because the water found in bogs has low levels of nitrogen and oxygen.

This page titled 6.1.4: Aquatic Biomes is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **44.4: Aquatic Biomes** by OpenStax is licensed CC BY 4.0.

Biogeochemical Cycles

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 90 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Discuss the biogeochemical cycles of water, carbon, nitrogen, phosphorus, and sulfur
- Explain how human activities have impacted these cycles and the potential consequences for Earth

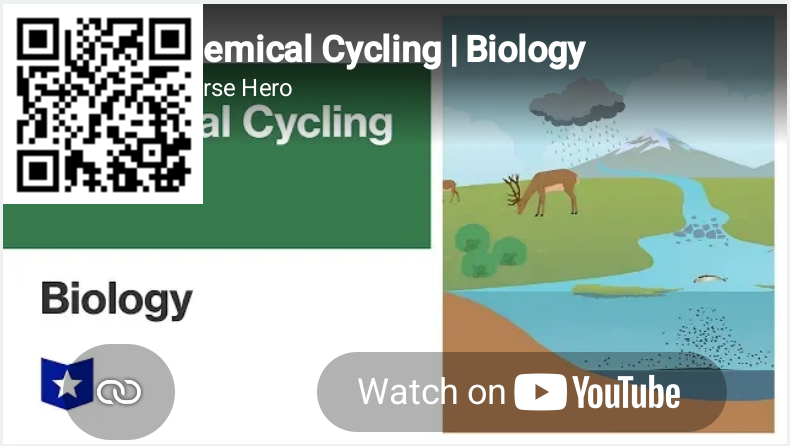
Introduction

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. Geologic processes through the **geosphere**, or rock of the Earth, such as weathering, erosion, water drainage, and the **subduction** of the continental plates, all play a role in this recycling of materials. Because geology and chemistry have major roles in the study of this process, the recycling of inorganic matter between living organisms and their environment is called a **biogeochemical cycle**.

Water contains hydrogen and oxygen, which is essential to all living processes. The **hydrosphere** is the area of the Earth where water movement and storage occurs: as liquid water on the surface and beneath the surface or frozen (rivers, lakes, oceans, groundwater, polar ice caps, and glaciers), and as water vapor in the atmosphere. Carbon is found in all organic macromolecules and is an important constituent of fossil fuels. Nitrogen is a major component of our nucleic acids and proteins and is critical to human agriculture. Phosphorus, a major component of nucleic acid (along with nitrogen), is one of the main ingredients in artificial fertilizers used in agriculture and their associated environmental impacts on our surface water. Sulfur, critical to the three-dimensional folding of proteins (as in disulfide binding), is released into the atmosphere by the burning of fossil fuels, such as coal.

The cycling of these elements is interconnected. For example, the movement of water is critical for the leaching of nitrogen and phosphate into rivers, lakes, and oceans. Furthermore, the ocean itself is a major reservoir for carbon. Thus, mineral nutrients are cycled, either rapidly or slowly, through the entire biosphere, from one living organism to another, and between the biotic and abiotic world.

Video



In this 6-minute video, you will examine how chemicals (nutrients) are recycled in an ecosystem and how energy flows through the ecosystem.

Questions after watching: A house plant in a terrarium with good soil is an isolated ecosystem. Is this closed ecosystem capable of recycling all of its needed chemicals? What are its sources of nutrients (chemicals) and energy?

The Water (Hydrologic) Cycle

Water is the basis of all living processes. The human body is more than 50% water and human cells are more than 70% water. Thus, most land animals need a supply of fresh water to survive. However, when examining the stores of water on Earth, 97.5 percent of it is non-potable salt water (Figure 6.1.5.1). Of the remaining water, 99 percent is locked underground as water or as ice. Thus, less than 1% of fresh water is easily accessible from lakes and rivers. Many living things, such as plants, animals, and fungi, are dependent on the small amount of fresh surface water supply, a lack of which can have massive effects on ecosystem dynamics. Humans, of course, have developed technologies to increase water availability, such as digging wells to harvest groundwater, storing rainwater, and using desalination to obtain drinkable water from the ocean. Although this pursuit of drinkable water has been ongoing throughout human history, the supply of fresh water is still a major issue in modern times.

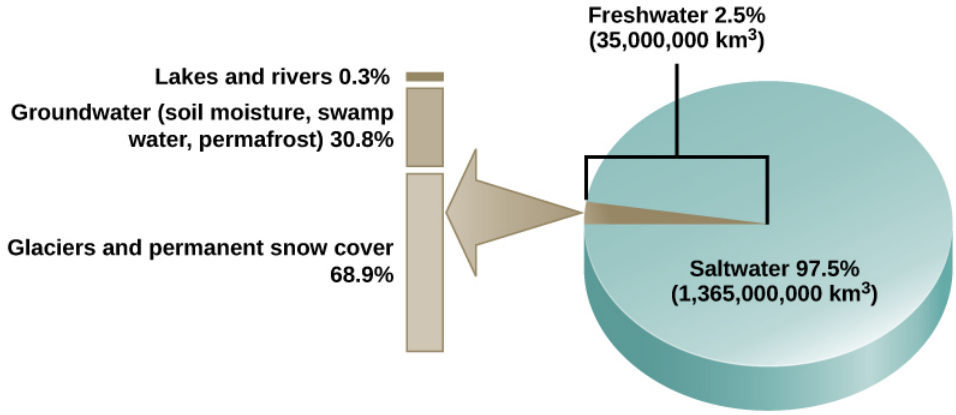


Figure 6.1.5.1: Only 2.5 percent of water on Earth is fresh water, and less than 1% of fresh water is easily accessible to living things.

Water cycling is extremely important to ecosystem dynamics. Water has a major influence on climate and, thus, on the environments of ecosystems, some located on distant parts of the Earth. Most of the water on Earth is stored for long periods in the oceans, underground, and as ice. Figure 6.1.5.2 illustrates the average time that an individual water molecule may spend in the Earth's major water reservoirs. **Residence time** is a measure of the average time an individual molecule stays in a particular reservoir. A large amount of the Earth's water is locked in place in these reservoirs as ice, beneath the ground, and in the ocean, and, thus, is unavailable for short-term cycling (only surface water can evaporate).

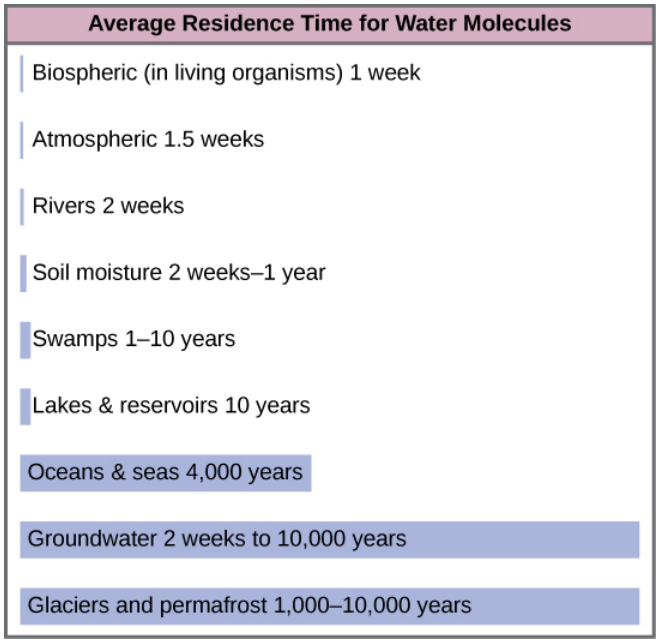


Figure 6.1.5.2: This graph shows the average residence time for water molecules in the Earth's water reservoirs.

There are various processes that occur during the cycling of water, shown in Figure 6.1.5.3. These processes include the following:

- evaporation/sublimation
- condensation/precipitation
- subsurface water flow
- surface runoff/snowmelt
- streamflow

The water cycle is driven by the Sun's energy as it warms the oceans and other surface waters. This leads to the **evaporation** (water to water vapor) of liquid surface water and the **sublimation** (ice to water vapor) of frozen water, which deposits large amounts of water vapor into the atmosphere. Over time, this water vapor condenses into clouds as liquid or frozen droplets and is eventually followed by **precipitation** (rain or snow), which returns water to the Earth's surface. Rain eventually **infiltrates** into the ground, where it may evaporate again if it is near the surface, flow beneath the surface, or be stored for long periods. More easily observed is surface **runoff**: the flow of fresh water either from rain or melting ice. Runoff can then make its way through streams and lakes to the oceans or flow directly to the oceans themselves.

Rain and surface runoff are major ways in which minerals, including carbon, nitrogen, phosphorus, and sulfur, are cycled from land to water. The environmental effects of runoff will be discussed later as these cycles are described.

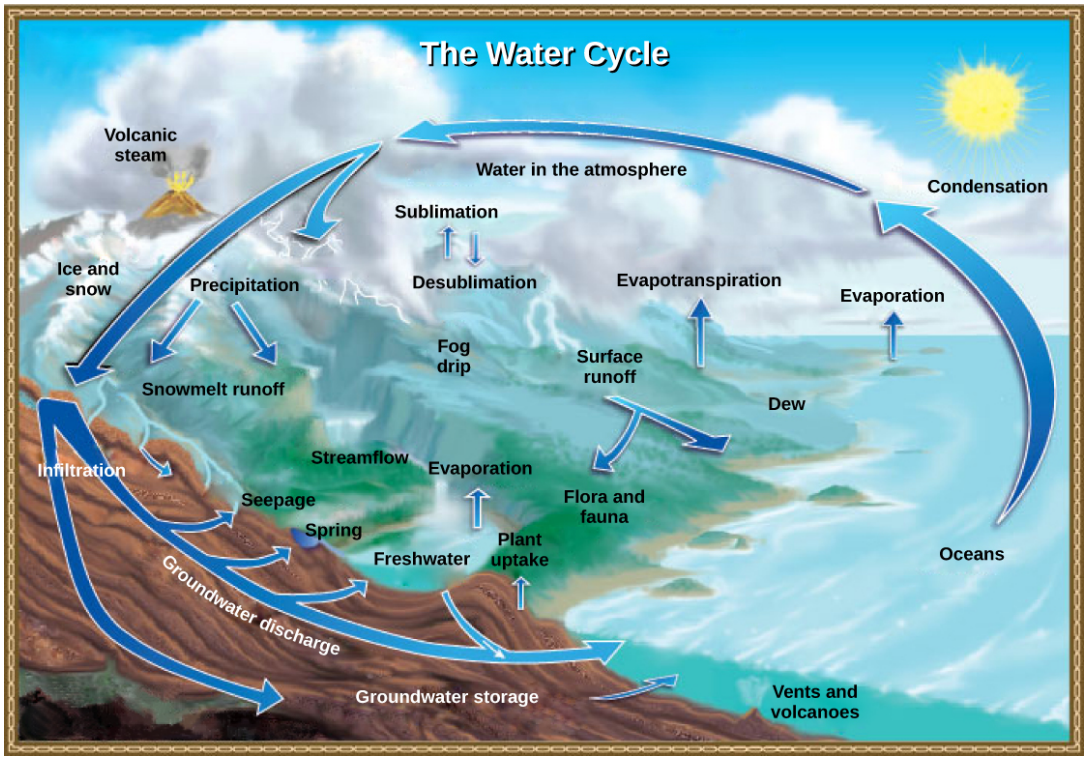


Figure 6.1.5.3: Water from the land and oceans enters the atmosphere by evaporation or sublimation, where it condenses into clouds and falls as rain or snow. Precipitated water may enter freshwater bodies or infiltrate the soil. The cycle is complete when surface or groundwater reenters the ocean. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

The Carbon Cycle

Carbon is the second most abundant element in living organisms. 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, a **carbon footprint** is based on how much carbon dioxide is produced by an individual or per capita 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 6.1.5.4.

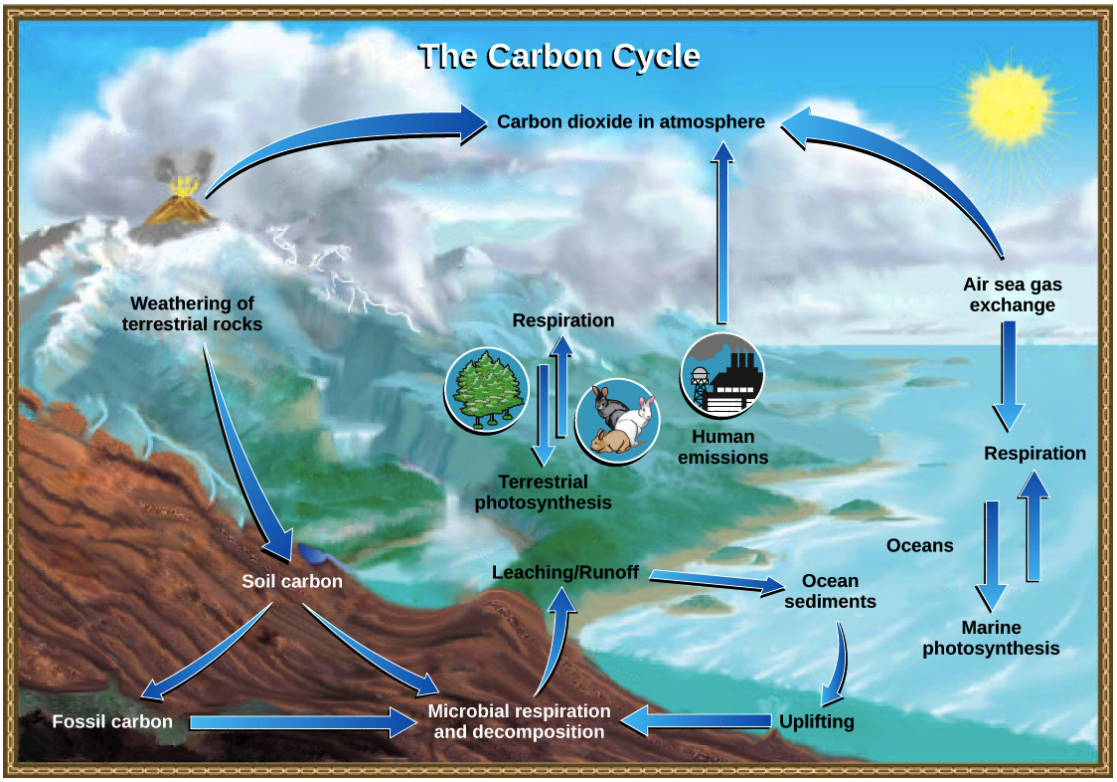


Figure 6.1.5.4: Carbon dioxide gas exists in the atmosphere and is dissolved in water. Photosynthesis converts carbon dioxide gas to organic carbon, and respiration cycles the organic carbon back into carbon dioxide gas. Long-term storage of organic carbon occurs when matter from living organisms is buried deep underground and becomes fossilized. Volcanic activity and, more recently, human emissions, bring this stored carbon back into the carbon cycle. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

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 acquire it in the dissolved form (carbonic acid, $H_2CO_3^-$). However carbon dioxide is acquired, a by-product of the process is oxygen. Photosynthetic organisms are responsible for depositing approximately 21% of the atmosphere's 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 and releases carbon dioxide as a by-product (this is a source). 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, or sinks, 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 water reservoirs 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 water and combines with water molecules to form carbonic acid, and then it ionizes to carbonate and bicarbonate ions.

More than 90 percent of the carbon in the ocean is found as bicarbonate ions. Some of these ions combine with seawater calcium to form calcium carbonate ($CaCO_3$), a major component of marine organism shells. 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 **non-renewable 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.

Carbon dioxide is also added to the atmosphere by the animal husbandry practices of humans. 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 animal 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 fossils fuels, scientists take natural processes, such as volcanoes and respiration, into account as they model and predict the future impact of this increase.

? Optional Activity 6.1.5.1

Carbon is present in the atmosphere as

a. carbon dioxide
b. carbonate ion
c. carbon dust
d. carbon monoxide

Answer

a. carbon dioxide

The Nitrogen Cycle

Getting nitrogen into the living world is difficult. Plants and phytoplankton are not equipped to incorporate nitrogen from the atmosphere due to its chemistry, even though this molecule comprises approximately 78 percent of the atmosphere. Nitrogen enters the living world via free-living and symbiotic bacteria, which incorporate nitrogen into their macromolecules through nitrogen fixation (conversion of N_2 into organic molecules) (see Unit 3.4.2). Cyanobacteria live in most aquatic ecosystems where sunlight is present; they play a key role in nitrogen fixation. Cyanobacteria are able to use inorganic sources of nitrogen to "fix" nitrogen. *Rhizobium* bacteria live symbiotically in the root nodules of legumes (such as peas, beans, and peanuts) and provide them with the organic nitrogen they need. Free-living bacteria, such as *Azotobacter*, are also important nitrogen fixers.

Organic nitrogen is especially important to the study of ecosystem dynamics since many ecosystem processes, such as primary production and decomposition, are limited by the available supply of nitrogen. As shown in Figure 6.1.5.5, the nitrogen that enters living systems by nitrogen fixation is successively converted from organic nitrogen back into nitrogen gas by bacteria. This process occurs in three steps in terrestrial systems: ammonification, nitrification, and denitrification. First, the ammonification process converts nitrogenous waste from living animals or from the remains of dead animals into ammonium (NH_4^+) by certain bacteria and fungi. Second, the ammonium is converted to nitrites (NO_2^-) by bacteria, such as *Nitrosomonas*, through nitrification.

Subsequently, nitrites are converted to nitrates (NO_3^-) by similar organisms. Third, the process of denitrification occurs, whereby bacteria, such as *Pseudomonas* and *Clostridium*, convert the nitrates into nitrogen gas, allowing it to re-enter the atmosphere.

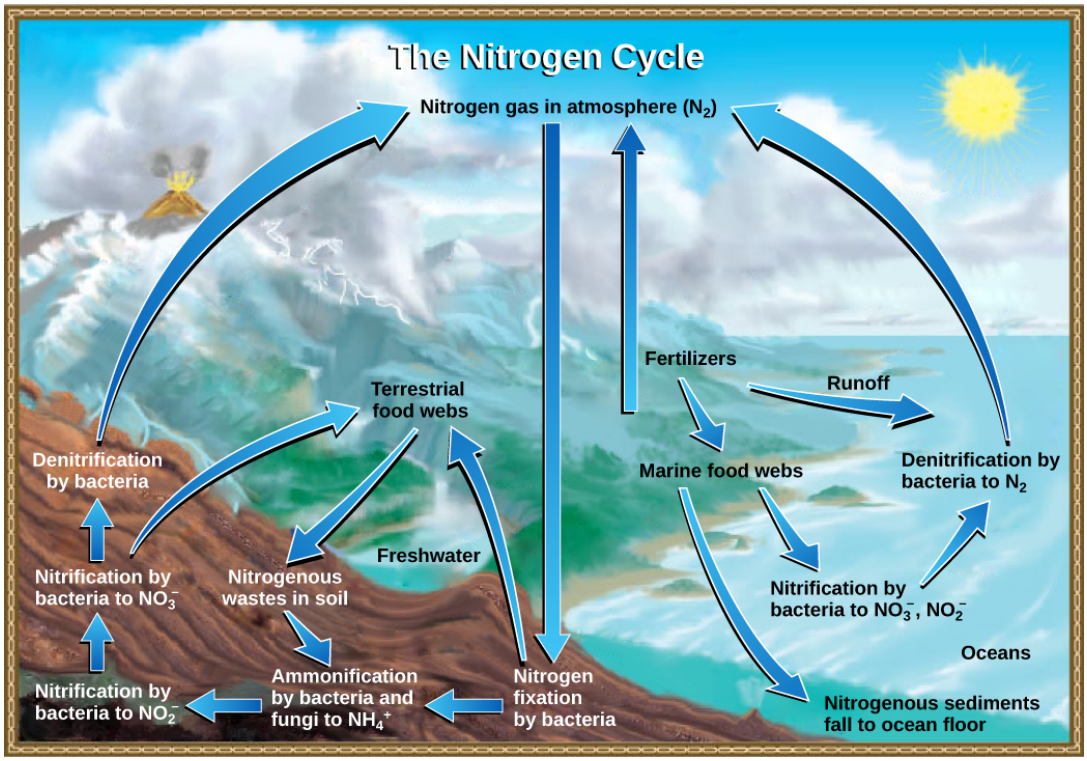


Figure 6.1.5.5: Nitrogen enters the living world from the atmosphere via nitrogen-fixing bacteria. This nitrogen and nitrogenous waste from animals is then processed back into gaseous nitrogen by soil bacteria, which also supply terrestrial food webs with the organic nitrogen they need. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

? Optional Activity 6.1.5.2

Which of the following statements about the nitrogen cycle is false?

A. Ammonification converts organic nitrogenous matter from living organisms into ammonium (NH_4^+).
B. Denitrification by bacteria converts nitrates (NO_3^-) to nitrogen gas (N_2).
C. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).
D. Nitrogen fixing bacteria convert nitrogen gas (N_2) into organic compounds.

Answer

C. Nitrification by bacteria converts nitrates (NO_3^-) to nitrites (NO_2^-).

Human activity can release nitrogen into the environment by two primary means: the combustion of fossil fuels, which releases different nitrogen oxides, and by the use of artificial fertilizers in agriculture, which are then washed into lakes, streams, and rivers by surface runoff. Atmospheric nitrogen is associated with several effects on Earth's ecosystems including the production of acid rain (as nitric acid, HNO_3) and greenhouse gas (as nitrous oxide, N_2O) potentially causing climate change. A major effect from fertilizer runoff is saltwater and freshwater eutrophication, a process whereby nutrient runoff causes the excess growth of microorganisms, depleting dissolved oxygen levels and killing ecosystem fauna.

A similar process occurs in the marine nitrogen cycle, where the ammonification, nitrification, and denitrification processes are performed by marine bacteria. Some of this nitrogen falls to the ocean floor as sediment, which can then be moved to land in geologic time by uplift of the Earth's surface and thereby incorporated into terrestrial rock. Although the movement of nitrogen from rock directly into living systems has been traditionally seen as insignificant compared with nitrogen fixed from the

atmosphere, a recent study showed that this process may indeed be significant and should be included in any study of the global nitrogen cycle.[1]

The Phosphorus Cycle

Phosphorus is an essential nutrient for living processes; it is a major component of nucleic acid and phospholipids, and, as calcium phosphate, makes up the supportive components of our bones. Phosphorus is often the limiting nutrient (necessary for growth) in aquatic ecosystems (Figure 6.1.5.6).

Phosphorus occurs in nature as the phosphate ion (PO_4^{3-}). In addition to phosphate runoff as a result of human activity, natural surface runoff occurs when it is leached, or chemically pulled, from phosphate-containing rock by weathering, thus sending phosphates into rivers, lakes, and the ocean. This rock has its origins in the ocean. Phosphate-containing ocean sediments form primarily from the bodies of ocean organisms and from their excretions. However, in remote regions, volcanic ash, aerosols, and mineral dust may also be significant phosphate sources. This sediment then is moved to land over geologic time by the uplifting of areas of the Earth's surface.

Phosphorus is also reciprocally exchanged between phosphate dissolved in the ocean and marine ecosystems. The movement of phosphate from the ocean to the land and through the soil is extremely slow, with the average phosphate ion having an oceanic residence time between 20,000 and 100,000 years.

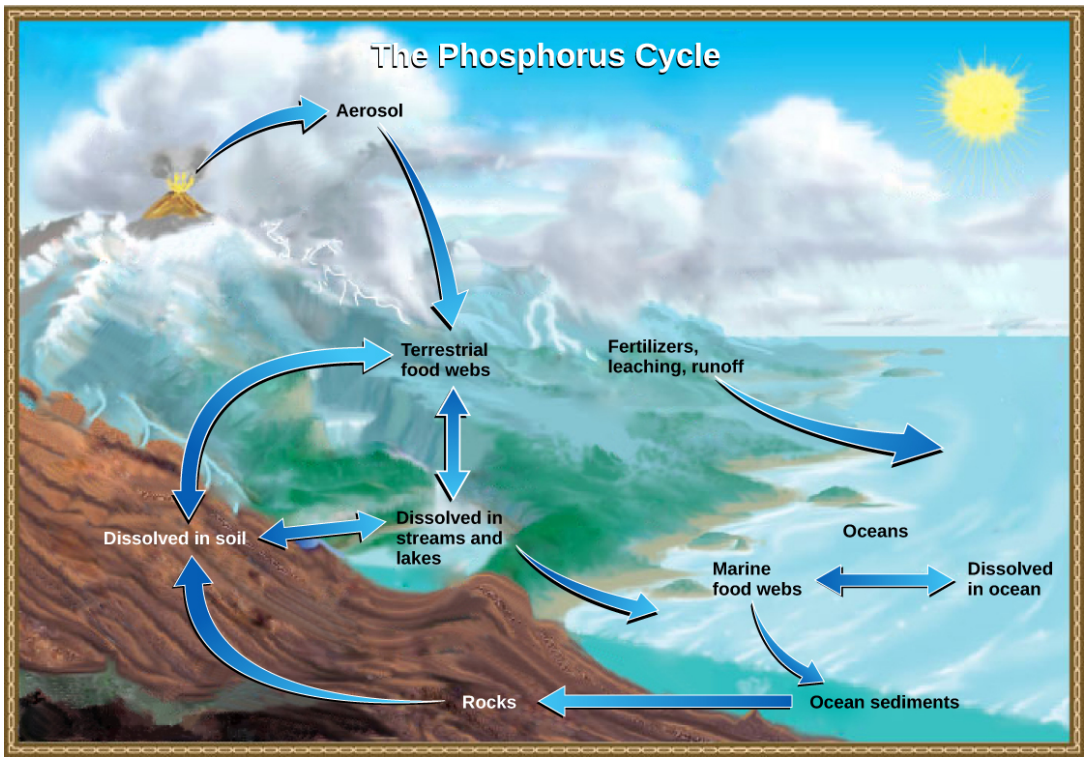


Figure 6.1.5.6: In nature, phosphorus exists as the phosphate ion (PO_4^{3-}). Weathering of rocks and volcanic activity releases phosphate into the soil, water, and air, where it becomes available to terrestrial food webs. Phosphate enters the oceans via surface runoff, groundwater flow, and river flow. Phosphate dissolved in ocean water cycles into marine food webs. Some phosphate from the marine food webs falls to the ocean floor, where it forms sediment. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

Excess phosphorus and nitrogen that enters these ecosystems from fertilizer runoff and from sewage causes excessive growth of microorganisms and depletes the dissolved oxygen, which leads to the death of many ecosystem fauna, such as shellfish and finfish. This process is responsible for dead zones in lakes and at the mouths of many major rivers (Figure 6.1.5.7).

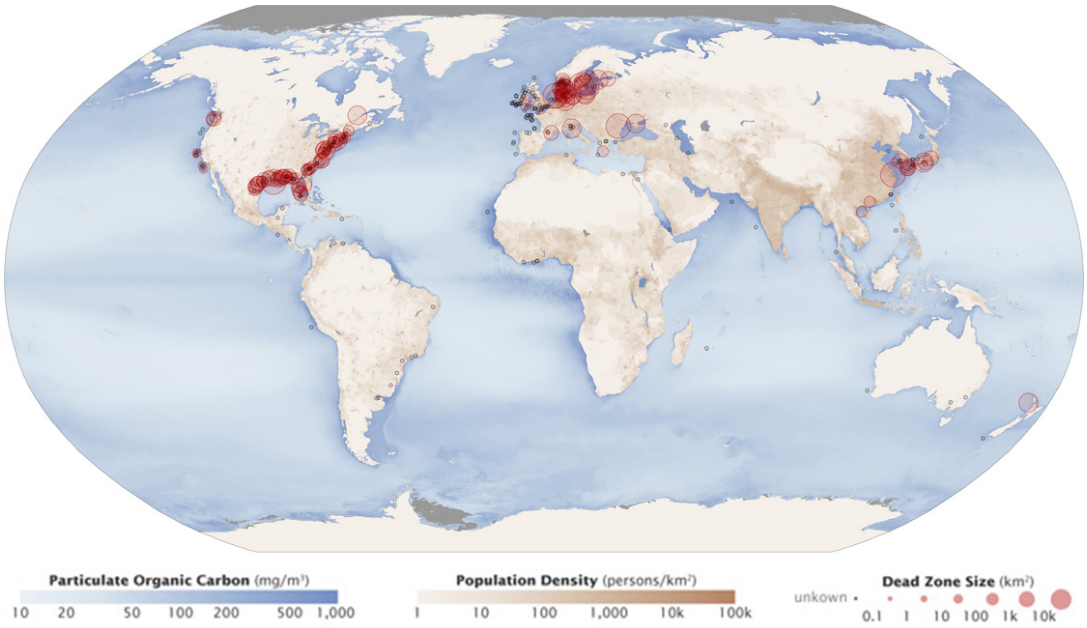
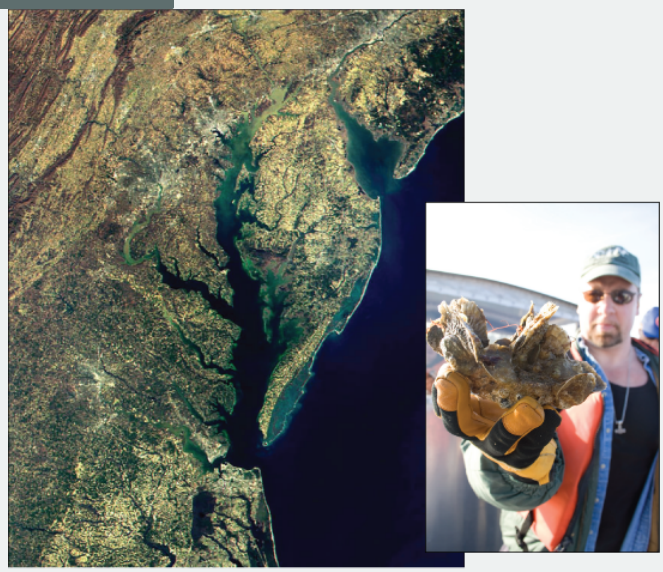


Figure 6.1.5.7: Dead zones occur when phosphorus and nitrogen from fertilizers cause excessive growth of microorganisms, which depletes oxygen and kills fauna. Worldwide, large dead zones are found in coastal areas of high population density. (credit: NASA Earth Observatory)

A **dead zone** is an area within a freshwater or marine ecosystem where large areas are depleted of their normal flora and fauna; these zones can be caused by eutrophication, oil spills, dumping of toxic chemicals, and other human activities. The number of dead zones has been increasing for several years, and more than 400 of these zones were present as of 2008. One of the worst dead zones is off the coast of the United States in the Gulf of Mexico, where fertilizer runoff from the Mississippi River basin has created a dead zone of over 21,919 km^2. Phosphate and nitrate runoff from fertilizers also negatively affect several lake and bay ecosystems including the Chesapeake Bay in the eastern United States (Figure 6.1.5.8).

Everyday Connection: Chesapeake Bay



(a) (b)

Figure 6.1.5.8: This (a) satellite image shows the Chesapeake Bay, an ecosystem affected by phosphate and nitrate runoff. A (b) member of the Army Corps of Engineers holds a clump of oysters being used as a part of the oyster restoration effort in the bay. (credit a: modification of work by NASA/MODIS; credit b: modification of work by U.S. Army)

The Chesapeake Bay has long been valued as one of the most scenic areas in the United States; it is now in distress and is recognized as a declining ecosystem. In the 1970s, the Chesapeake Bay was one of the first ecosystems to have identified dead zones, which continue to kill many fish and bottom-dwelling species, such as clams, oysters, and worms. Several species have declined in the Chesapeake Bay due to surface water runoff containing excess nutrients from artificial fertilizer used on land. The source of the fertilizers (with high nitrogen and phosphate content) is not limited to agricultural practices. There are many nearby urban areas and more than 150 rivers and streams empty into the bay that are carrying fertilizer runoff from lawns and gardens. Thus, the decline of the Chesapeake Bay is a complex issue and requires the cooperation of industry, agriculture, and everyday homeowners.

Of particular interest to conservationists is the oyster population; it is estimated that more than 80,937 hectares of oyster reefs existed in the bay in the 1700s, but that number has now declined to only 14,569 hectares. Oyster harvesting was once a major industry for Chesapeake Bay, but it declined 88 percent between 1982 and 2007. This decline was due not only to fertilizer runoff and dead zones but also to overharvesting. Oysters require a certain minimum population density because they must be in close proximity to reproduce. Human activity has altered the oyster population and locations, greatly disrupting the ecosystem.

The restoration of the oyster population in the Chesapeake Bay has been ongoing for several years with mixed success. Not only do many people find oysters good to eat, but they also clean up the bay. Oysters are filter feeders, and as they eat, they clean the water around them. In the 1700s, it was estimated that it took only a few days for the oyster population to filter the entire volume of the bay. Today, with changed water conditions, it is estimated that the present population would take nearly a year to do the same job.

Restoration efforts have been ongoing for several years by non-profit organizations, such as the Chesapeake Bay Foundation. The restoration goal is to find a way to increase population density so the oysters can reproduce more efficiently. Many disease-resistant varieties (developed at the Virginia Institute of Marine Science for the College of William and Mary) are now available and have been used in the construction of experimental oyster reefs. Efforts to clean and restore the bay by Virginia and Delaware have been hampered because much of the pollution entering the bay comes from other states, which stresses the need for inter-state cooperation to gain successful restoration.

The new, hearty oyster strains have also spawned a new and economically viable industry—oyster aquaculture—which not only supplies oysters for food and profit, but also has the added benefit of cleaning the bay.

Learn about the ecology of *natural* dead zones in the Saanich Inlet in British Columbia here: https://www.uvic.ca/science/home/news/archive/saanich%20inlet%20project.php

The Sulfur Cycle

Sulfur is an essential element for the macromolecules of living things. As a part of the amino acid cysteine, it is involved in the formation of disulfide bonds within proteins, which help to determine their 3-D folding patterns, and hence their functions. As shown in Figure 6.1.5.9, sulfur cycles between the oceans, land, and atmosphere. Atmospheric sulfur is found in the form of sulfur dioxide (SO_2) and enters the atmosphere in three ways: from the decomposition of organic molecules, from volcanic activity and geothermal vents, and from the burning of fossil fuels by humans.

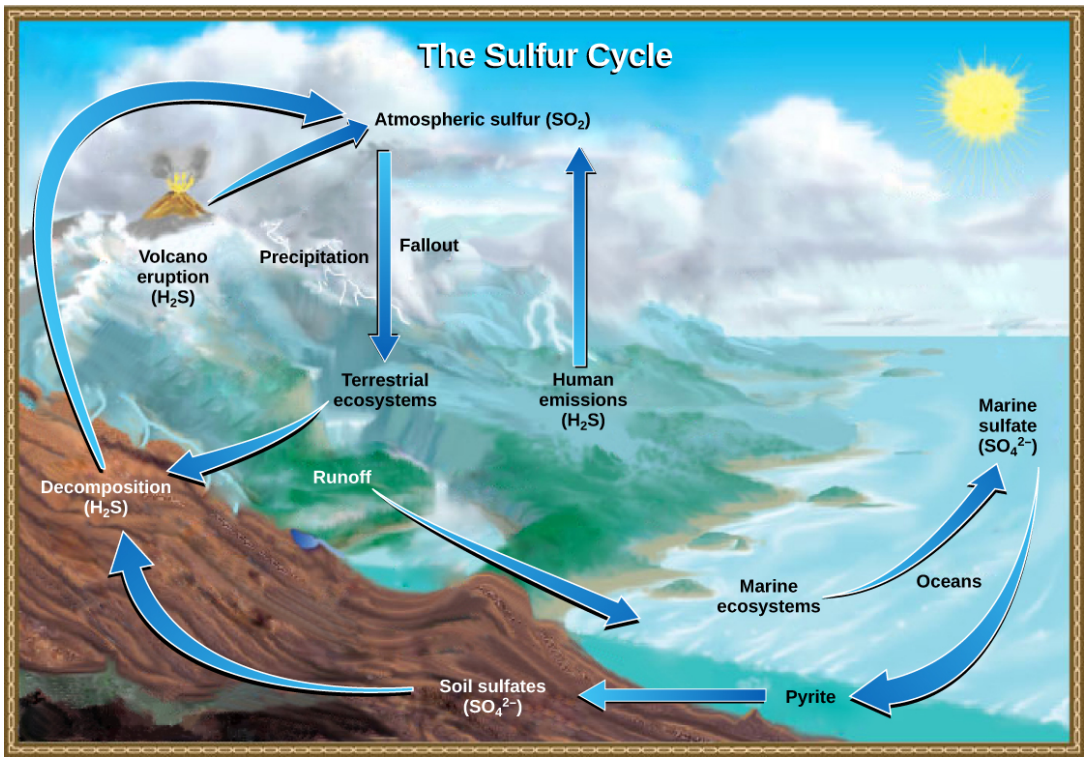


Figure 6.1.5.9: Sulfur dioxide from the atmosphere becomes available to terrestrial and marine ecosystems when it is dissolved in precipitation as weak sulfuric acid or when it falls directly to the Earth as fallout. Weathering of rocks also makes sulfates available to terrestrial ecosystems. Decomposition of living organisms returns sulfates to the ocean, soil and atmosphere. (credit: modification of work by John M. Evans and Howard Perlman, USGS)

On land, sulfur is deposited in four major ways: precipitation, direct fallout from the atmosphere, rock weathering, and geothermal vents (Figure 6.1.5.10). Atmospheric sulfur is found in the form of sulfur dioxide (SO_2), and as rain falls through the atmosphere, sulfur is dissolved in the form of weak sulfuric acid (H_2SO_4). Sulfur can also fall directly from the atmosphere in a process called **fallout**.

Also, the weathering of sulfur-containing rocks releases sulfur into the soil. These rocks originate from ocean sediments that are moved to land by the geologic uplifting of ocean sediments. Terrestrial ecosystems can then make use of these soil sulfates (SO_4^{2-}), and upon the death and decomposition of these organisms, release the sulfur back into the atmosphere as hydrogen sulfide (H_2S) gas. Sulfur enters the ocean via runoff from land, from atmospheric fallout, and from underwater geothermal vents. Some ecosystems rely on chemoautotrophs using sulfur as a biological energy source. This sulfur then supports marine ecosystems in the form of sulfates.



Figure 6.1.5.10: At this sulfur vent in Lassen Volcanic National Park in northeastern California, the yellowish sulfur deposits are visible near the mouth of the vent.

Human activities have played a major role in altering the balance of the global sulfur cycle. The burning of large quantities of fossil fuels, especially coal, releases larger amounts of hydrogen sulfide gas into the atmosphere. As rain falls through this gas, it creates the phenomenon known as acid rain. **Acid rain** is corrosive rain caused by rainwater falling to the ground through sulfur dioxide gas, turning it into weak sulfuric acid, which causes damage to aquatic ecosystems. Acid rain damages the natural environment by lowering the pH of lakes, which kills many of the resident fauna; it also affects the man-made environment through the chemical degradation of buildings. For example, many marble monuments, such as the Lincoln Memorial in Washington, DC, have suffered significant damage from acid rain over the years. These examples show the wide-ranging effects of human activities on our environment and the challenges that remain for our future.

? Optional Activity 6.1.5.3

The average time a molecule spends in its reservoir is known as _____.

a. residence time
b. restriction time
c. resilience time
d. storage time

Answer

a. residence time

? Optional Activity 6.1.5.4

The process whereby nitrogen is brought into organic molecules is called _____.

a. ammonification
b. denitrification
c. nitrogen fixation
d. nitrogen cycling

Answer

c. nitrogen fixation

Footnotes

1. 1 Scott L. Morford, Benjamin Z. Houlton, and Randy A. Dahlgren, “Increased Forest Ecosystem Carbon and Nitrogen Storage from Nitrogen Rich Bedrock,” *Nature* 477, no. 7362 (2011): 78–81.

This page titled 6.1.5: Biogeochemical Cycles is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **46.3: Biogeochemical Cycles** by OpenStax is licensed CC BY 4.0.

6.1.6: Biogeography

Biogeography

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 30 minutes.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Define biogeography
- List and describe abiotic factors that affect the global distribution of plant and animal species
- Compare the impact of abiotic forces on aquatic and terrestrial environments
- Summarize the effects of abiotic factors on net primary productivity

Introduction

As noted in Unit 2, **biogeography** is the study of the geographic distribution of living things and the abiotic factors that affect their distribution. Abiotic factors such as temperature and rainfall vary based mainly on latitude and elevation. As these abiotic factors change, the composition of plant and animal communities also changes. For example, if you were to begin a journey at the equator and walk north, you would notice gradual changes in plant communities. At the beginning of your journey, you would see tropical wet forests with broad-leaved evergreen trees, which are characteristic of plant communities found near the equator. As you continued to travel north, you would see these broad-leaved evergreen plants eventually give rise to seasonally dry forests with scattered trees. You would also begin to notice changes in temperature and moisture. At about 30 degrees north, these forests would give way to deserts, which are characterized by low precipitation.

Moving farther north, you would see that deserts are replaced by grasslands or prairies. Eventually, grasslands are replaced by deciduous temperate forests. These deciduous forests give way to the boreal forests found in the subarctic, the area south of the Arctic Circle. Finally, you would reach the Arctic tundra, which is found at the most northern latitudes. This trek north reveals gradual changes in both climate and the types of organisms that have adapted to environmental factors associated with ecosystems found at different latitudes. However, different ecosystems exist at the same latitude due in part to abiotic factors such as jet streams, the Gulf Stream, and ocean currents. If you were to hike up a mountain, the changes you would see in the vegetation would parallel those as you move to higher latitudes.

Ecologists who study biogeography examine patterns of species distribution. No species exists everywhere; for example, the Venus flytrap is endemic to a small area in North and South Carolina. An **endemic** species is one that is naturally found only in a specific geographic area that is usually restricted in size. Other species are generalists: species that live in a wide variety of geographic areas; the raccoon, for example, is native to most of North and Central America.

Species distribution patterns are based on biotic and abiotic factors and their influences during the very long periods of time required for species evolution; therefore, early studies of biogeography were closely linked to the emergence of evolutionary thinking in the eighteenth century. Some of the most distinctive assemblages of plants and animals occur in regions that have been physically separated for millions of years by geographic barriers. Biologists estimate that Australia, for example, has between 600,000 and 700,000 species of plants and animals. Approximately 3/4 of living plant and mammal species are endemic species found solely in Australia (Figure 6.1.6.1).



(a) (b)

Figure 6.1.6.1: Australia is home to many endemic species. The (a) wallaby (*Wallabia bicolor*), a medium-sized member of the kangaroo family, is a pouched mammal, or marsupial. The (b) echidna (*Tachyglossus aculeatus*) is an egg-laying mammal. (credit a: modification of work by Derrick Coetzee; credit b: modification of work by Allan Whittome)

Sometimes ecologists discover unique patterns of species distribution by determining where species are *not* found. Hawaii, for example, has no native land species of reptiles or amphibians, and has only one native terrestrial mammal, the hoary bat. Most of New Guinea, as another example, lacks placental mammals.

Plants can be endemic or generalists: endemic plants are found only in specific regions of the Earth, while generalists are found in many regions. Isolated land masses—such as Australia, Hawaii, and Madagascar—often have large numbers of endemic plant species. Some of these plants are endangered due to human activity. The forest gardenia (*Gardenia brighamii*), for instance, is endemic to Hawaii; only an estimated 15–20 trees are thought to exist (Figure 6.1.6.2).



Figure 6.1.6.2: Listed as federally endangered, the forest gardenia (*Gardenia brighamii*) is a small tree with distinctive flowers. It is found only in five of the Hawaiian Islands in small populations consisting of a few individual specimens. (credit: Forest & Kim Starr)

Energy Sources

Energy from the sun is captured by plants, algae, cyanobacteria, and photosynthetic protists. These organisms convert solar energy into the chemical energy needed by all living things. Light availability can be an important force directly affecting the evolution of adaptations in photoautotrophs. For instance, plants in the understory of a temperate forest are shaded when the trees above them in the canopy completely leaf out in the late spring. Not surprisingly, understory plants have adaptations to successfully capture available light. One such adaptation is the rapid growth of spring ephemeral plants such as the springbeauty (*Claytonia virginica*) (Figure 6.1.6.3). These spring flowers achieve much of their growth and finish their life cycle (reproduce) early in the season before the trees in the canopy develop leaves.



Figure 6.1.6.3: The springbeauty (*Claytonia virginica*) is an ephemeral spring plant that flowers early in the spring to avoid competing with larger forest trees for sunlight. (credit: John Beetham)

In aquatic ecosystems, the availability of light may be limited because sunlight is absorbed by water, plants, suspended particles, and resident microorganisms. Toward the bottom of a lake, pond, or ocean, there is a zone that light cannot reach. Photosynthesis cannot take place there and, as a result, a number of adaptations have evolved that enable living things to survive without light. For instance, aquatic plants have photosynthetic tissue near the surface of the water; for example, think of the broad, floating leaves of a water lily—water lilies cannot survive without light. In environments such as hydrothermal vents, some bacteria extract energy from inorganic chemicals because there is no light for photosynthesis.

The availability of nutrients in aquatic systems is also an important aspect of energy or photosynthesis. Many organisms sink to the bottom of the ocean when they die in the open water; when this occurs, the energy found in that living organism is sequestered for some time unless ocean upwelling occurs. **Ocean upwelling** is the rising of deep ocean waters that occurs when prevailing winds blow along surface waters near a coastline (Figure 6.1.6.4). As the wind pushes ocean waters offshore, water from the bottom of the ocean moves up to replace this water. As a result, the nutrients once contained in dead organisms become available for reuse by other living organisms.

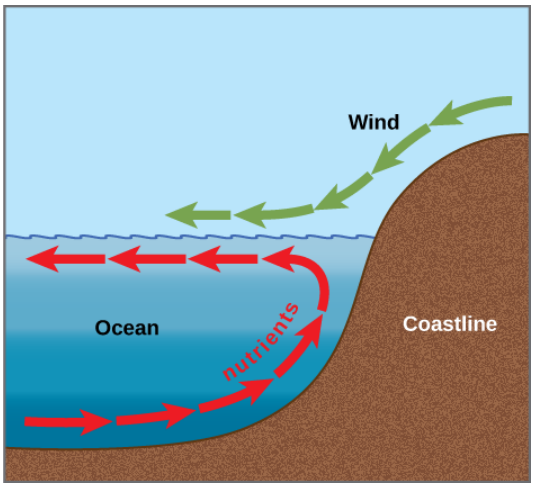


Figure 6.1.6.4: Ocean upwelling is an important process that recycles nutrients and energy in the ocean. As wind (green arrows) pushes offshore, it causes water from the ocean bottom (red arrows) to move to the surface, bringing up nutrients from the ocean depths. It is prevalent on the west coasts of continents, like in BC, and important to those ocean ecosystems and the maintenance of its biodiversity.

In freshwater systems, the recycling of nutrients occurs in response to air temperature changes. The nutrients at the bottom of lakes are recycled twice each year: in the spring and fall turnover. Spring and fall **turnovers** are seasonal processes that recycle nutrients and oxygen from the bottom of a freshwater ecosystem to the top of a body of water (Figure 6.1.6.5). These turnovers are caused by the formation of a **thermocline**: a layer of water with a temperature that is significantly different from that of the surrounding layers. In wintertime, the surface of lakes found in many northern regions is frozen. However, the water under the ice is slightly

warmer, and the water at the bottom of the lake is warmer yet at 4°C to 5°C. Water is densest at 4°C; therefore, the deepest water is also the densest. The deepest water is oxygen-poor because the decomposition of organic material at the bottom of the lake uses up available oxygen that cannot be replaced by means of oxygen diffusion into the water due to the surface ice layer.

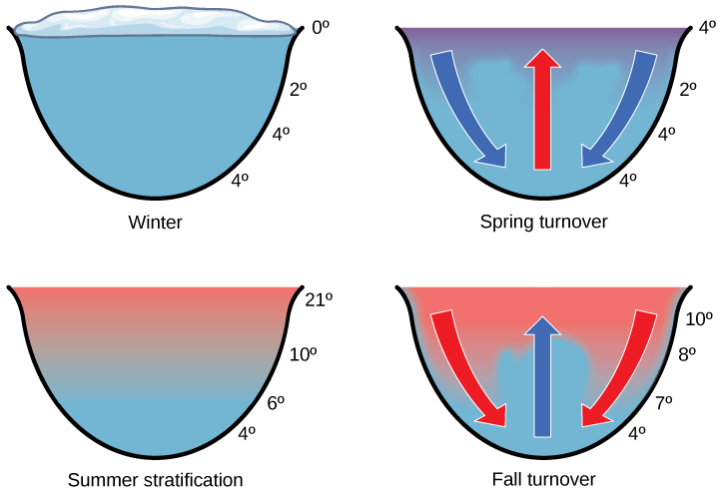


Figure 6.1.6.5: The spring and fall turnovers are important processes in freshwater lakes that act to move the nutrients and oxygen at the bottom of deep lakes to the top. Turnover occurs because water has a maximum density at 4 °C. Surface water temperature changes as the seasons progress, and denser water sinks.

In springtime, air temperatures increase and surface ice melts. When the temperature of the surface water begins to reach 4°C, the water becomes heavier and sinks to the bottom. The water at the bottom of the lake is then displaced by the heavier surface water and, thus, rises to the top. As that water rises to the top, the sediments and nutrients from the lake bottom are brought along with it. During the summer months, the lake water stratifies, or forms layers, with the warmest water at the lake surface.

As air temperatures drop in the fall, the temperature of the lake water cools to 4°C; therefore, this causes fall turnover as the heavy cold water sinks and displaces the water at the bottom. The oxygen-rich water at the surface of the lake then moves to the bottom of the lake, while the nutrients at the bottom of the lake rise to the surface (Figure 6.1.6.5). During the winter, the oxygen at the bottom of the lake is used by decomposers and other organisms requiring oxygen, such as fish.

? Optional Activity 6.1.6.1

Figure 6.1.6.5: How might turnover in tropical lakes differ from turnover in lakes that exist in temperate regions?

Answer

Tropical lakes don’t freeze, so they don’t undergo spring turnover in the same way temperate lakes do. However, stratification does occur, as well as seasonal turnover.

Temperature

Temperature affects the physiology of living things as well as the density and state of water. Temperature exerts an important influence on organisms because few living things can survive at temperatures below 0°C due to metabolic constraints. It is also rare for living things to survive at temperatures exceeding 45°C; this is a reflection of evolutionary response to typical temperatures. Enzymes are most efficient within a narrow and specific range of temperatures; below that chemical reactions happen too slowly to support most life and biomolecules become rigid, above that enzyme degradation can occur. Therefore, organisms either must maintain an internal temperature or they must inhabit an environment that will keep the body within a temperature range that supports metabolism. Some animals have adapted to enable their bodies to survive significant temperature fluctuations, such as seen in hibernation or reptilian torpor. Similarly, some bacteria are extremophiles, living in extremely hot temperatures such as geysers.

Temperature can limit the distribution of living things. Animals faced with temperature fluctuations may respond with adaptations, such as migration, in order to survive. **Migration**, the movement from one place to another, is an adaptation found in many

animals, including many that inhabit seasonally cold climates. Migration solves problems related to temperature, locating food, and finding a mate. In migration, for instance, the Arctic tern (*Sterna paradisaea*) makes a 40,000 km round trip flight each year between its feeding grounds in the southern hemisphere and its breeding grounds in the Arctic Ocean. Monarch butterflies (*Danaus plexippus*) live in the eastern United States in the warmer months and migrate to Mexico and southeastern Canada in the wintertime. Some species of mammals also make migratory forays. Reindeer (*Rangifer tarandus*) travel about 5,000 km each year to find food. Amphibians and reptiles are more limited in their distribution because they lack migratory ability. Not all animals that can migrate do so: migration carries risk and comes at a high energy cost.

Some animals hibernate or estivate to survive hostile temperatures. Hibernation enables animals to survive cold conditions, and estivation allows animals to survive the hostile conditions of a hot, dry climate. Animals that hibernate or estivate enter a state known as torpor: a condition in which their metabolic rate is significantly lowered. This enables the animal to wait until its environment better supports its survival. Some amphibians, such as the wood frog (*Rana sylvatica*), have an antifreeze-like chemical in their cells, which retains the cells' integrity and prevents them from bursting when temperatures fall below 0°C.

Water

Water is required by all living things because it is critical for cellular processes. Since terrestrial organisms lose water to the environment by simple diffusion, they have evolved many adaptations to retain water.

- Plants have a number of interesting features on their leaves, such as leaf hairs and a waxy cuticle, that serve to decrease the rate of water loss via transpiration.
- Freshwater organisms are surrounded by water and are constantly in danger of having water rush into their cells because of osmosis. Many adaptations of organisms living in freshwater environments have evolved to ensure that solute concentrations in their bodies remain within appropriate levels. One such adaptation is the excretion of dilute urine.
- Marine organisms are surrounded by water with a higher solute concentration than the organism and, thus, are in danger of losing water to the environment because of osmosis. These organisms have morphological and physiological adaptations to retain water and release solutes into the environment. For example, marine iguanas (*Amblyrhynchus cristatus*), sneeze out water vapor that is high in salt in order to maintain solute concentrations within an acceptable range while swimming in the ocean and eating marine plants.

Inorganic Nutrients and Soil

Inorganic nutrients, such as nitrogen and phosphorus, are important in the distribution and abundance of living things. Plants obtain these inorganic nutrients from the soil when water moves into the plant through the roots. Therefore, soil structure (particle size of soil components), soil pH, and soil nutrient content play an important role in the distribution of plants. Aquatic autotrophs such as algae, aquatic plants, and cyanobacteria absorb nutrients directly from the water.

Heterotrophs such as many protists, animals, and fungi obtain inorganic nutrients from the organisms they consume. Therefore, heterotroph distributions are related to the distribution of what they eat. In some cases, heterotrophs will follow their food resource as it moves through the environment.

Other Abiotic Factors

Some abiotic factors, such as gasses like oxygen and carbon dioxide, are important in aquatic ecosystems as well as terrestrial environments. Terrestrial organisms obtain needed gasses directly from the air. Gas availability can be an issue for organisms living at very high elevations where there are fewer molecules of oxygen in the air.

Aquatic organisms obtain necessary gasses from those dissolved in the water. In aquatic systems, the concentration of dissolved gasses is related to water temperature and the speed at which the water moves. Cold water has more dissolved gasses than warmer water. In addition, salinity, currents, and tides can be important abiotic factors in aquatic ecosystems.

For terrestrial systems, wind can be an important abiotic factor because it influences the rate of evaporation and transpiration. The physical force of wind is also important because it can move soil, water, or other abiotic factors, as well as an ecosystem's organisms.

Fire is another terrestrial factor that can be an important agent of disturbance in terrestrial ecosystems. Some organisms are adapted to fire and, thus, require the high heat associated with fire to complete a part of their life cycle. For example, the jack pine (*Pinus banksiana*), a coniferous tree, requires heat from fire for its seed cones to open (Figure 6.1.6.6). Through the burning of pine needles, fire adds nitrogen to the soil and limits competition by destroying undergrowth.



Figure 6.1.6.6: The mature cones of the jack pine (*Pinus banksiana*) open only when exposed to high temperatures, such as during a forest fire. Fire is likely to kill most vegetation, so a seedling that germinates after a fire is more likely to receive ample sunlight than one that germinates under normal conditions. (credit: USDA)

Abiotic Factors Influencing Plant Growth

Temperature and moisture are important influences on plant production (primary productivity) and the amount of organic matter available as food (net primary productivity). Net primary productivity is an important variable when considering differences in biomes. Very productive biomes have a high level of aboveground biomass. Aboveground biomass produces several important resources for other living things, including habitat and food.

Annual biomass production is directly related to the abiotic components of the environment. Environments with the greatest amount of biomass have conditions in which photosynthesis, plant growth, and the resulting net primary productivity are optimized. The climate of these areas is warm and wet. Photosynthesis can proceed at a high rate, enzymes work efficiently, and stomata can remain open without the risk of excessive transpiration; together, these factors lead to the maximal amount of carbon dioxide (CO_2) moving into the plant, resulting in high biomass production. Conversely, dry and/or cold environments have lower photosynthetic rates and therefore less biomass. Heterotrophs living in these environments will then be affected by the decrease in available food.

? Optional Activity 6.1.6.2

Which of the following is a biotic factor?

a. disease-causing microbe
b. temperature
c. soil particle size
d. wind

Answer

a. disease-causing microbe

This page titled 6.1.6: Biogeography is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **44.2: Biogeography** by OpenStax is licensed CC BY 4.0.

6.1.S: Chapter Resources

Summary

Ecosystems exist underground, on land, at sea, and in the air. Organisms in an ecosystem acquire energy in a variety of ways, which is transferred between trophic levels as the energy flows from the base to the top of the food web, with energy being lost at each transfer. Mineral nutrients are cycled through ecosystems and their environment. Of particular importance are water, carbon, nitrogen, phosphorus, and sulfur. All of these cycles have major impacts on ecosystem structure and function. Ecosystems have been damaged by a variety of human activities that alter the natural biogeochemical cycles due to pollution, oil spills, and events causing global climate change. The health of the biosphere depends on understanding these cycles and how to protect the environment from irreversible damage. Earth has terrestrial and aquatic biomes. There are eight major terrestrial biomes: tropical rainforests, savannas, subtropical deserts, chaparral, temperate grasslands, temperate forests, boreal forests, and Arctic tundra. Temperature and precipitation, and variations in both, are key abiotic factors that shape the composition of animal and plant communities in terrestrial biomes. Sunlight is an important factor in bodies of water, especially those that are very deep, because of the role of photosynthesis in sustaining certain organisms. Other important factors include temperature, water movement, and salt content. Aquatic biomes include both freshwater and marine environments. Like terrestrial biomes, aquatic biomes are influenced by abiotic factors. In the case of aquatic biomes the abiotic factors include light, temperature, flow regime, and dissolved solids.

Review Questions

1. Secondary consumers would eat which one following?
   A. Producers
   B. Plants
   C. Herbivores
   D. Carnivores
   E. Tertiary consumers
2. If you are concerned about biomagnification of toxins, which one of the following would you most want to avoid eating?
   A. Tuna (tertiary consumer)
   B. Seaweed (producer)
   C. Urchin (primary consumer)
   D. Sculpin (secondary consumer)
   E. Any photoautotroph
3. Which one of the following is not a biogeochemical cycle?
   A. Energy cycle
   B. Nitrogen cycle
   C. Carbon cycle
   D. Phosphorus cycle
   E. Water cycle
4. Which one of the following would not increase the amount of water in the atmosphere?
   A. Evaporation
   B. Transpiration
   C. Sublimation
   D. Infiltration
   E. Evapotranspiration
5. Which one of the following processes would remove nitrates from contaminated water by converting it into nitrogen gas?
   A. Nitrification
   B. Nitrogen fixation
   C. Denitrification
   D. Assimilation
   E. Ammonification

6. What do deserts and chaparral have in common?
   A. Dry and hot summers
   B. Dominated by abundant evergreen shrubs
   C. Both can exist as either the hot or cold variety
   D. Very small amounts of rainfall consistently throughout the year
   E. Very low biodiversity
7. Which one of the following would most likely live within the benthic realm of the ocean?
   A. Squid
   B. Tuna
   C. Phytoplankton
   D. Marine worm
   E. Shark
8. What two variables most strongly contribute to the type of biome that exists in a particular area?
   A. Precipitation levels and temperature
   B. Type of producers and density of herbivores
   C. Amount of sunlight and annual rainfall
   D. Soil type and amount of O_2
   E. Distance from ocean and elevation
9. The conversion of nitrogen gas (N_2) into ammonia (NH_3) happens during which specific process?
   A. Ammonification
   B. Dentification
   C. Nitrification
   D. Nitrogenous cycling
   E. Nitrogen fixation
10. Use your knowledge of the relative energy content among trophic levels to answer the following question: A larger human population could be supported if all humans derived their food from which trophic level?
    A. Producers
    B. Primary consumers
    C. Secondary consumers
    D. Tertiary consumers
    E. Quaternary consumers

See Appendix for answers

Attributions

OpenStax College. (2013). *Concepts of biology*. Retrieved from http://cnx.org/contents/b3c1e1d2-839...9a8aafbdd@8.10. OpenStax CNX. Available under Creative Commons Attribution License 3.0 (CC BY 3.0). Modified from Original.

Page attribution: Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0. “Review Questions” is licensed under CC BY 4.0 by Matthew R. Fisher.

This page titled 6.1.S: Chapter Resources is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg via source content that was edited to the style and standards of the LibreTexts platform.

- **3.5: Chapter Resources** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.

CHAPTER OVERVIEW

6.2: Biodiversity and HIPPPOC

Conservation biology is the management of nature and of Earth's biodiversity with the aim of protecting species, their habitats, and ecosystems from excessive rates of extinction and the erosion of biotic interactions. It is an interdisciplinary subject drawing on natural and social sciences and the practice of natural resource management.

Video



This 3-minute video summarizes Unit 5.2.

Question after watching: What areas from the video are you already familiar with? What topics are you unfamiliar with?

6.2.1: Introduction to Biodiversity

6.2.2: Importance of Biodiversity

6.2.3: The Biodiversity Crisis - HIPPPOC

6.2.4: Preserving Biodiversity

6.2.S: Chapter Resources

This page titled 6.2: Biodiversity and HIPPPOC is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

Introduction to Biodiversity

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Define biodiversity
- Explain what is meant by the 'biodiversity crisis'
- Provide examples of anthropogenic extinctions

Introduction

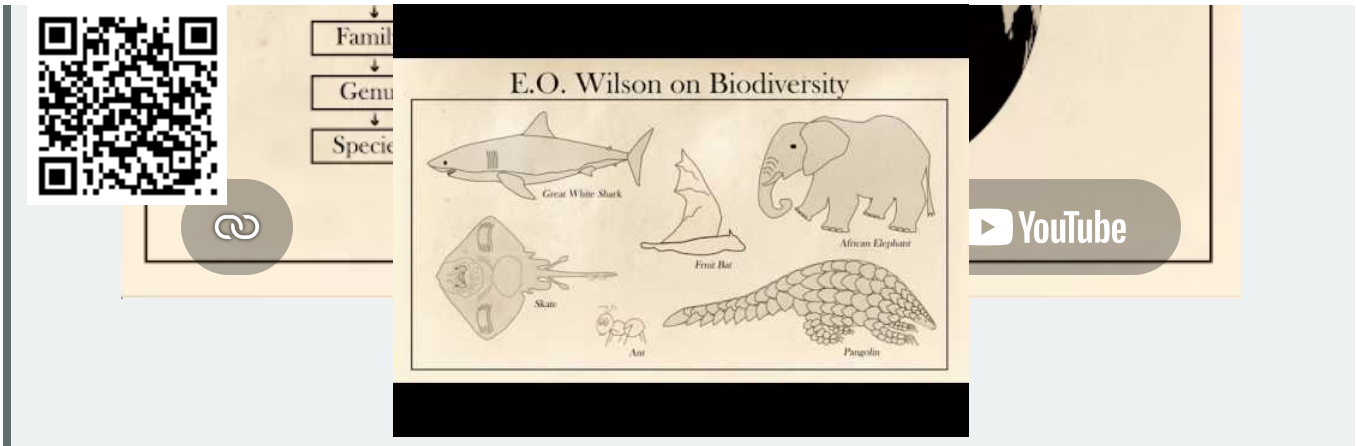
In the 1980s, biologists working in Lake Victoria in Africa discovered one of the most extraordinary products of evolution on the planet. Located in the Great Rift Valley, Lake Victoria (Figure 6.2.1.1) is a large lake about 68,900 km^2 in area (larger than Lake Huron, the second largest of North America's Great Lakes). Biologists were studying species of a family of fish called cichlids. They found that as they sampled for fish in different locations of the lake, they never stopped finding new species, and they identified nearly 500 evolved types of cichlids. But while studying these variations, they quickly discovered that the invasive Nile Perch was destroying the lake's cichlid population, bringing hundreds of cichlid species to extinction with devastating rapidity.



Figure 6.2.1.1: Cichlids are some of the most biodiverse fish on the planet but are also a casualty of devastating biodiversity loss. (credit: modification of work by Rishabh Tatiraju, using NASA World Wind software)

Video





Watch a 1-minute presentation by biologist E.O. Wilson (1929-2021) on the importance of biodiversity.

What is Biodiversity?

Biodiversity is a broad term for biological variety, and it can be measured at a number of organizational levels. Traditionally, ecologists have measured biodiversity by taking into account both the number of species and the number of individuals of each species (known as **relative abundance**). However, biologists are using different measures of biodiversity, including genetic diversity, to help focus efforts to preserve the biologically and technologically important elements of biodiversity.

Species Diversity

Scientists accept that the term biodiversity generally describes the number and kinds of species in a location or on the planet. This is known as **species diversity**. Species can be difficult to define, but most biologists still feel comfortable with the concept and are able to identify and count eukaryotic species in most contexts.

For example, the American Ornithologists' Union lists 2078 species of birds in North and Central America. This is one measure of the bird biodiversity on the continent. More sophisticated measures of diversity take into account the relative abundances of species. An ecologist analyzing a forest with 10 equally common species of trees would note that this first forest is more diverse than a forest that has the same 10 species of trees but where just one of those species makes up 95 percent of the trees.

In addition to these measures of species diversity, biologists have identified alternate measures of biodiversity, some of which are important in planning how to preserve biodiversity.

Genetic Diversity

One alternate concept of biodiversity, **genetic diversity**, is the raw material for evolutionary adaptation in a species and is represented by the variety of genes present within a population. A species' potential to adapt to changing environments or new diseases depends on this genetic diversity. The same is true for higher taxonomic categories. A genus with very different types of species will have more genetic diversity than a genus with species that look alike and have similar ecologies. If there were a choice between one of these genera of species being preserved, the one with the greatest potential for subsequent evolution is the most genetically diverse one. It would be ideal not to have to make such choices, but increasingly this may be the norm.

Beyond ecological importance, genetic diversity has potential benefits for humans as sources of pharmaceuticals, so it provides one way to measure diversity that is important to human health and welfare. Humans have also generated diversity through domestic animals, plants, and fungi. This diversity is suffering losses because of migration, market forces, and increasing globalism in agriculture, especially in heavily populated regions such as China, India, and Indonesia. The human population directly depends on this diversity as a stable food source, and its decline is troubling biologists and agricultural scientists.

Ecosystem Diversity

It is also useful to define **ecosystem diversity**, meaning the number of different ecosystems on the planet or in a given geographic area (Figure 6.2.1.2). Whole ecosystems can disappear even if some of the species might survive by adapting to other ecosystems. The loss of an ecosystem means the loss of interactions between species, the loss of unique features of coadaptation, and the loss of

biological productivity that an ecosystem is able to create. An example of a large, nearly extinct ecosystem in North America are the prairies (Figure 6.2.1.2*b*). Prairies once spanned central North America from the boreal forest in northern Canada down into Mexico. They are now all but gone, replaced by crop fields, pasture lands, and suburban sprawl. Many of the individual species survive but the hugely productive ecosystem as a whole has fallen apart. As a consequence, the most productive agricultural soils on the planet are disappearing or must be maintained at greater expense.



Figure 6.2.1.2: The variety of ecosystems on Earth—from (a) coral reef to (b) prairie—enables a great diversity of species to exist. (credit a: modification of work by Jim Maragos, USFWS; credit b: modification of work by Jim Minnerath, USFWS)

How Many Species?

As of August 2022, taxonomists have described nearly 2.3 million species that share this planet with us. While this total may seem impressive, available evidence suggests that this estimate vastly underestimates the true extent of Earth's biodiversity. In fact, even now, after all the exploration in years gone by, several thousand new species are described each year. Many new discoveries are made by skilled researchers recognizing new species by discerning variation in morphological characters; that includes the discoveries of a new small forest antelope from West Africa and a new species of shark off the coast of Mozambique. New genetic technologies have highlighted that there are many thousands of species yet to be described. Both traditional and genetic techniques rely heavily on the availability of specimens in Natural History Museums collections to help identify and describe new species. A lack of taxonomists and natural history collections in many of the world's most biodiverse countries means there is still a great deal of work to do.

The most exciting and newsworthy discoveries of new species generally involve higher-level taxa, especially living fossils. For example, in 1938, biologists across the world were stunned by the report of a strange fish caught in the Indian Ocean off South Africa. This fish, subsequently named *Latimeria chalumnae*, belongs to a group of marine fishes known as coelacanths that were common in ancient seas but were thought to have gone extinct 65 million years ago. Coelacanths are of interest to evolutionary biologists because they show certain features of muscles and bones in their fins that are comparable to the limbs of the first vertebrates that crawled onto land. Following the initial discovery, coelacanths have been found along Africa's Indian Ocean coast from South Africa to the Comoros and through to Kenya. Unfortunately, the entire coelacanth population, estimated at fewer than 500 individuals, is currently highly threatened because of ongoing fishing pressures.

Although field surveys have proven to be of great importance for discovering new species and populations, perhaps the greatest taxonomic progress has come from advances in genetic analyses which help to separate cryptic species previously lumped under more widespread species. For example, advances in genetic research recently highlighted that the African clawed frog *Xenopus laevis*—a popular model organism in biomedical research—consists of seven distinct species.

Molecular genetics and data processing and storage technologies are maturing to the point where cataloging the planet's species in an accessible way is close to feasible. DNA barcoding is one molecular genetic method, which takes advantage of rapid evolution in a mitochondrial gene present in eukaryotes, except the plants, to identify species using the sequence of portions of the gene. Plants are barcoded using a combination of chloroplast genes. Rapid mass sequencing machines make the molecular genetics portion of the work relatively inexpensive and quick. Computer resources store and make available large volumes of data. Projects are currently underway to use DNA barcoding to catalog museum specimens, which have already been named and studied, as well as testing the method on less studied groups. As of mid-2020, close to 750,000 named species had been barcoded. Early studies suggest there are significant numbers of undescribed species that looked too much like sibling species to previously be recognized as different. These now can be identified with DNA barcoding.

Numerous computer databases now provide information about named species and a framework for adding new species. However, at the present rate of description of new species, it would still take close to 500 years before the complete catalog of life is known. Many, perhaps most, species on the planet do not have that much time given the **anthropogenic**, or human-caused, pressures on species around the world (Unit 5.2.3).

The presence of so many undiscovered species and communities makes precise estimates of species diversity incredibly difficult. Biologists' most recent estimates, combining genetic analysis of well-known groups with mathematical patterns, suggests there are between 1–6 billion distinct species on Earth, of which there are only about 163 million animals and 340 thousand plants. This is obviously much greater than the current catalog of around 2.3 million species.

Anthropogenic Extinctions

A review of the previous five mass extinctions can be found in Unit 3.3. The sixth, or Holocene, mass extinction appears to have begun earlier than previously believed and has mostly to do with the activities of *Homo sapiens*. Since the beginning of the Holocene period, there are numerous recent extinctions of individual species that are recorded in human writings. Most of these are coincident with the expansion of the European colonies since the 1500s.

Recent Extinctions

One of the earlier and popularly known examples is the dodo bird. The dodo bird lived in the forests of Mauritius, an island in the Indian Ocean. The dodo bird became extinct around 1662. It was hunted for its meat by sailors and was easy prey because the dodo, which did not evolve with humans, would approach people without fear. Introduced pigs, rats, and dogs brought to the island by European ships also killed dodo young and eggs (Figure 6.2.1.3).



Figure 6.2.1.3. The dodo bird was hunted to extinction around 1662. (credit: Ed Uthman, taken in Natural History Museum, London, England)

Steller's sea cow became extinct in 1768; it was related to the manatee and probably once lived along the northwest coast of North America. Steller's sea cow was first discovered by Europeans in 1741 and was hunted for meat and oil. The last sea cow was killed in 1768. That amounts to 27 years between the sea cow’s first contact with Europeans and extinction of the species.

In 1914, the last living passenger pigeon died in a zoo in Cincinnati, Ohio. This species had once darkened the skies of North America during its migrations, but it was hunted and suffered from habitat loss through the clearing of forests for farmland. In 1918, the last living Carolina parakeet died in captivity. This species was once common in the eastern United States, but it suffered from habitat loss. The species was also hunted because it ate orchard fruit when its native foods were destroyed to make way for farmland. The Japanese sea lion, which inhabited a broad area around Japan and the coast of Korea, became extinct in the 1950s due to fishermen. The Caribbean monk seal was distributed throughout the Caribbean Sea but was driven to extinction via hunting by 1952.

These are only a few of the recorded extinctions in the past 500 years.

The Red List

There is also the problem of understanding which species known to science are currently threatened and to what degree they are threatened. The International Union for Conservation of Nature (IUCN), an international non-profit, keeps a list of extinct and endangered species called the Red List, supported by scientific research. The list is not complete, but it describes 380 species of vertebrates that went extinct after 1500 AD, 86 of which were driven extinct by overhunting or overfishing. In 2011, the list contained 61,000 species. It is categorized by taxonomy, type of threat, and other criteria (Figure 6.2.1.4).

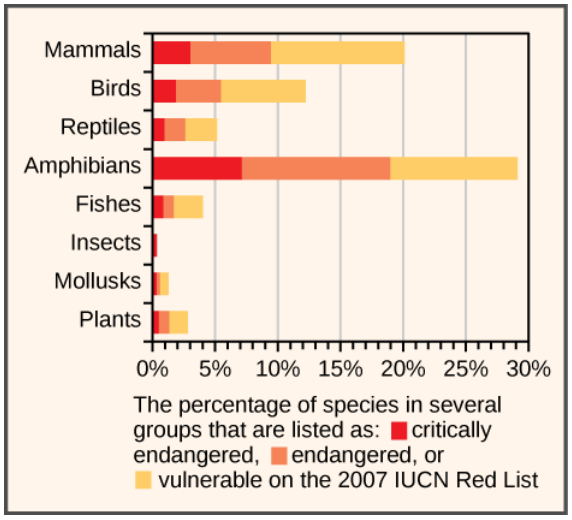


Figure 6.2.1.4: This chart shows the percentage of various animal species, by group, on the IUCN Red List as of 2007.

Optional Activity 6.2.1.1

Which of the following statements is NOT supported by Figure 6.2.1.4?

A. There are more vulnerable fishes than critically endangered and endangered fishes combined.
B. There are more critically endangered amphibians than vulnerable, endangered, and critically endangered reptiles combined.
C. Within each group, there are more critically endangered species than vulnerable species.
D. A greater percentage of bird species are critically endangered than mollusk species.

Answer

C. Within each group, there are more critically endangered species than vulnerable species.

Evolution Connection: Lake Victoria cichlids

The Lake Victoria cichlids provide an example through which we can begin to understand biodiversity. The biologists studying cichlids in the 1980s discovered hundreds of cichlid species representing a variety of specializations to particular habitat types and specific feeding strategies: eating plankton floating in the water, scraping and then eating algae from rocks, eating insect larvae from the bottom, and eating the eggs of other species of cichlid. The cichlids of Lake Victoria are the product of adaptive radiation. Adaptive radiation is a rapid (less than three million years in the case of the Lake Victoria cichlids) branching through speciation of a phylogenetic tree into many closely related species; typically, the species “radiate” into different habitats and niches. The Galápagos finches are an example of a modest adaptive radiation with 15 species. The cichlids of Lake Victoria are an example of a spectacular adaptive radiation that includes about 500 species.

At the time biologists were making this discovery, some species began to quickly disappear. A culprit in these declines was a species of large fish that was introduced to Lake Victoria by fisheries to feed the people living around the lake. The Nile perch was introduced in 1963, but lay low until the 1980s when its populations began to surge. The Nile perch population grew by consuming cichlids, driving species after species to the point of extinction (the disappearance of a species). In fact, there were several factors that played a role in the extinction of perhaps 200 cichlid species in Lake Victoria: the Nile perch, declining lake water quality due to agriculture and land clearing on the shores of Lake Victoria, and increased fishing pressure. Scientists had not even cataloged all of the species present—so many were lost that were never named. The diversity is now a shadow of what it once was.

The cichlids of Lake Victoria are a thumbnail sketch of contemporary rapid species loss that occurs all over Earth and is caused by human activity. Extinction is a natural process of macroevolution that occurs at the rate of about one out of 1 million species becoming extinct per year. The fossil record reveals that there have been five periods of mass extinction in history with much higher rates of species loss, and the rate of species loss today is comparable to those periods of mass extinction. However, there

is a major difference between the previous mass extinctions and the current extinction we are experiencing: human activity. Specifically, three human activities have a major impact: the destruction of habitat, introduction of exotic species, and over-harvesting. Predictions of species loss within the next century, a tiny amount of time on geological timescales, range from 10 percent to 50 percent. Extinctions on this scale have only happened five other times in the history of the planet, and they have been caused by cataclysmic events that changed the course of the history of life in each instance. Earth is now in one of those times.

Estimates of Present-day Extinction Rates

Estimates of extinction rates are hampered by the fact that most extinctions are probably happening without being observed. The extinction of a bird or mammal is often noticed by humans, especially if it has been hunted or used in some other way. But there are many organisms that are less noticeable to humans (not necessarily of less value) and many that are undescribed.

The **background extinction rate** is estimated to be about 1 per million species years (E/MSY). One "species year" is one species in existence for one year. One million species years could be one species persisting for one million years, or a million species persisting for one year. If it is the latter, then one extinction per million species years would be one of those million species becoming extinct in that year. For example, if there are 10 million species in existence, then we would expect 10 of those species to become extinct in a year. This is the background rate.

One contemporary extinction-rate estimate uses the extinctions in the written record since the year 1500. For birds alone, this method yields an estimate of 26 E/MSY, almost three times the background rate. However, this value may be underestimated for three reasons. First, many existing species would not have been described until much later in the time period and so their loss would have gone unnoticed. Second, biologists know the number is higher than the written record suggests because now extinct species are being described from skeletal remains that were never mentioned in written history. And third, some species are probably already extinct even though conservationists are reluctant to name them as such. Taking these factors into account raises the estimated extinction rate to nearer 100 E/MSY. The predicted rate by the end of the century is 1500 E/MSY.

A second approach to estimating present-time extinction rates is to correlate species loss with habitat loss, and it is based on measuring forest-area loss and understanding species–area relationships. The species-area relationship is the rate at which new species are seen when the area surveyed is increased (Figure 6.2.1.5). Likewise, if the habitat area is reduced, the number of species seen will also decline. This kind of relationship is also seen in the relationship between an island's area and the number of species present on the island: as one increases, so does the other, though not in a straight line.

Estimates of extinction rates based on habitat loss and species–area relationships have suggested that with about 90 percent of habitat loss an expected 50 percent of species would become extinct. Reducing forest area from 100 km^2 to 10 km^2, a decline of 90 percent, reduces the number of species by about 50 percent (Figure 6.2.1.5). Species–area estimates have led to estimates of present-day species extinction rates of about 1000 E/MSY and higher.

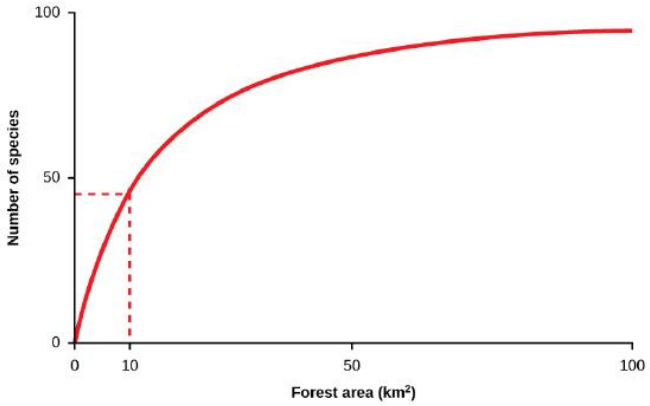


Figure 6.2.1.5. A typical species-area curve shows the cumulative number of species found as more and more area is sampled. The curve has also been interpreted to show the effect on species numbers of destroying habitat; a reduction in habitat of 90 percent from 100 km^2 to 10 km^2 reduces the number of species supported by about 50 percent.

Video



In this 9-minute video, discover why the current impacts of humans are as devastating to biodiversity as a large meteor.

Question after watching: What is lost when a species goes extinct? Consider all of the things that are lost, not just the biological ones.

This page titled 6.2.1: Introduction to Biodiversity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **47.0: Prelude to Conservation Biology and Biodiversity** by OpenStax is licensed CC BY 4.0.
- **47.2: The Importance of Biodiversity to Human Life** by OpenStax is licensed CC BY 4.0.
- **47.1: The Biodiversity Crisis** by OpenStax is licensed CC BY 4.0.
- **3.4: Patterns of Biodiversity** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **47.4: Preserving Biodiversity** by OpenStax is licensed CC BY 4.0.
- **5.5: Preserving Biodiversity** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.

Importance of Biodiversity

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Summarize the benefits of biodiversity

Introduction

It may not be clear why biologists are concerned about biodiversity loss. When biodiversity loss is thought of as the extinction of the passenger pigeon, the dodo bird, and even the woolly mammoth, the loss may appear to be an emotional one. However, is the loss practically important for the welfare of the human species? The loss of a keystone species can lead to ecological disaster and the extinction of many other species. But, from the perspective of evolution and ecology, the loss of one or two individual species may be relatively unimportant. Extinction is a normal part of macroevolution. Humans have accelerated the extinction rate, though, leading to losses of tens of thousands of species within our lifetimes. These losses are likely to have dramatic effects on human welfare through the collapse of ecosystems and added costs to maintain food production, clean air and water, and human health. There are strategies to avoid some of these losses and the field of study to preserve biodiversity is known as **conservation biology**.

Video



Watch this 4-minute video for an understanding of the importance of biodiversity.
Question after watching: Humans have cut and frayed the woven tapestry of Earth's biodiversity. List and describe three ways.

The Biodiversity Crisis

Biologists estimate that species extinctions are currently 500–1,000 times the normal, or **background**, rate seen previously in Earth's history. The current high rates will cause a precipitous decline in the biodiversity of the planet in the next century or two. The loss of biodiversity will include many species we know today. Although it is sometimes difficult to predict which species will become extinct, many are listed as **endangered** (at great risk of extinction). However, many extinctions will affect species that biologists have not yet discovered.

Most of these “invisible” species that will become extinct currently live in tropical rainforests like those of the Amazon basin or on coral reefs. Rainforests are the most diverse terrestrial ecosystems on the planet and are being destroyed rapidly by deforestation (Figure 6.2.2.1). Between 1970 and 2011, almost 20 percent of the Amazon rainforest was lost. Coral reefs are being lost to overharvesting, warming oceans, and pollution.



Figure 6.2.2.1. This tropical lowland rainforest in Madagascar is an example of a high biodiversity habitat. This particular location is protected within a national forest, yet only 10 percent of the original coastal lowland forest remains, and research suggests half the original biodiversity has been lost. (credit: Frank Vassen)

Biodiversity loss refers to the reduction of biodiversity due to displacement or extinction of species. The loss of a particular individual species may seem unimportant to some, especially if it is not a **charismatic species** like the Bengal tiger or the bottlenose dolphin. However, the current accelerated extinction rate means the loss of tens of thousands of species within our lifetimes. Much of this loss is occurring in tropical rainforests as mentioned above, which are very high in biodiversity but are being cleared for timber and agriculture. This is likely to have dramatic effects on human welfare through the collapse of ecosystems.

Biologists recognize that human populations are embedded in ecosystems and are dependent on them, just as is every other species on the planet. Agriculture began after early hunter-gatherer societies first settled in one place and heavily modified their immediate environment. This cultural transition has made it difficult for many modern humans to recognize their dependence on living things other than crops and domesticated animals on the planet. Today our technology smooths out the harshness of existence and allows many of us to live longer, more comfortable lives, but ultimately the human species cannot exist without its surrounding ecosystems. Our ecosystems provide us with food, medicine, clean air and water, recreation, and spiritual and aesthetical inspiration.

Current Species Diversity

Despite considerable effort, knowledge of the species that inhabit the planet is limited. A recent estimate suggests that only 13% of eukaryotic species have been named (Table 1). Estimates of numbers of prokaryotic species are largely guesses, but biologists agree that science has only just begun to catalog their diversity. Some scientists estimate that there may be over 100 million species of prokaryotes alone. Given that Earth is losing species at an accelerating pace, science knows little about what is being lost.

Table 1. This table shows the estimated number of species by taxonomic group—including both described (named and studied) and predicted (yet to be named) species.

Estimated Numbers of Described and Predicted species						
	Source: Mora et al 2011		Source: Chapman 2009		Source: Groombridge and Jenkins 2002	
	Described	Predicted	Described	Predicted	Described	Predicted
Animals	1,124,516	9,920,000	1,424,153	6,836,330	1,225,500	10,820,000
Photosynthetic protists	17,892	34,900	25,044	200,500	—	—
Fungi	44,368	616,320	98,998	1,500,000	72,000	1,500,000
Plants	224,244	314,600	310,129	390,800	270,000	320,000
Non-photosynthetic protists	16,236	72,800	28,871	1,000,000	80,000	600,000
Prokaryotes	—	—	10,307	1,000,000	10,175	—
Total	1,438,769	10,960,000	1,897,502	10,897,630	1,657,675	13,240,000

There are various initiatives to catalog described species in accessible and more organized ways, and the internet is facilitating that effort. Nevertheless, at the current rate of species description, which according to the State of Observed Species reports is 17,000–20,000 new species a year, it would take close to 500 years to describe all of the species currently in existence. The task, however, is becoming increasingly impossible over time as extinction removes species from Earth faster than they can be described.

Naming and counting species may seem an unimportant pursuit given the other needs of humanity, but it is not simply an accounting. Describing species is a complex process by which biologists determine an organism's unique characteristics and whether or not that organism belongs to any other described species. It allows biologists to find and recognize the species after the initial discovery to follow up on questions about its biology. That subsequent research will produce the discoveries that make the species valuable to humans and to our ecosystems. Without a name and description, a species cannot be studied in depth and in a coordinated way by multiple scientists.

Patterns of Biodiversity

Biodiversity is not evenly distributed on the planet. Lake Victoria contained almost 500 species of cichlids (just one family of fishes that are present in the lake) before the introduction of an exotic species in the 1980s and 1990s caused a mass extinction. All of these species were found only in Lake Victoria, which is to say they were endemic. Endemic species with highly restricted distributions, like the ciclids, are particularly vulnerable to extinction.

Lake Huron contains about 79 species of fish, all of which are found in many other lakes in North America. What accounts for the difference in diversity between Lake Victoria and Lake Huron? Lake Victoria is a tropical lake, while Lake Huron is a temperate lake. Lake Huron in its present form is only about 7,000 years old, while Lake Victoria in its present form is about 15,000 years old. These two factors, latitude and age, are two of several hypotheses biogeographers have suggested to explain biodiversity patterns on Earth.

Biogeography is the study of the distribution of the world's species both in the past and in the present (Unit 4.4.5). The work of biogeographers is critical to understanding our physical environment, how the environment affects species, and how changes in environment impact the distribution of a species.

There are three main fields of study under the heading of biogeography: ecological biogeography, historical biogeography (called paleobiogeography), and conservation biogeography. Ecological biogeography studies the current factors affecting the distribution of plants and animals. Historical biogeography, as the name implies, studies the past distribution of species. Conservation biogeography, on the other hand, is focused on the protection and restoration of species based upon the known historical and current ecological information.

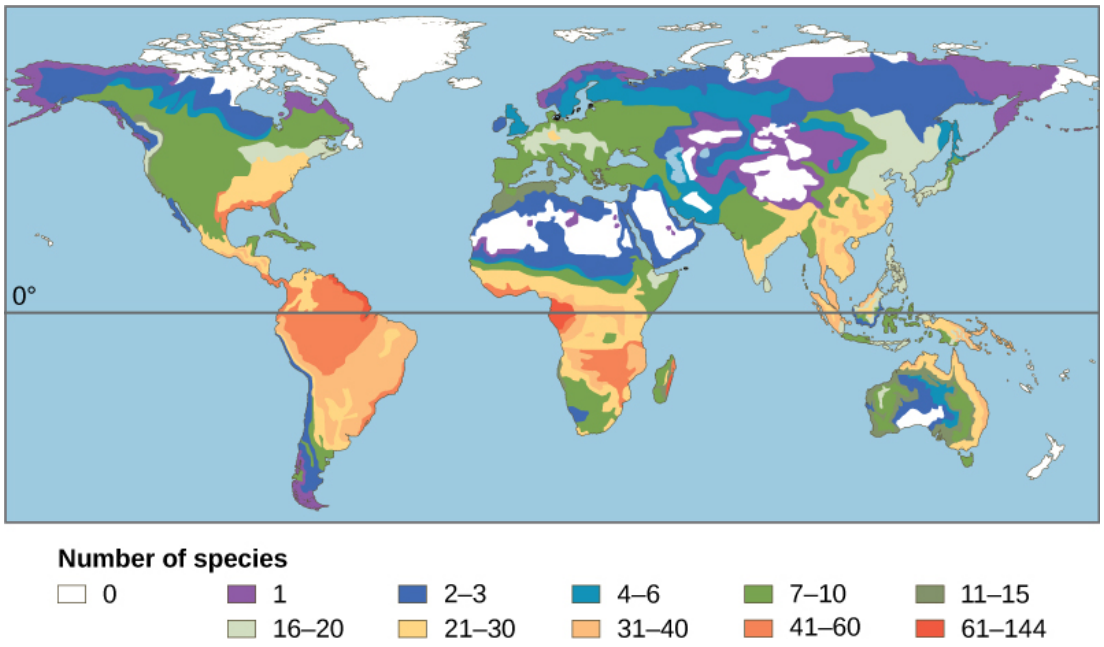


Figure 6.2.2.3. This map illustrates the number of amphibian species across the globe and shows the trend toward higher biodiversity at lower latitudes. A similar pattern is observed for most taxonomic groups.

One of the oldest observed patterns in ecology is that biodiversity typically increases as latitude decreases. In other words, biodiversity increases closer to the equator (Figure 6.2.2.3).

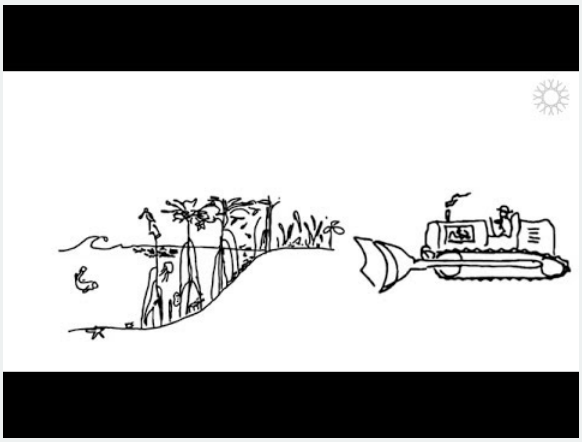
It is not yet clear why biodiversity increases closer to the equator, but hypotheses include the greater age of the ecosystems in the tropics versus temperate regions, which were largely devoid of life or drastically impoverished during the last ice age. The greater age provides more time for speciation, the evolutionary process of creating new species. Another possible explanation is the greater energy the tropics receive from the sun. But scientists have not been able to explain how greater energy input could translate into more species. The complexity of tropical ecosystems may promote speciation by increasing the habitat complexity, thus providing more ecological niches. Lastly, the tropics have been perceived as being more stable than temperate regions, which have a pronounced climate and day-length seasonality. The stability of tropical ecosystems might promote speciation. Regardless of the mechanisms, it is certainly true that biodiversity is greatest in the tropics. There are also high numbers of endemic species.

Importance of Biodiversity

Loss of biodiversity may have reverberating consequences on ecosystems because of the complex interrelations among species. For example, the extinction of one species may cause the extinction of another. Biodiversity is important to the survival and welfare of human populations because it has impacts on our health and our ability to feed ourselves through agriculture and harvesting populations of wild animals. Much of the importance of biodiversity comes from what is known as **ecosystem services** (Unit 5.2.3).

Video





In this 9-minute video by the California Academy of Sciences, the many ecosystem services that biodiversity provides are described.

Question after watching: Describe three different services and several examples of how biodiversity is important to humans.

Health

Many medications are derived from natural chemicals made by a diverse group of organisms. For example, many plants produce compounds meant to protect the plant from insects and other animals that eat them. Some of these compounds also work as human medicines. Contemporary societies that live close to the land often have a broad knowledge of the medicinal uses of plants growing in their area. For centuries in Europe, older knowledge about the medical uses of plants was compiled in herbals—books that identified the plants and their uses. Humans are not the only animals to use plants for medicinal reasons. The other great apes, orangutans, chimpanzees, bonobos, and gorillas as well as many other organisms such as elephants, bees, lizards, and canids have all been observed self-medicating with plants.

Modern pharmaceutical science also recognizes the importance of these plant compounds. Examples of significant medicines derived from plant compounds include aspirin (from the white willow, *Salix alba*), codeine (from the poppy, *Papaver somniferum*), digoxin (from the genus *Digitalis)*, atropine (from the belladonna, *Atropa belladonna)*, and vincristine (Figure 6.2.2.4). Many medications were once derived from plant extracts but are now synthesized. It is estimated that, at one time, 25 percent of modern

drugs contained at least one plant extract. That number has probably decreased to about 10 percent as natural plant ingredients are replaced by synthetic versions of the plant compounds. Antibiotics, which are responsible for extraordinary improvements in health and lifespans in developed countries, are compounds largely derived from fungi and bacteria.



Figure 6.2.2.4. *Catharanthus roseus*, the Madagascar periwinkle, has various medicinal properties. Among other uses, it is a source of vincristine, a drug used in the treatment of lymphomas. (credit: Forest and Kim Starr)

In recent years, animal venoms and poisons have excited intense research for their medicinal potential. By 2007, the FDA had approved five drugs based on animal toxins to treat diseases such as hypertension, chronic pain, and diabetes. Another five drugs are undergoing clinical trials and at least six drugs are being used in other countries. Other toxins under investigation come from mammals, snakes, lizards, various amphibians, fish, snails, octopuses, and scorpions.

Aside from representing billions of dollars in profits, these medications improve people's lives. Pharmaceutical companies are actively looking for new natural compounds that can function as medicines. It is estimated that more than 30% of pharmaceutical research and development is spent on natural compounds and that about 35% of new drugs brought to market between 1981 and 2002 were from natural compounds.

Agriculture

Since the beginning of human agriculture more than 10,000 years ago, human groups have been breeding and selecting crop varieties. This crop diversity matched the cultural diversity of highly subdivided populations of humans. For example, potatoes were domesticated beginning around 7,000 years ago in the central Andes of Peru and Bolivia. The potatoes grown in that region belong to seven species and the number of varieties likely is in the thousands. Each variety has been bred to thrive at particular elevations and soil and climate conditions. The diversity is driven by the diverse demands of the topography, the limited movement of people, and the demands created by crop rotation for different varieties that will do well in different fields.

Potatoes are only one example of human-generated diversity. Every plant, animal, and fungus that has been cultivated by humans has been bred from original wild ancestor species into diverse varieties arising from the demands for food value, adaptation to growing conditions, and resistance to pests. The potato demonstrates a well-known example of the risks of low crop diversity: the tragic Irish potato famine when the single variety grown in Ireland became susceptible to potato blight, wiping out the crop. The loss of the crop led to famine, death, and mass emigration. Resistance to disease is a chief benefit to maintaining crop biodiversity, and the lack of diversity in contemporary crop species carries similar risks. Seed companies, which are the source of most crop varieties in developed countries, must continually breed new varieties to keep up with evolving pest organisms. These same seed companies, however, have participated in the decline of the number of varieties available as they focus on selling fewer varieties in more areas of the world.

The ability to create new crop varieties relies on the diversity of varieties available and the accessibility of wild forms related to the crop plant. These wild forms are often the source of new gene variants that can be bred with existing varieties to create varieties with new attributes. Loss of wild species related to a crop will mean the loss of potential in crop improvement. Maintaining the genetic diversity of wild species related to domesticated species ensures our continued food supply.

Since the 1920s, government agriculture departments have maintained seed banks of crop varieties as a way to maintain crop diversity. This system has flaws because, over time, seed banks are lost through accidents, and there is no way to replace them. In 2008, the Svalbard Global Seed Vault (Figure 6.2.2.5) began storing seeds from around the world as a backup system to the regional

seed banks. If a regional seed bank stores varieties in Svalbard, losses can be replaced from Svalbard. The seed vault is located deep into the rock of an arctic island. Conditions within the vault are maintained at ideal temperature and humidity for seed survival, but the deep underground location of the vault in the arctic means that failure of the vault's systems will not compromise the climatic conditions inside the vault.



Figure 6.2.2.5. The Svalbard Global Seed Vault is a storage facility for seeds of Earth's diverse crops. (credit: Mari Tefre, Svalbard Global Seed Vault)

? Optional Activity 6.2.2.1

Figure 6.2.2.5: The Svalbard Global Seed Vault is located on Spitsbergen island in Norway, which has an arctic climate. Why might an arctic climate be good for seed storage?

Answer

The ground is permanently frozen so the seeds will keep even if the electricity fails.

Crop success is largely dependent on the quality of the soil. Although some agricultural soils are rendered sterile using controversial cultivation and chemical treatments, most contain a huge diversity of organisms that maintain nutrient cycles—breaking down organic matter into nutrient compounds that crops need for growth. These organisms also maintain soil texture that affects water and oxygen dynamics in the soil that are necessary for plant growth. If farmers had to maintain arable soil using alternate means, the cost of food would be much higher than it is now. These kinds of processes are called ecosystem services. They occur within ecosystems, such as soil ecosystems, as a result of the diverse metabolic activities of the organisms living there, but they provide benefits to human food production, drinking water availability, and breathable air.

Other key ecosystem services related to food production are plant pollination and crop pest control. Over 150 crops in the United States require pollination to produce. One estimate of the benefit of honeybee pollination within the United States is $1.6 billion per year; other pollinators contribute up to $6.7 billion more.

Many honeybee populations are managed by apiarists who rent out their hives' services to farmers. Honeybee populations in North America have been suffering large losses caused by a syndrome known as colony collapse disorder, whose cause is unclear. Other pollinators include a diverse array of other bee species and various insects and birds. Loss of these species would make growing crops requiring pollination impossible, increasing dependence on other crops.

Finally, humans compete for their food with crop pests, most of which are insects. Pesticides control these competitors; however, pesticides are costly and lose their effectiveness over time as pest populations adapt. They also lead to collateral damage by killing non-pest species and risking the health of consumers and agricultural workers. Ecologists believe that the bulk of the work in removing pests is actually done by predators and parasites of those pests, but the impact has not been well studied. A review found that in 74 percent of studies that looked for an effect of landscape complexity on natural enemies of pests, the greater the complexity, the greater the effect of pest-suppressing organisms. An experimental study found that introducing multiple enemies of pea aphids (an important alfalfa pest) increased the yield of alfalfa significantly. This study shows the importance of landscape diversity via the question of whether a diversity of pests is more effective at control than one single pest; the results showed this to be the case. Loss of diversity in pest enemies will inevitably make it more difficult and costly to grow food.

Optional Activity 6.2.2.2

Which of the following agricultural crops is most likely to survive a catastrophic event?

A. a monoculture of a crop on a large surface
B. diverse varieties of a crop surrounded by a diverse ecosystem
C. a single crop surrounded by a diverse ecosystem
D. diverse varieties of a crop in a simple ecosystem

Answer

B. diverse varieties of a crop surrounded by a diverse ecosystem.

Video



In this short 1.5-minute video, learn how biodiversity for food and agriculture is indispensable to food security, sustainable development, and the supply of many vital ecosystem services.
Question after watching: In what ways could you diversify your own diet and support local food growers?

Wild Food Sources

In addition to growing crops and raising food animals, humans obtain food resources from wild populations, primarily wild fish populations. For about one billion people, aquatic resources provide the main source of animal protein. But since 1990, production from global fisheries has declined. Despite considerable effort, few fisheries on Earth are managed sustainability.

Fishery extinctions rarely lead to complete extinction of the harvested species, but rather to a radical restructuring of the marine ecosystem in which a dominant species is so over-harvested that it becomes a minor player, ecologically. In addition to humans losing a food source, these alterations affect many other species in ways that are difficult or impossible to predict. The collapse of fisheries has dramatic and long-lasting effects on local human populations that work in the fishery. In addition, the loss of an inexpensive protein source to populations that cannot afford to replace it will increase the cost of living and limit societies in other ways. In general, the fish taken from fisheries have shifted to smaller species and the larger species are overfished. The ultimate outcome could clearly be the loss of aquatic systems as food sources.

Psychological and Moral Value

Finally, it has been argued that humans benefit psychologically from living in a biodiverse world. The chief proponent of this idea was famed entomologist E. O. Wilson. He argued that human evolutionary history has adapted us to living in a natural environment and that built environments generate stresses that affect human health and well-being. There is considerable research into the psychologically regenerative benefits of natural landscapes that suggest the hypothesis may hold some truth. In addition, there is a moral argument that humans have a responsibility to inflict as little harm as possible on other species.

Video



This 5.5-minute video from the EU's Science for Environment Policy summarizes many of the ecosystem services and benefits discussed above.

Question after watching: What is your opinion of using monetary values for nature to convince people to preserve or restore natural systems?

This page titled 6.2.2: Importance of Biodiversity is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **47.2: The Importance of Biodiversity to Human Life** by OpenStax is licensed CC BY 4.0.
- **5.3: Importance of Biodiversity** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.

The Biodiversity Crisis - HIPPPOC

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1.5 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify and explain the major causes of anthropogenic global change and their impacts on biodiversity.

Introduction

The core threat to biodiversity on the planet, and therefore a threat to human welfare, is the combination of human population growth and the resources used by that population. The human population requires resources to survive and grow, and many of those resources are being removed unsustainably from the environment. The three greatest proximate threats to biodiversity are habitat loss, overexploitation (also known as overharvesting), pollution, predator losses, and introduction of invasive species. These are a direct result of human population growth, resource use, increased mobility, and trade (Unit 4.2.6). One of the major causes of extinction, **anthropogenic climate change**, is covered in more depth in the next section (Unit 5.3).

Together, these threats are known as **HIPPPOC**: **h**abitat loss, **i**nvasive species, **p**ollution, **p**opulation (human), **p**redator loss, **o**verexploitation, and **c**limate change.

Habitat Loss

Humans rely on technology to modify their environment and make it habitable. Other species cannot do this. Elimination of their habitat—whether it is a forest, coral reef, grassland, or flowing river—will kill the individuals in the species. Remove the entire habitat and the species will become extinct, unless they are among the few species that do well in human-built environments. Human destruction of habitats accelerated in the latter half of the twentieth century.

Consider the exceptional biodiversity of Sumatra: it is home to one species of orangutan, a species of critically endangered elephant, and the Sumatran tiger, but half of Sumatra's forest is now gone. The neighboring island of Borneo, home to the other species of orangutan, has lost a similar area of forest. Forest loss continues in protected areas of Borneo. The orangutan in Borneo is listed as endangered by the International Union for Conservation of Nature (IUCN), but it is simply the most visible of thousands of species that will not survive the disappearance of the forests of Borneo. The forests are removed for timber and to plant palm oil plantations (Figure 6.2.3.1). Palm oil is used in many products including food products, cosmetics, and biodiesel in Europe. A 5-year estimate of global forest cover loss for the years from 2000 to 2005 was 3.1%. Much loss (2.4%) occurred in the tropics where forest loss is primarily from timber extraction. These losses certainly also represent the extinction of species unique to those areas.



(a)



(b)



(c)



(d)



(e)

Figure 6.2.3.1: (a) One species of orangutan, *Pongo pygmaeus*, is found only in the rainforests of Borneo, and the other species of orangutan (*Pongo abelii*) is found only in the rainforests of Sumatra. These animals are examples of the exceptional biodiversity of (c) the islands of Sumatra and Borneo. Other species include the (b) Sumatran tiger (*Panthera tigris sumatrae*) and the (d) Sumatran elephant (*Elephas maximus sumatranus*), both critically endangered species. Rainforest habitat is being removed to make way for (e) oil palm plantations such as this one in Borneo's Sabah Province. (credit a: modification of work by Thorsten Bachner; credit b: modification of work by Dick Mudde; credit c: modification of work by U.S. CIA World Factbook; credit d: modification of work by "Nonprofit Organizations"/Flickr; credit e: modification of work by Dr. Lian Pin Koh)

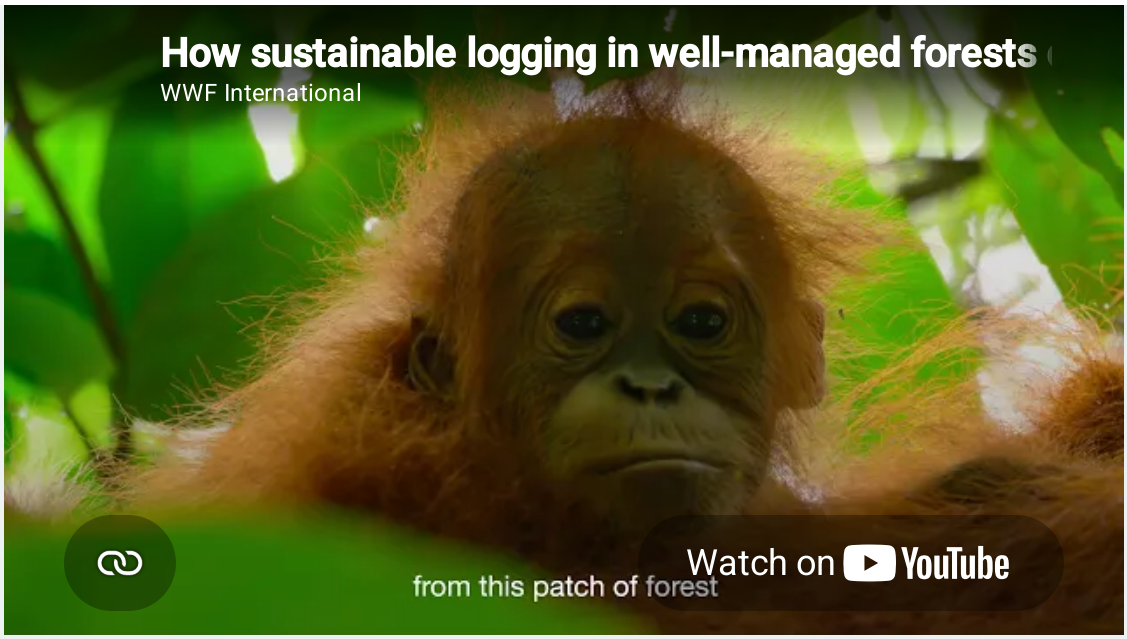
Preventing Habitat Destruction with Wise Wood Choices

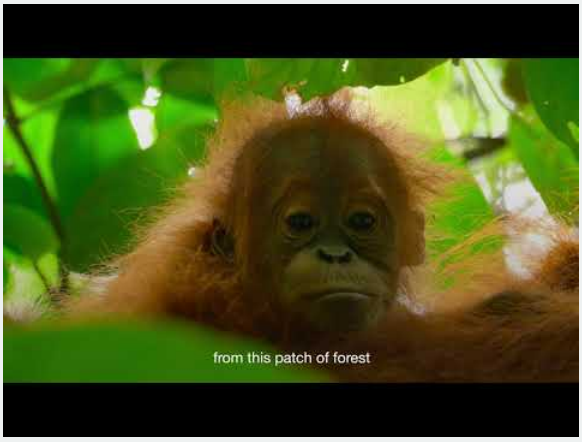
Most consumers do not imagine that the home improvement products they buy might be contributing to habitat loss and species extinctions. Yet the market for illegally harvested tropical timber is huge, and the wood products often find themselves in building supply stores. How is it possible to determine if a wood product, such as flooring, was harvested sustainably or even legally?

Various certifications can identify sustainably harvested forest products. Looking for certifications on flooring and other hardwood products is one way to ensure that the wood has not been taken illegally from a tropical forest. Some of these certifications are run by timber companies, however, thus creating a conflict of interest. Another approach is to buy domestic wood species. While it would be great if there was a list of legal versus illegal woods, it is not that simple. Logging and forest management laws vary from country to country; what is illegal in one country may be legal in another. Where and how a product is harvested and whether the forest from which it comes is being sustainably maintained all factor into whether a wood product will be certified. It is always a good idea to ask questions about where a wood product came from and how the supplier knows that it was harvested legally.

Habitat destruction can affect ecosystems other than forests. Rivers and streams are important ecosystems and are frequently the target of habitat modification. Damming of rivers affects flow and access to habitat. Altering a flow regime can reduce or eliminate populations that are adapted to seasonal changes in flow. Many fish species, including salmon, have seen declines caused by river damming and habitat loss.

Research has confirmed that species of amphibians that must carry out parts of their life cycles in both aquatic and terrestrial habitats are at greater risk of population declines and extinction because of the increased likelihood that one of their habitats or access between them will be lost. This is of particular concern because amphibians have been declining in numbers and going extinct more rapidly than many other groups for a variety of possible reasons.





Foresters identify strategies to manage forest habitats sustainably by mimicking natural processes in this 3.5-minute video from the World Wildlife Fund.
Question after watching: What are benefits to sustainable logging as described in the video?

Invasive Species

Non-native species are those that have been intentionally or unintentionally introduced by humans into an ecosystem in which they did not evolve. Human transportation of people and goods, including the intentional transport of organisms for trade, has dramatically increased the introduction of species into new ecosystems. These new introductions are often at distances that are well beyond the capacity of the species to ever travel on its own, and outside the range of the species' natural predators.

Most non-native species introductions probably fail because of the low number of individuals introduced or poor adaptation to the ecosystem they enter. Some species, however, have characteristics that can make them especially successful in a new ecosystem. These non-native species may undergo dramatic population increases in their new habitat and reset the ecological conditions in the new environment, threatening the native species that already exist there. When this happens, the non-native species is termed an **invasive species**. Invasive species can threaten other species through competition for resources, increased predation, or by causing new diseases.

Many invasive species are well suited evolutionarily to exploiting human transportation as a means to migrate, whether by air, sea, or land. The accidental introduction of the brown tree snake via aircraft (Figure 6.2.3.2) from the Solomon Islands to Guam in 1950 led to the extinction of three species of birds and three to five species of reptiles endemic to the island. Several other species are

still threatened. Islands do not make up a large area of land on the globe, but they do contain a disproportionate number of endemic species because of their isolation from mainland ancestors.

Lakes and islands are particularly vulnerable to extinction threats from non-native species. In Lake Victoria, the intentional introduction of the Nile perch was largely responsible for the extinction of about 200 species of cichlids. Many introductions of aquatic species, both marine and freshwater, have occurred when ships have dumped ballast water taken on at a port of origin into waters at a destination port. Water from the port of origin is pumped into tanks on a ship empty of cargo to increase stability. The water is drawn from the ocean or estuary of the port and typically contains living organisms such as plant parts, microorganisms, eggs, larvae, or aquatic animals. The water is then pumped out before the ship takes on cargo at the destination port, which may be on a different continent.

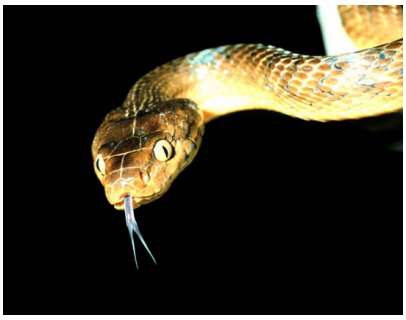


Figure 6.2.3.2. The brown tree snake, *Boiga irregularis*, is an exotic species that has caused numerous extinctions on the island of Guam since its accidental introduction in 1950. (credit: NPS)

Invading exotic species can also be disease organisms. It now appears that the global decline in amphibian species recognized in the 1990s is, in some part, caused by the fungus *Batrachochytrium dendrobatidis*, which causes the disease chytridiomycosis (Figure 6.2.3.3). There is evidence that the fungus is native to Africa and may have been spread throughout the world by transport of a commonly used laboratory and pet species: the African clawed frog, *Xenopus laevis*. It may well be that biologists themselves are responsible for spreading this disease worldwide. The North American bullfrog, *Rana catesbeiana*, which has also been widely introduced as a food animal but which easily escapes captivity, survives most infections of *B. dendrobatidis* and can act as a reservoir for the disease.



Figure 6.2.3.3. This Limosa harlequin frog (*Atelopus limosus*), an endangered species from Panama, died from a fungal disease called chytridiomycosis. The red lesions are symptomatic of the disease. (credit: Brian Gratwicke)

Video





In this 5-minute video, discover the devastating impact that invasive species can have on ecosystems. Question after watching: Do some research to find out what invasive species are a problem in your area? What is being done to combat them?

Optional Activity 6.2.3.1

Invasive predator species are especially threatening to what kind of ecosystem?

A. deserts
B. marine ecosystems
C. islands
D. tropical forests

Answer

C. islands

Pollution

Air Pollution

Air pollution occurs in many forms but can generally be thought of as gaseous and particulate contaminants that are present in the earth's atmosphere. Chemicals discharged into the air that have a direct impact on the environment are called **primary pollutants**. These primary pollutants sometimes react with other chemicals in the air to produce **secondary pollutants**.

Outdoor air pollution involves exposures that take place outside of the built environment. Examples include fine particles produced by the burning of coal, noxious gases such as sulfur dioxide, nitrogen oxides and carbon monoxide; ground-level ozone and tobacco smoke. **Indoor air pollution** involves exposures to particulates, carbon oxides, and other pollutants carried by indoor air or dust. Examples include household products and chemicals, out-gassing of building materials, allergens (cockroach and mouse dropping, mold, pollen), and tobacco smoke.

A **point source** of air pollution refers to an emission source that does not move including factories, power plants, and dry cleaners. The term **non-point sources** is used to describe many sources of air pollution located together whose individual emissions may be below thresholds of concern, but whose collective emissions can be significant. Non-point sources include the construction of housing developments, runoff from asphalt, and landfills. In crop production, the misapplication of fertilizers, herbicides, and pesticides can potentially result in aerial drift of these materials and harm may be caused.

Video



In this 4-minute video from National Geographic, learn how greenhouse gasses, smog, and toxic pollutants affect climate change and human health.

Question after watching: What strategies beyond those discussed in the video do you think will help to reduce air pollution?

Unlike the above-mentioned sources of air pollution, air pollution caused by **natural sources** is not caused by people or their activities. An erupting volcano emits particulate matter and gases, forest and prairie fires can emit large quantities of pollutants, dust storms can create large amounts of particulate matter, and plants and trees naturally emit volatile organic compounds which can form aerosols that can cause a natural blue haze.

Water Pollution

Water pollution is the contamination of water by an excess amount of a substance that can cause harm to human beings and/or the ecosystem. The level of water pollution depends on the abundance of the pollutant, the ecological impact of the pollutant, and the use of the water. Pollutants are derived from biological, chemical, or physical processes. Although natural processes such as volcanic eruptions or evaporation sometimes can cause water pollution, most pollution is derived from human, land-based activities (Figure 6.2.3.4).



Figure 6.2.3.4. Water Pollution. Obvious water pollution in the form of floating debris, largely plastics; microscopic and chemical water pollutants are often much more harmful than visible ones. Source: Stephen Codrington at Wikimedia Commons

Water pollutants can move through different water reservoirs, as the water carrying them progresses through stages of the water cycle (Figure 6.2.3.5). **Water residence time** (the average time that a water molecule spends in a water reservoir) is very important to pollution problems because it affects pollution potential. Water in rivers has a relatively short residence time, so pollution usually is there only briefly. Of course, pollution in rivers may simply move to another reservoir, such as the ocean, where it can cause further problems. Groundwater is typically characterized by slow flow and longer residence time, which can make groundwater pollution particularly problematic. Finally, **pollution residence time** can be much greater than the water residence time because a pollutant may be taken up for a long time within the ecosystem or absorbed onto sediment.

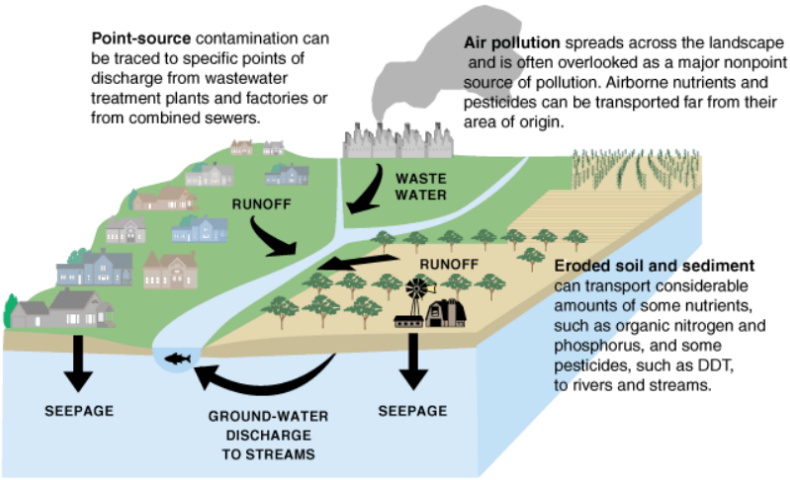


Figure 6.2.3.5. Sources of Water Contamination. Sources of some water pollutants and movement of pollutants into different water reservoirs of the water cycle. Source: U.S. Geological Survey

Like air pollution, water pollutants may enter the water cycle from point sources, which include identifiable and (generally) relatively small locations, or nonpoint sources, which include large and more diffuse areas. Point sources of pollution include animal factory farms (Figure 6.2.3.6) that raise a large number and high density of livestock such as cows, pigs, and chickens.



Figure 6.2.3.6. Large animal farms are often referred to as concentrated feeding operations (CFOs). These farms are considered potential point sources of pollution because untreated animal waste may enter nearby waterbodies as untreated sewage. Credit: ehp.gov

Included in point sources are pipes from factories or sewage treatment plants. Combined sewer systems that have a single set of underground pipes to collect both sewage and stormwater runoff from streets for wastewater treatment can be major point sources of pollutants. During heavy rain, stormwater runoff may exceed sewer capacity, causing it to back up and spilling untreated sewage directly into surface waters (Figure 6.2.3.7).

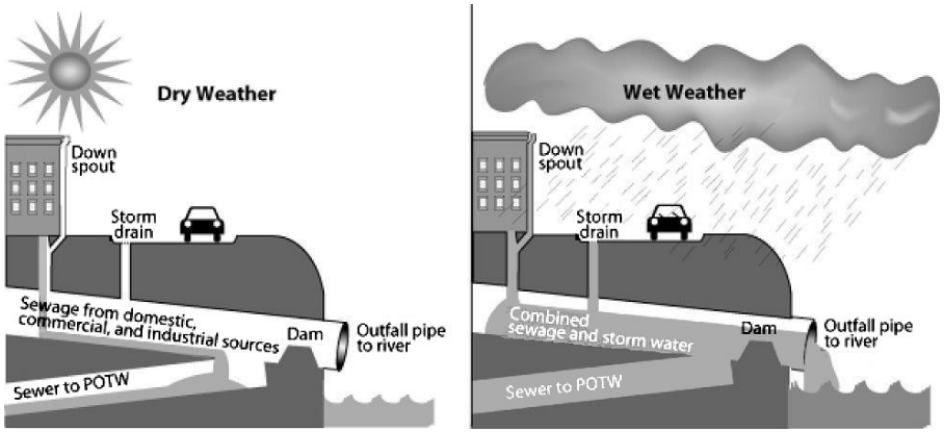


Figure 6.2.3.7. Combined Sewer System A combined sewer system is a possible major point source of water pollution during heavy rain due to overflow of untreated sewage. During dry weather (and small storms), all flows are handled by the publicly-owned treatment works. During large storms, the relief structure allows some of the combined stormwater and sewage to be discharged untreated to an adjacent water body. Source: U.S. Environmental Protection Agency at Wikimedia Commons

Non-point sources of pollution include agricultural fields, cities, and abandoned mines. Rainfall runs over the land and through the ground, picking up pollutants such as herbicides, pesticides, and fertilizer from agricultural fields and lawns; oil, antifreeze, animal waste, and road salt from urban areas; and acid and toxic elements from abandoned mines. Then, this pollution is carried into surface water bodies and groundwater. Non-point source pollution, which is the leading cause of water pollution, is usually much more difficult and expensive to control than point source pollution because of its low concentration, multiple sources, and much greater volume of water.

Video



In this 9-minute video, discover how the plastic we dump into the ocean might be hiding in plain sight. Question after watching: What is the ultimate solution to plastic waste in the ocean? What part can individuals play in this solution? What part can corporations play?

Population

Humans, while subject to the same ecological constraints as any other species (a need for nutrients, water, etc.), have some features as individuals and some as a population that make them a unique species. Unlike most other organisms, humans have the capacity to alter their number of offspring, level of resource consumption and distribution. While most women around the world could potentially have the same number of children during their lives, the number they actually have is affected by many factors. Depending upon technological, cultural, economic and educational factors, people around the world have families of different sizes. Additionally, unlike other organisms, humans invent and alter technology, which allows them to change their environment. This ability makes it difficult to determine the human carrying capacity (Figure 6.2.3.8).

For example, families in developing nations are often larger, but less resource-intensive (e.g., they use fewer resources per person) than those in more developed nations. However, increasingly, human populations wish to have a "western" standard of living. An increase in the world's average standard of living significantly lowers the potential human carrying capacity of the earth. Therefore, in order to reduce their impact as a species, humans must not only reduce the resources they use per person, they must also reduce their average family size.

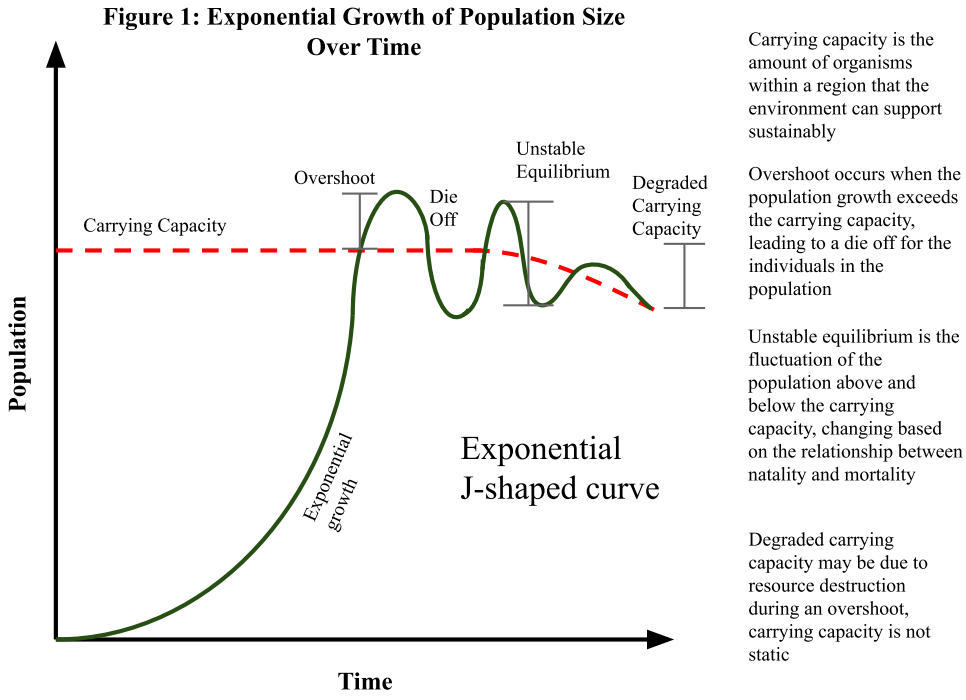


Figure 6.2.3.8: Reaching carrying capacity through exponential growth, followed by die-off and carrying capacity degradation (Copyright; Nchisick CC BY-SA 4.0)

Human Resource Utilization

Humans have always made an impact on the environment through their use of resources. For example, early humans were primarily hunter-gatherers who used tools to survive. They fashioned wood and stone tools for hunting and food preparation, and used fire for cooking. Early humans developed methods for changing habitats to suit their needs and herding wild animals. As time passed, humans developed more tools and techniques and came to rely on that technology in their daily lives. Although the tools of early humans were primitive by today's standards, they significantly affected the environment and probably hastened the extinction of some large Ice Age mammals.

Over the last 10,000 years, land clearing for agriculture has destroyed and degraded the habitats of many species of plants and animals. Today, growing populations in less developed countries are rapidly clearing tropical forests and savannas for agricultural use. These tropical rainforests and savannas provide habitat for most of the earth's species. It has become clear that modern agricultural practices are not sustainable. Once-fertile areas are becoming infertile because of overgrazing, erosion and nutrient depletion. Furthermore, modern agriculture requires large inputs of energy and fertilizers, usually produced from nonrenewable fossil fuels.

Advanced industrialization leads to many changes in human society, and some of those changes negatively affect the supply of natural resources and result in environmental degradation. These changes include: increased production and consumption of goods by humans, dependence on non-renewable resources such as oil and coal, production of synthetic materials (which may be toxic or non-biodegradable), and consumption of large amounts of energy at home and work. For example, if everyone on the planet lived as the average Canadian, humanity would need the equivalent of 5.1 Earths to support everyone.

Other changes may have positive benefits. These include: creation and mass production of useful and affordable products, significant increases in the average **gross national product** per person, large increases in agricultural productivity, sharp rises in average life expectancy and a gradual decline in population growth rates. The information age was born with the invention of miniaturized electronics such as integrated circuits and computer central processing units. This stage in human development has changed and continues to change society as we know it. By making good use of information technologies, less developed countries may be able to reduce potential environmental problems as their economies expand in the future. With so much information easily

available, developing countries may not repeat the environmental mistakes that more developed countries made as they became industrialized.

Predator Losses

"The loss of apex consumers is arguably humankind's most pervasive influence on the natural world. This is true in part because it has occurred globally and in part because extinctions are by their very nature perpetual, whereas most other environmental impacts are potentially reversible on decadal to millenial time scales. Recent research suggests that the disappearance of these animals reverberates further than previously anticipated, with far-reaching effects on processes as diverse as the dynamics of disease; fire; carbon sequestration; invasive species; and biogeochemical exchanges among Earth's soil, water, and atmosphere."[1] The loss of these predators leads to what is known as **trophic cascades**.

"Predation is ubiquitous in nature and can be an important component of both ecological and evolutionary interactions. One of the most striking features of predators is how often they cause evolutionary diversification in natural systems. Predators are effective agents of natural selection because they possess key traits that allow them to capture and consume their prey; they adopt different strategies to do so, and they are common, but not too common, such that they can drive prey evolution without driving prey species to extinction."[2]

"Classic ecological studies that viewed predators as static entities that interact with prey in fixed ways resulting in predictable population dynamics are likely too simplistic. Today it is recognized that both predator and prey populations evolve—and that this evolution can happen very rapidly, even on ecological time scales, often with more than two species involved."[2]

"Ecosystems may be shaped by the loss of consumers. The loss of a single predator species may reverberate through the community. The loss of apex consumers reduces food chain length, thus altering the intensity of herbivory and the abundance and composition of plants in largely predictable ways. The transitions in ecosystems that characterize such changes are often abrupt, are sometimes difficult to reverse, and commonly lead to radically different patterns and pathways of energy and [matter]."[2]

Video



Scientists have discovered that reintroducing apex predators has led to successful recovery of previously damaged ecosystems, profiled in this 6-minute video from the IUCN.

Question after watching: Why do apex predators play such a crucial role in ecosystems and how can we effectively preserve them?

? Optional Activity 6.2.3.2

Wolves are a keystone species in Yellowstone National Park, Wyoming, USA. Predict what would happen if they were hunted to extinction.

A. Many species would increase and the elk population would disappear.
B. Many species would disappear and the elk population would initially increase.
C. Many species along with elk population would increase.
D. Many species, along with the elk population, would disappear.

Answer

B. Many species would disappear and the elk population would initially increase.

Overharvesting

Overharvesting is a serious threat to many species, but particularly to aquatic species. There are many examples of regulated fisheries (including hunting of marine mammals and harvesting of crustaceans and other species) monitored by fisheries scientists that have nevertheless collapsed. The western Atlantic cod fishery is the most spectacular recent collapse. While it was a hugely productive fishery for 400 years, the introduction of modern factory trawlers in the 1980s and the pressure on the fishery led to it becoming unsustainable. The causes of fishery collapse are both economic and political in nature.

Most fisheries are managed as a common resource, available to anyone willing to fish, even when the fishing territory lies within a country's territorial waters. Common resources are subject to an economic pressure known as the tragedy of the commons, in which fishers have little motivation to exercise restraint in harvesting a fishery when they do not own the fishery. The general outcome of harvests of resources held in common is their overexploitation. While large fisheries are regulated to attempt to avoid this pressure, it still exists in the background. This overexploitation is exacerbated when access to the fishery is open and unregulated and when technology gives fishers the ability to overfish. In a few fisheries, the biological growth of the resource is less than the potential growth of the profits made from fishing if that time and money were invested elsewhere. In these cases—whales are an example—economic forces will drive toward fishing the population to extinction.

Video



Learn about overfishing and its effects on ecosystems, food security, jobs, economies, and coastal cultures in this 4.5-minute video.

Question after watching: What can communities do to ensure their local waters are fished sustainably?

Coral reefs are extremely diverse marine ecosystems that face peril from several processes. Reefs are home to 1/3 of the world's marine fish species—about 4,000 species—despite making up only one percent of marine habitat. Most home marine aquaria house coral reef species that are wild-caught organisms—not cultured organisms. Although no marine species is known to have been driven extinct by the pet trade, there are studies showing that populations of some species have declined in response to harvesting,

indicating that the harvest is not sustainable at those levels. There are also concerns about the effect of the pet trade on some terrestrial species such as turtles, amphibians, birds, plants, and even the orangutans Figure 6.2.3.9.



Figure 6.2.3.9. Harvesting of pangolins for their scales and meat, and as curiosities, has led to a drastic decline in population size for this fascinating creature. *This work by David Brossard is licensed under CC BY 4.0*

Many around the world eat wild animals for food. Hunting is practiced throughout the world, but hunting practices, particularly in equatorial Africa and parts of Asia, are believed to threaten several species with extinction. Traditionally, wild meat in Africa was hunted to feed families directly. However, recent commercialization of the practice now has wild meat available in grocery stores, which has increased harvest rates to the level of unsustainability. Additionally, human population growth has increased the need for protein foods that are not being met from agriculture. Species threatened by the wild meat trade are mostly mammals including many monkeys and the great apes living in the Congo basin.

Climate Change

Climate change, and specifically the anthropogenic (meaning, caused by humans) warming trend presently underway, is recognized as a major extinction threat, particularly when combined with other threats such as habitat loss. Extinction rate estimates range from 15 percent to 40 percent of species committed to extinction by 2050 due to climate change. Climate change will alter regional climates, including rainfall and snowfall patterns, making habitats less hospitable to the species living in them. The warming trend will shift colder climates toward the north and south poles, forcing species to move with their adapted climate norms while facing habitat gaps along the way.

The shifting ranges will impose new competitive regimes on species as they find themselves in contact with other species not present in their historic range. One such unexpected species contact is between polar bears and grizzly bears (Figure 6.2.3.10). Previously, these two species had separate ranges. Now, their ranges are overlapping and there are documented cases of these two species mating and producing viable offspring. Changing climates also throw off species' delicate timing adaptations to seasonal food resources and breeding times. Many contemporary mismatches to shifts in resource availability and timing have already been documented.



Figure 6.2.3.10: Since 2008, grizzly bears (*Ursus arctos horribilis*) have been spotted farther north than their historic range, a possible consequence of climate change. As a result, grizzly bear habitat now overlaps polar bear (*Ursus maritimus*) habitat. The two kinds of bears, which are capable of mating and producing viable offspring, are considered separate species as historically they lived in different habitats and never met. However, in 2006 a hunter shot a wild grizzly-polar bear hybrid known as a grolar bear, the first wild hybrid ever found.

Range shifts are already being observed: for example, some European bird species ranges have moved 91 km northward. The same study suggested that the optimal shift based on warming trends was double that distance, suggesting that the populations are not moving quickly enough. Range shifts have also been observed in plants, butterflies, other insects, freshwater fishes, reptiles, and mammals.

Climate gradients will also move up mountains, eventually crowding species higher in altitude and eliminating the habitat for those species adapted to the highest elevations. Some climates will completely disappear. The rate of warming appears to be accelerated in the arctic, which is recognized as a serious threat to polar bear populations that require sea ice to hunt seals during the winter months: seals are the only source of protein available to polar bears. A trend to decreasing sea ice coverage has occurred since observations began in the mid-twentieth century. The rate of decline observed in recent years is far greater than previously predicted by climate models.

Finally, climate change will raise ocean levels due to meltwater from glaciers and the greater volume of warmer water. Shorelines will be inundated, reducing island size, which will have an effect on some species, and a number of islands will disappear entirely. Additionally, the gradual melting and subsequent refreezing of the poles, glaciers, and higher-elevation mountains—a cycle that has provided freshwater to environments for centuries—will also be jeopardized. This could result in an overabundance of salt water and a shortage of fresh water.

More on climate change follows in Unit 5.3.

Video



This 6-minute video from PBS discusses that as the world figures out how to live with a rapidly changing climate, traditional knowledge from indigenous cultures could help Western Science understand just how things are transforming.

Question after watching: In what ways is Indigenous Science dynamic regarding climate change? In what areas are Indigenous people facing discrimination in science?

Optional Activity 6.2.3.3

Converting a prairie to a farm field is an example of _____.

A. overharvesting
B. habitat loss
C. exotic species
D. climate change

Answer

B. habitat loss

Optional Activity 6.2.3.4

Loss of biodiversity and acceleration of extinction rates have several causes. Which of the following situations causes direct loss of biodiversity owing to overexploitation?

A. fishing cod at a rate that is greater than natural replacement
B. building a housing subdivision in place of second-growth forest
C. introduction of an invasive ornamental plant in a new ecosystem
D. emission of greenhouse gases increasing the average temperatures of an area

Answer

A. fishing cod at a rate that is greater than natural replacement

Video



In this 3.5-minute video, learn of a 2019 United Nations report that says humans are transforming the planet's natural habitat at an unprecedented rate.

Question after watching: Are you optimistic or pessimistic of humans' capability to change and reduce their collective ecological footprint?

Footnotes:

1. Estes, J.A. et al. 2011. Trophic Downgrading of Planet Earth. *Science.* 333(6040): 301-306: https://doi.org/10.1126/science.1205106

2. Johnson, J.B. and M.C. Belk. 2020. Predators as Agents of Selection and Diversification. *Diversity.* 12(11): 415; https://doi.org/10.3390/d12110415

This page titled 6.2.3: The Biodiversity Crisis - HIPPPOC is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **5.4: Threats to Biodiversity** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.
- **10.3: Habitat Loss** by Melissa Ha and Rachel Schleiger is licensed CC BY-SA 4.0.
- **10.1: Atmospheric Pollution** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.
- **7.3: Water Pollution** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.
- **1.7: Carrying Capacity** is licensed CC BY 2.0. Original source: https://cnx.org/contents/ApdCwdkA.
- **1.6: History and Global Distribution** is licensed CC BY 2.0. Original source: https://cnx.org/contents/ApdCwdkA.
- **47.3: Threats to Biodiversity** by OpenStax is licensed CC BY 4.0.

Preserving Biodiversity

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.



Introduction

Preserving biodiversity is an extraordinary challenge that must be met by a greater understanding of biodiversity itself, changes in human behavior and beliefs, and various preservation strategies. The threats to biodiversity have been recognized for some time. Today, the main efforts to preserve biodiversity involve legislative approaches to regulate human and corporate behavior, setting aside protected areas, and habitat restoration. A lofty goal is to protect 50% of the Earth's natural spaces for wildlife known as the Half-Earth Project, as described by the late Dr. E.O. Wilson below. Others, such as David Attenborough and Dr. Sylvia Earle, weigh in on the issue as well.

Videos





6-minute video with famed conservationist David Attenborough



6-minute video with famed biologist E.O. Wilson



3-minute video with famed marine biologist Sylvia Earle

Question after watching: What common themes do you find in the messages of these conservation ambassadors?

Changing Human Behavior

Ultimately, human behavior will change when human values change. At present, the growing urbanization of the human population is a force that poses challenges to the valuing of biodiversity. Legal avenues can help to protect biodiversity in the meantime.

International Legislation

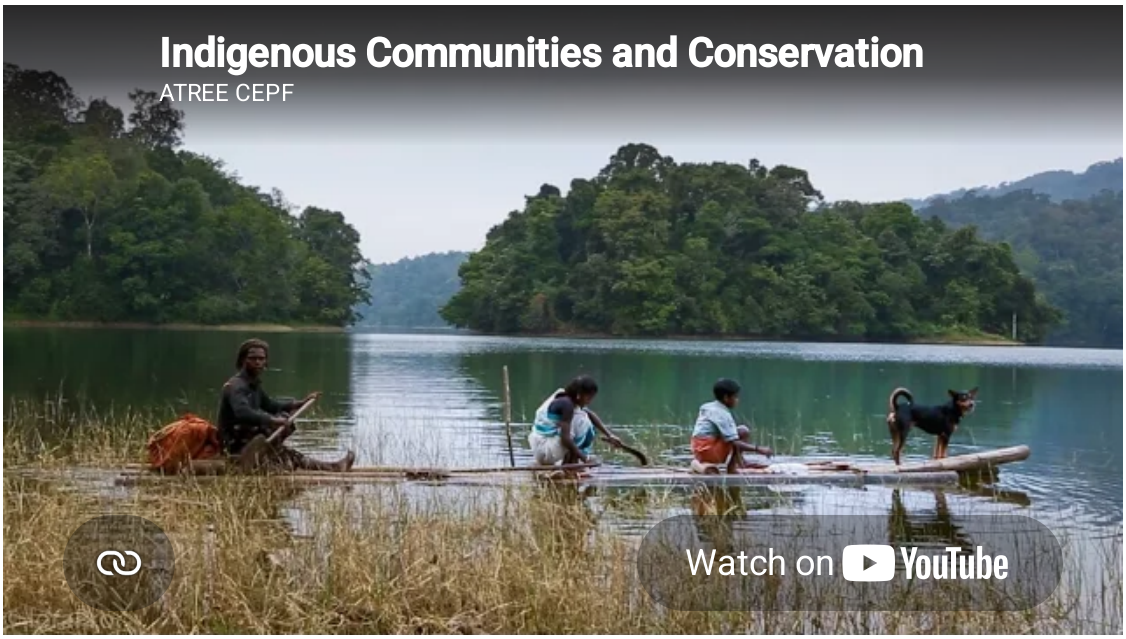
Legislation throughout the world has been enacted to protect species. The legislation includes international treaties as well as national and provincial laws. The Convention on International Trade in Endangered Species of Wild Fauna and Flora (**CITES**) agreement came into force in 1975. The agreement, and the national legislation that supports it in Canada and most other countries, provides a legal framework for preventing approximately 33,000 listed species from being transported across national borders, thus protecting them from being caught or killed when international trade is involved. The treaty is limited in its reach because it only deals with the international movement of organisms or their parts. It is also limited by some countries' ability or willingness to enforce the treaty and supporting legislation. The illegal trade in organisms and their parts is probably a market in the hundreds of millions of dollars. Illegal wildlife trade is monitored by a non-profit: Trade Records Analysis of Flora and Fauna in Commerce (**TRAFFIC**).

The **Convention on Biological Diversity** is now the leading international treaty to advance the conservation of biodiversity, within the context of a comprehensive agenda for sustainable development. The three key goals of the Convention are the conservation of biodiversity, the sustainable use of its components, and the equitable sharing of benefits from the use of genetic resources. The 194 ratified parties to the Convention are engaged in a multitude of cooperative initiatives and information and technology sharing, and are committed to identify and conserve their biodiversity.

A key action is to periodically undertake science assessments of the status of global biodiversity. Broadly speaking, the most recent assessment found that the prospects of biodiversity were rapidly worsening in many parts of the world, although considerable progress was being made in cooperative planning and in the designation of protected areas and other conservation measures in many countries. It is too soon to tell whether these international actions will be successful because the programs began only in the late 1970s (as an earlier program called the World Conservation Strategy). However, it is encouraging to know that this sort of comprehensive international effort exists and that almost all of Earth's nations are participating, including countries in all stages of economic development.

On an international level, important wilderness lands have been designated by the United Nations through its "**Man and the Biosphere Program**." This program was established in 1973 to protect examples of major natural regions throughout the world, and provide opportunities for ecological research and education.

Biosphere reserves are organized into three interrelated zones: the **core area**, the **buffer zone** and the **transition area**. The core area contains the landscape and ecosystems to be preserved. The buffer zone is an area where activities are controlled to protect the core area. The outer transition area contains a variety of agricultural activities, human settlements and other uses. Local communities, conservation agencies, scientists and private enterprises that have a stake in the management of the region work together to make the reserves work. Mt Kenya in Africa and the Galapagos Islands are examples of wilderness areas protected under this provision.





Optional Activity 6.2.4.1

The Convention on International Trade in Endangered Species (CITES) passed a resolution to protect rhinoceroses in the wild. Rhinoceroses have been hunted to the brink of extinction because their horns, which are made of the protein keratin, the same as humans' fingernails and hair, are considered an aphrodisiac and a powerful drug in some cultures. Why does the protection of rhinoceroses require an international agreement?

A. The rhinoceroses are hunted in their native countries, but the trade crosses borders.
B. The use of rhinoceros' horns as an aphrodisiac has showed negative effects internationally.
C. The hunters from different countries travel to the native country to hunt for rhinoceroses.
D. Their demand is greater in foreign countries as compared to their native countries.

Answer

A. The rhinoceroses are hunted in their native countries, but the trade crosses borders.

US Legislation

Within many countries there are laws that protect endangered species and that regulate hunting and fishing. In the United States, the **Endangered Species Act** (ESA) was enacted in 1973. When an at-risk species is listed by the Act, the U.S. Fish & Wildlife Service is required by law to develop a management plan to protect the species and bring it back to sustainable numbers. The ESA,

and others like it in other countries, is a useful tool, but it suffers because it is often difficult to get a species listed or to get an effective management plan in place once a species is listed.

The **Migratory Bird Treaty Act** (MBTA) is an agreement between the United States and Canada that was signed into law in 1918 in response to declines in North American bird species caused by hunting. The Act now lists over 800 protected species. It makes it illegal to disturb or kill the protected species or distribute their parts (much of the hunting of birds in the past was for their feathers). Examples of protected species include northern cardinals, the red-tailed hawk, and the American black vulture.

The ESA recognizes five categories of risk, each of which has a specific meaning in terms of imminent threats to the future survival of the species (COSEWIC, 2015).

- **Extinct** refers to any species of wildlife that was formerly indigenous to the US but no longer exists anywhere in the world.
- **Extirpated** refers to any species or subspecies that was formerly indigenous to the US but now only survives in the captivity or elsewhere, usually in Canada or Mexico.
- **Endangered** refers to native species that are faced with imminent extinction or extirpation throughout all or a significant portion of their range.
- **Threatened** refers to any indigenous taxon that is likely to become critically imperiled unless factors affecting its status are reversed.
- **Vulnerable** refers to any indigenous species that is not currently imperiled but is at risk of becoming so because of small or declining numbers, occurrence at the fringe of its range or in restricted areas, habitat fragmentation, or some other reason.

It must be recognized that the designation of species at risk is a continuing and always incomplete process. For instance, because the conservation status of only a few species of invertebrates has been investigated, critically imperiled species in this group are enormously under-represented in the ESA list. Unfortunately, more rapid progress is constrained by a shortage of funding for research and monitoring of endangered species, and by a lack of specialists with the necessary taxonomic and ecological skills and knowledge.

Of course, it is not sufficient merely to designate species as being at risk of extirpation or extinction. If their status is to be improved, the species and their habitats must also be protected. Remarkably, the US federal government has not yet enacted effective legislation to protect endangered species and their habitat across the whole of the country. However, this situation is starting to change.

However, federal legislation has little direct influence on the status of the many threatened and vulnerable species that are living on state, private, or Indigenous land. Most importantly, the Act does not fully address the protection of habitat of critically threatened species off federal land. To some degree, this deficiency is covered by legislation that has been enacted by states. However, their legislations are also not very effective, because they, too, do not protect the habitat of species at risk, especially on private land. Such a piecemeal approach results in uneven levels of protection for species-at-risk, which is unacceptable from the conservation viewpoint.

The lack of effective protection of species-at-risk in US is raising controversy. Governments feel the need to demonstrate that they are making rapid progress toward sustainability, an important component of which involves the protection of native species and their habitats. Unfortunately, the progress to date has been lacking and is not yet effective in protecting our biodiversity most at-risk. Hopefully, the lobbying efforts of non-governmental organizations (NGOs) will result in appropriate changes to the currently weak legislation of all levels of government.

Most of the natural ecosystems of the United States now exist only as small remnants of their former extent. Because of this, they are as endangered as the species they support. The most endangered of our natural ecosystems are:

- the tall-grass prairie of the Midwest
- old-growth forests of all of the US
- dry coastal forests of the southeast
- deserts of the southwest
- most freshwater wetlands

Some of these ecosystems are also rich in endangered species. It is imperative that the remaining areas of these endangered ecosystems become preserved in parks and other kinds of protected areas.

Video



In this 3 min video, you will be introduced to the argument that biodiversity loss results in economic loss in diverse ways, therefore natural resource management practices need to be applied.
Question after watching: Do you agree that biodiversity loss should be treated with natural resource management practices? What are the advantages and disadvantages of doing this?

Indigenous Connections: Preserving Salmon Fisheries

"Pacific salmon—fish known by a host of Indigenous names throughout their vast geographic range (genus Oncorhynchus)—have been in a state of decline in British Columbia (BC), Canada for several decades (Price et al. 2017) such that a growing number of wild salmon populations have been assessed as “at risk”’ (from Special Concern (n = 5 populations) to Threatened (n = 3) to Endangered (n = 10)) by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Government of Canada 2018). As both ecological and cultural keystone species, without the continued existence of salmon, ecosystems and societies alike would be entirely transformed (Willson and Halupka 1995; Garibaldi and Turner 2004)."[1]

"For the Nisga’a, which sits on the BC–Alaska border (and to which the lead author belongs), salmon are vital. They shape *ayuukhl* (code of law) and *adaawak* (oral histories), they figure centrally in *yukw* (feasts, known externally as “potlatches”), and they are a focal point of the Nisga’a Treaty (2000) that defines Nisga’a rights tied specifically to salmon. As Nisga’a and indeed many Indigenous nations identify as “Salmon People” (Columbia River Inter-Tribal Fish Commission 2020; Earth Economics 2021), there is serious concern about what will become of salmon-linked cultures, economies, knowledges, languages, laws, well-being, and worldviews as the annual return of these anadromous fish to rivers across the Pacific Northwest become increasingly unpredictable and, in many systems, Indigenous fisheries for wild salmon become a shadow of their former selves (Jacob, McDaniels and Hinch 2010; Atlas et al. 2021). Decolonial research strategies that respect Indigenous intellectual traditions and affirm Indigenous control over Indigenous knowledge are critical to the maintenance and recovery of salmon-based knowledge systems and salmon populations (Simpson 2004; Bingham et al. 2021)."[1]

> *Not only would it behoove fisheries scientists to use all and the best tools and knowledge available at this time of [social-ecological] crisis, irrespective of their origin and the perceived objectivity and superiority of Western scientific approaches, but this would importantly serve decolonial and reconciliatory efforts that help rectify uneven power relations, knowledge inequalities, and other racially linked and unjust dynamics in fisheries.*[3]

"Indigenous peoples have been managing landscapes more or less sustainably for thousands of years. Indigenous peoples’ successes stem, in part, from the fact that many Indigenous worldviews recognize that species do not exist in isolation; they are part of a natural system."[2]

"TEK provides invaluable time-tested resource management practices that can be used alongside WS to develop more workable and effective approaches to current resource management strategies than either could accomplish alone. In fact, it has become a policy requirement in Canada, and in particular Northern Canada, that TEK be incorporated into environmental assessments affecting wildlife management including: migratory birds, species at risk, forest practices, and fisheries management (Usher, 2000)."3

The Nisga'a Nation's understanding of, and work with, Pacific salmon is an excellent example of the role that Indigenous Science plays in understanding biodiversity and how to protect species and habitat in a sustainable manner.

"Through partnerships with 18 communities of “Salmon People” and semi-structured interviews with 48 knowledge holders (i.e., Elders), we learned that, on average, Elders spent more than half of a century actively engaged in salmon fishing and processing. Modern salmon catches are reported to be approximately one-sixth of what they were estimated to be five to seven decades ago, and the top five threats to salmon identified by Elders included (i) aquaculture, (ii) climate change, (iii) contaminants, (iv) industrial development, and (v) infectious diseases. Threat priorities varied regionally, reflecting distinct lived experiences and regional variation in the prevalence and impact of different threats. Elders perceived threats to salmon equally as threats to aquatic health and human well-being, with evidence that the relationships between people and water, and salmon and people, are being profoundly transformed."[1]

"The Nisga’a people of northern British Columbia live in the Nass Valley near Alaska. Every spring, members of some Nisga’a families still walk their salmon streams to ensure that spawning channels are clear of debris and that salmon are not obstructed in their ascent to spawning grounds. Concerned with the multiple perils faced by their Nass River salmon, the Nisga’a have themselves implemented a salmon protection project that uses both the ancient technology and wisdom practices, as well as modern statistical methods of data analysis to provide more reliable fish counts than electronic tracking systems (Figure 6.2.4.1). The Nisga’a project, which earned a Department of Fisheries and Oceans Canada award, is described in the following account by Corsiglia and Snively (1997)

> *"Observing that electronic fish counters can be inaccurate, the Nisga’a have instituted an ingenious fish counting system in the Nass River that combines ancient fish wheel technology with modern statistical methods. The ancient fish wheel was made of cedar wood and nettle fibre mesh, and the elongated axle of the fish wheel was fitted with three parallel vanes constructed in the form of large, flattened dip nets. The swift moving downstream current turned the wheel by exerting force against the submerged vanes, and as the companion vanes rose in turn, they gently caught and uplifted the fish as they swam upriver. As each vane rose from the horizontal, the fish slid toward wooden baffles that guided them out of the side of the fish wheel and into submerged holding baskets. This technology provided the Nisga’a with an effortless fishing technique as well as a ready supply of fresh salmon."[3] (p. 19)*

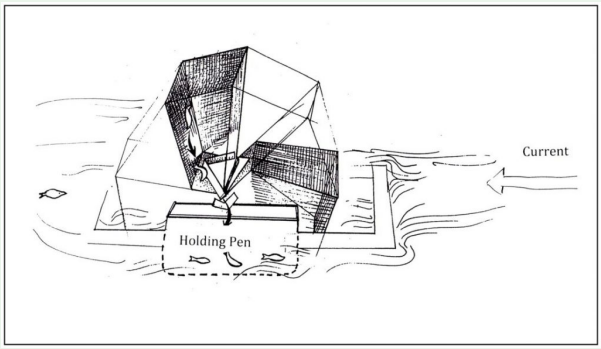


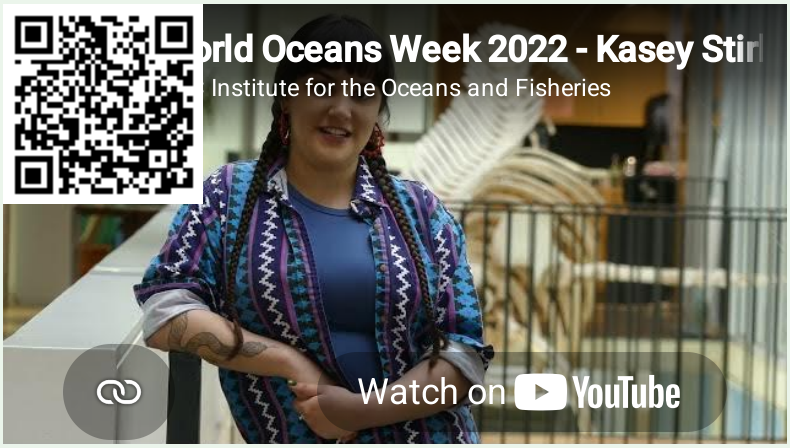
Figure 6.2.4.1. *Nisga’a fish wheel showing holding pen. Illustration by Laura Corsiglia (1997).*

"Modern Nisga'a fishing wheels are made of aircraft aluminum and nylon mesh. Like their predecessors, these fish wheels allow fish to be captured live and held in holding tanks. This enables the Nisga'a to tag and count the fish by means of statistical analysis. Returning salmon are first caught using a fish wheel at a lower river station where fish are tagged. Fish are also caught at an upper fish station where the proportion of tagged fish is used to calculate returns. Reportedly, "this system provides more accurate and reliable data than that collected by electronic tracking systems alone" (Chief Harry Nyce, personal communication to John Corsiglia, 1986)."[3]

In a similar context, the Wuikinuxv of central British Columbia identify the season's quotas for salmon not only with humans in mind but also with bears. They recognize that not only are the bears an important part of their ecosystem and culture but, if the bears are well-fed with salmon, they are less likely to seek out food in areas where humans live. The forest and other inhabitants that the Wuikinuxv rely on are nourished in one way or another by the remains of the salmon.[2]

"The Wuikinuxv calculate fishing quotas based on salmon availability and existing bear density, assuming that, as salmon populations recover, the bear population will grow until it is limited by some other factor. Salmon and bear numbers are then balanced against the benefits of salmon to human fishers. Spawning targets aim to balance the costs felt by humans and bears, the latter of which encompasses the needs of other beings in the ecosystem. In contrast, Canada manages salmon at the federal level, while bears are managed provincially, making holistic management difficult. The smaller, more intimate scale of Indigenous management efforts, in contrast, allows closer observation of the landscape...and demonstrates how local knowledge is often undervalued".[2]

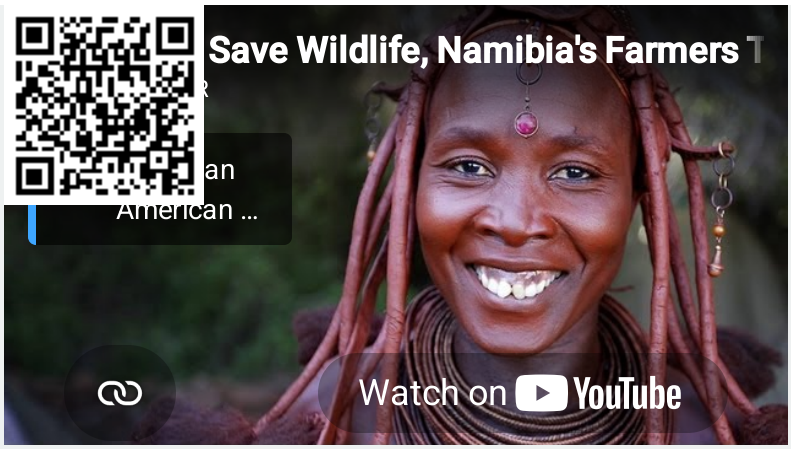
"In a decolonized approach to conservation, the observations of people living in the area would be given proper respect, and systems would be in place to incorporate those observations into models. Another step toward decolonizing conservation...is for settler governments to work with Indigenous communities as equals rather than as just one of many stakeholders. Resource stewardship should be inseparable from Indigenous sovereignty, assert the study's authors."[2]



In this 2.5-minute video, you will meet Kasey Stirling, a Nlaka'pamux, Mi'kmaq, and Acadienne researcher, is a master's student in the Centre for Indigenous Fisheries at the Institute for the Oceans and Fisheries (IOF). Stirling works in partnership with the First Nations Fisheries Legacy Fund, a collective of six Lower Fraser First Nations (Katzie, Kwantlen, Kwikwetlem, Musqueam, Tsleil-Waututh, and Tsawwassen), to co-develop a more culturally relevant framework for watershed health assessment, which directly impacts salmon populations.

Question after watching: What might be gained from scientists working in partnership with Indigenous communities to preserve diversity? What type of knowledge and perspective can each group bring to the partnership?

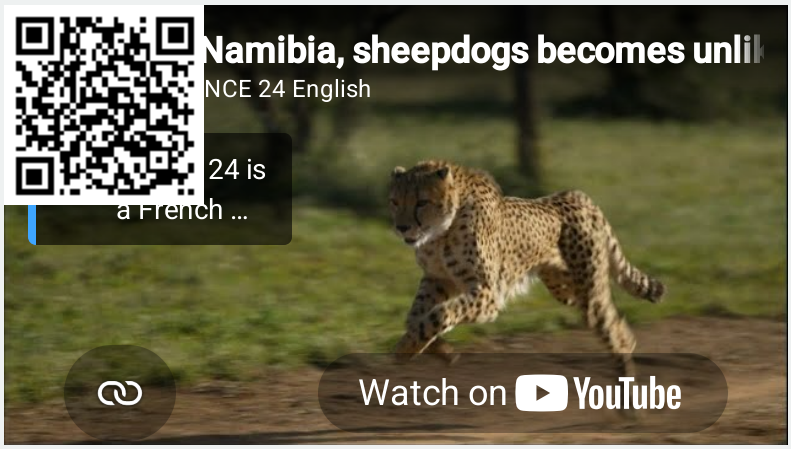
Video



Imagine the U.S. government told people who live around Yellowstone, say, all those bears and wolves are now yours to take care of, and for doing that you get to keep the money from tourists who come to see those animals. It can sound radical, but that's essentially what the government of Namibia is doing right now. And as a result, wildlife numbers are rising there - unlike much of Africa.

Question after watching:

Video



Namibia is home to around 3,500 cheetahs, or half the world's cheetah population. But the animals there are threatened by farmers, who often shoot them on sight to defend their herds. To protect the big cats, one wildlife sanctuary had the idea of training sheepdogs.

Question after watching:

Adapting to and Mitigating Climate Change

More on climate change is discussed in the next section, but it should be clear to anyone that climate change has the potential to greatly restructure the world's ecosystems, ecosystem services, and national economies. Many coastal areas will experience rising sea levels and increased flooding, while inland areas may experience desertification and less favorable growing conditions for crops. Poorer countries and communities will suffer the consequences disproportionately because of their limited mobility, high dependence on ecosystem services, and general lack of disaster management infrastructure.

If we are to mitigate the far-reaching impacts of climate change, we must carefully monitor and study changes in biological communities and ecosystem functioning, and how they relate to changes in climate and other stressors. While we may lose some species in a warmer world, we can also prevent many extinctions with proactive wildlife management. It is likely that many existing protected areas will no longer preserve some of the rare and threatened species that currently live in them, necessitating

careful planning when establishing new protected areas. Even if climate change is not as severe as predicted, the steps we take now to safeguard biodiversity can only help in the future.

The widespread and dramatic impacts of climate change rightfully deserve much attention. But it is also important to remember that we continue to destroy habitats at a massive scale and increasing pace and this loss of habitat is currently the main cause of species extinctions. The highest priorities for conservation must continue to be the preservation of healthy, intact, and connected ecosystems, and the restoration of degraded ecosystems. These actions will simultaneously reduce the impacts of climate change, by reducing carbon emissions, increasing carbon sequestration, and giving wildlife more opportunities to adjust their ranges, in their own time, as the world's climate changes.

Videos



Indigenous communities in British Columbia are preparing for climate change, as detailed in this 5-minute video. Question after watching: How are Indigenous communities reconnecting to the land in a changing climate? What other strategies are they utilizing internally and sharing with non-Indigenous communities?

Conservation in Preserves

Video



This 10-minute video by Hank Green provides an overview of both conservation science and restoration efforts, described in further detail below.

Question after watching: What conserved spaces are nearest to you? Do you visit them? Do you know of any restoration efforts near where you live?

The establishment of wildlife and ecosystem **preserves** is one of the key tools in conservation efforts (Figure 6.2.4.2). A preserve is an area of land set aside with varying degrees of protection for the organisms that exist within the boundaries of the preserve. Preserves can be effective in the short term for protecting both species and ecosystems, but they face challenges that scientists are still exploring to strengthen their viability as long-term solutions. Human behavior can still be problematic in these areas as well. For example, the public's misbehavior at national parks has become an increasing problem for governments in many countries.



Figure 6.2.4.2: National parks, such as Kootenay National Park in British Columbia, help conserve biodiversity. (Parks Canada)

Video



This 3-minute video from the National Resources Defense Council profiles the importance of Canada's boreal forest and current threats to this ecosystem.

Question after watching: What strategies might be used to preserve these habitats?

US Preservation

An important human-centered benefit of undeveloped land is their recreational value. Every year, millions of people visit recreational lands such as parks and wilderness areas to experience attractions of the great outdoors: hiking among the giant sequoias in California, traveling on a photo safari in Kenya or just picnicking at a local county park. Besides providing people with obvious health benefits and aesthetic pleasures, recreational lands also generate considerable tourist money for government and local economies.

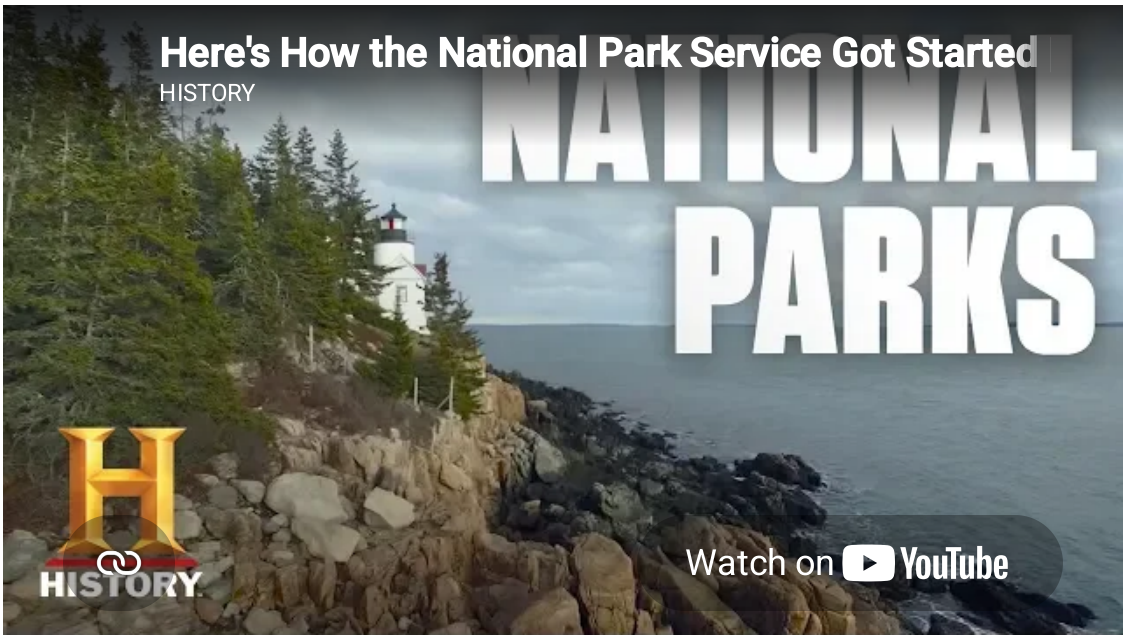
The United States has set aside more land for public recreational use than any other country. Several different federal organizations provide lands for recreational use: the National Forest System, the U.S. Fish and Wildlife Service, the National Park System and the National Wilderness Preservation System. The National Forest System manages more than 170 forestlands and grasslands, which are available for activities such as camping, fishing, hiking and hunting.

The U.S. Fish and Wildlife Service manage more than 500 National Wildlife Refuges, which not only protect animal habitats and breeding areas but also provide recreational facilities. The National Park System manages more than 380 parks, recreation areas, seashores, trails, monuments, memorials, battlefields and other historic sites. The National Wilderness Preservation System manages more than 630 roadless areas through the aforementioned government services as well as through the Bureau of Land Management.

The **National Park System** consists of more than 80 million acres nationwide. The largest national park is Wrangell-St. Elias National Park and Preserve in Alaska with over 13 million acres. California has eight national parks: Channel Islands, Death Valley, Joshua Tree, Lassen, Redwood, Sequoia, Kings Canyon and Yosemite. Many national parks such as Yosemite, Yellowstone and the Grand Canyon are such popular recreation destinations that the ecosystems of those parks are being severely tested by human activities.

In addition to their primary goal of conserving biodiversity, most parks serve additional purposes, including the support of economically important outdoor recreation and tourism. To some degree, the use of parks for these purposes is a challenge to their

ability to function as ecological reserves. For example, strictly interpreted, the ecological values of national parks are not compatible with consumptive uses of their natural resources (such as sport fishing) or with the development of infrastructure to support recreation and tourism (such as campgrounds, golf courses, hotels, roads, ski facilities, and even interpretation facilities).









Every state has also set aside significant amounts of land for recreational use. The California State Park System manages more than one million acres of parklands including: coastal wetlands, estuaries, scenic coastlines, lakes, mountains and desert areas. California's largest state park is Anza-Borrego Desert State Park, which is the largest state park in the United States with 600,000 acres. The stated mission of the California State Park System is: "To provide for the health, inspiration and education of the people of California by helping to preserve the state's extraordinary biological diversity, protecting its most valued natural and cultural resources and creating opportunities for high-quality outdoor recreation."

This is the basic goal of all recreational lands: to manage and conserve natural ecosystems, while supporting a sustainable and balanced level of human use of those areas. Unfortunately, it is a goal which is sometimes difficult to achieve due to the increasing popularity and use of recreational lands.

The "**Wilderness Act of 1964**" created the world's first wilderness system in the United States. Presently, the **National Wilderness Preservation System** contains more than 100 million acres of land that will forever remain wild. A wide range of recreation, scientific and outdoor activities are available in wilderness lands. Mining operations and livestock grazing are permitted to continue in certain wilderness areas where such operations existed prior to an area's designation. Hunting and fishing are also allowed in wilderness areas (except in national parks).

For most people, wilderness lands provide a means for various forms of recreation: hiking, horseback riding, bird watching, fishing, and hunting. People can escape the stress of modern-day life and enjoy an undisturbed look at nature. Wilderness lands provide an essential habitat for a wide array of fish, wildlife, and plants, and are particularly important in protecting endangered

species. For scientists, wilderness lands serve as natural laboratories, where studies can be performed that would not be possible in developed areas.

Several other types of public lands complement the designated wilderness land system. These include: national forest roadless areas, national trails system, natural research areas and state and private wilderness lands. The national forest roadless areas consist of millions of acres of wild, undeveloped land without roads that exist on National Forest land outside of designated wilderness lands.

The "**National Trail System**," established by Congress in 1968, includes trails in wilderness areas and other public lands. **Research Natural Areas** located throughout the country on public lands serve as outdoor laboratories to study natural systems. They are intended in part to serve as gene pools for rare and endangered species and as examples of significant natural ecosystems. Some wilderness lands are maintained by states or private organizations. For example, the state of New York has long preserved a region of the Adirondacks as wilderness.

In addition to their primary goal of conserving biodiversity, most parks serve additional purposes, including the support of economically important outdoor recreation and tourism. To some degree, the use of parks for these purposes is a challenge to their ability to function as ecological reserves. For example, strictly interpreted, the ecological values of national parks are not compatible with consumptive uses of their natural resources (such as sport fishing) or with the development of infrastructure to support recreation and tourism (such as campgrounds, golf courses, hotels, roads, ski facilities, and even interpretation facilities).

The ecological-reserve function of many protected areas is also threatened by land-use and management activities that are occurring in their surrounding area. Usually, the most important of the “external” stressors are associated with agriculture, forestry, mining, tourism, or hydroelectric development. In fact, all of the national parks in more southern regions of Canada are significantly threatened in this way.

Banff National Park in southwestern Alberta was the first national park to be established in Canada, in 1885. The original intent was to protect extremely scenic views and hot springs and to develop the area in support of the economic benefits of tourism. It was not until several decades later that the philosophical underpinning of national parks shifted toward the protection of natural values. In any event, the early development of Banff featured the enthusiastic construction of large hotels, golf courses, skiing facilities, major highways, a transcontinental railroad, several villages, and other structures. This pattern continues today with much ongoing construction, coupled with rapid development of the area east of the park for tourism, residential neighborhoods, forestry, and other uses. These facilities severely threaten the long-term viability of the natural values of Banff.

Provincial and territorial governments also have a responsibility to protect natural values within their jurisdiction. These governments have designated many ecological reserves and wilderness areas, supplemented by natural areas that are protected in provincial parks and conservation areas, which are also well-used for recreation. Some municipalities also have natural-area parks that provide habitat for native species. An outstanding example is the city of Windsor, Ontario, which is protecting important remnants of tall-grass prairie and Carolinian forest, and their many species-at-risk.

How Much Area to Preserve?

Due to the way protected lands are allocated (they tend to contain less economically valuable resources rather than being set aside specifically for the species or ecosystems at risk) and the way biodiversity is distributed, determining a target percentage of land or marine habitat that should be protected to maintain biodiversity levels is challenging. The IUCN World Parks Congress estimated that 11.5% of Earth’s land surface was covered by preserves of various kinds in 2003. This area is greater than previous goals; however, it only represents 9 out of 14 recognized major biomes. Research has shown that 12% of all species live only outside preserves; these percentages are much higher when only threatened species and high-quality preserves are considered. For example, high-quality preserves include only about 50% of threatened amphibian species. The conclusion must be that either the percentage of area protected must increase, the percentage of high-quality preserves must increase, or preserves must be targeted with greater attention to biodiversity protection. Researchers argue that more attention to the latter solution is required.

A **biodiversity hotspot** is a conservation concept developed by Norman Myers in 1988. Hotspots are geographical areas that contain high numbers of endemic species. The purpose of the concept was to identify important locations on the planet for conservation efforts, a kind of conservation triage. Protecting hotspots would be able to protect a larger number of species. The original criteria for a hotspot included the presence of 1,500 or more species of endemic plants and 70 percent of the area disturbed

by human activity. While many have still not been conserved, there are now 34 identified global biodiversity hotspots (Figure 6.2.4.3) that contain large numbers of endemic species, which include half of Earth's endemic plants. In addition to natural spaces, there are numerous human cultural sites preserved in the **UNESCO World Heritage Sites** list: https://whc.unesco.org/en/list/

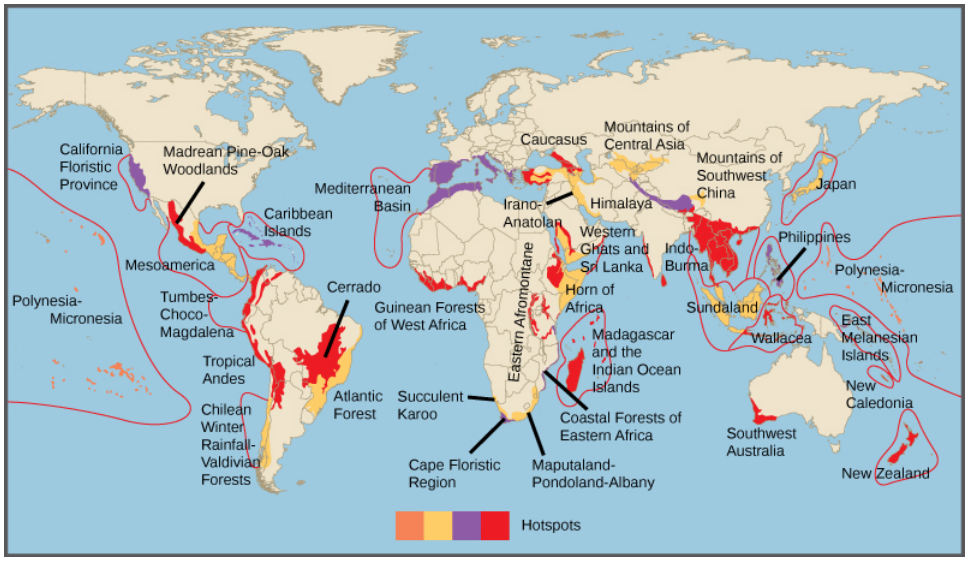


Figure 6.2.4.3. Conservation International has identified 34 biodiversity hotspots. Although these cover only 2.3 percent of the Earth's surface, 42 percent of the terrestrial vertebrate species and 50 percent of the world's plants are endemic to those hotspots.

? Optional Activity 6.2.4.2

Scientists are evaluating an island ecosystem for consideration as a biodiversity hotspot. What information should they collect and evaluate as part of their fieldwork to produce their final assessment?

a. the total number of endemic species in an ecosystem
b. the total number of organisms in an ecosystem
c. the total number of species divided by the area of the ecosystem
d. the total number of endangered species in an ecosystem

Answer

A. the total number of endemic species in an ecosystem.

Preserve Design

There has been extensive research into optimal preserve designs for maintaining biodiversity. The fundamental principle behind much of the research has been the seminal theoretical work of Robert H. MacArthur and Edward O. Wilson published in 1967 on island biogeography.[1] This work sought to understand the factors affecting biodiversity on islands. The fundamental conclusion was that biodiversity on an island was a function of the origin of species through migration, speciation, and extinction on that island. Islands farther from the mainland are harder to get to, so migration is lower and the equilibrium number of species is lower. Within island populations, evidence suggests that the number of species gradually increases to a level similar to the numbers on the mainland from which the species is suspected to have migrated. In addition, smaller islands are harder to find, so their immigration rates for new species are lower. Smaller islands are also less geographically diverse so there are fewer niches to promote speciation. And finally, smaller islands support smaller populations, so the probability of extinction is higher.

As islands get larger, the number of species accelerates, although the effect of island area on species numbers is not a direct correlation. Conservation preserves can be seen as "islands" of habitat within "an ocean" of non-habitat. For a species to persist in a preserve, the preserve must be large enough. The critical size depends, in part, on the home range that is characteristic of the species. A preserve for wolves, which ranges hundreds of kilometers, must be much larger than a preserve for butterflies, which might range within ten kilometers during its lifetime. But larger preserves have more core area of optimal habitat for individual

species, they have more niches to support more species, and they attract more species because they can be found and reached more easily.

Preserves perform better when there are buffer zones around them of suboptimal habitat. The buffer allows organisms to exit the boundaries of the preserve without immediate negative consequences from predation or lack of resources. One large preserve is better than the same area of several smaller preserves because there is more core habitat unaffected by edges. For this same reason, preserves in the shape of a square or circle will be better than a preserve with many thin "arms." If preserves must be smaller, then providing wildlife corridors between them so that individuals and their genes can move between the preserves, for example along rivers and streams, will make the smaller preserves behave more like one large one. All of these factors are taken into consideration when planning the nature of a preserve before the land is set aside.

In addition to the physical, biological, and ecological specifications of a preserve, there are a variety of policy, legislative, and enforcement specifications related to the uses of the preserve for functions other than the protection of species. These can include anything from timber extraction, mineral extraction, regulated hunting, human habitation, and non-destructive human recreation. Many of these policy decisions are made based on political pressures rather than conservation considerations. In some cases, wildlife protection policies have been so strict that subsistence-living Indigenous populations have been forced from ancestral lands that fell within a preserve. In other cases, even if a preserve is designed to protect wildlife, if the protections are not or cannot be enforced, the preserve status will have little meaning in the face of illegal poaching and timber extraction. This is a widespread problem with preserves in areas of the tropics.

? Optional Activity 6.2.4.3

A preserve design is proposed for a densely populated suburban area. Which overall design plan would be best for preservation of local ecosystems?

A. Set up many, small, unconnected, protected areas.
B. Select one, small area that is isolated from residences.
C. Plan buffer zones around all backyard spaces.
D. Set up several, connected, larger areas to be set aside for natural ecosystems.

Answer

D. Set up several, connected, larger areas to be set aside for natural ecosystems.

Limitations on Preserves

Some of the limitations of preserves as conservation tools are evident from the discussion of preserve design. Political and economic pressures typically make preserves smaller, never larger, so setting aside areas that are large enough is difficult. If the area set aside is sufficiently large, there may not be sufficient area to create a buffer around the preserve. In this case, an area on the outer edges of the preserve inevitably becomes a riskier suboptimal habitat for the species in the preserve. Enforcement of protections is also a significant issue in countries without the resources or political will to prevent poaching and illegal resource extraction.

Climate change will create inevitable problems with the location of preserves. The species within them will migrate to higher latitudes as the habitat of the preserve becomes less favorable. Scientists are planning for the effects of global warming on future preserves and striving to predict the need for new preserves to accommodate anticipated changes to habitats; however, the end effectiveness is tenuous since these efforts are prediction-based.

Finally, an argument can be made that conservation preserves reinforce the cultural perception that humans are separate from nature, can exist outside of it, and can only operate in ways that do damage to biodiversity. Creating preserves reduces the pressure on human activities outside the preserves to be sustainable and non-damaging to biodiversity. Ultimately, the political, economic, and human demographic pressures will degrade and reduce the size of conservation preserves if the activities outside them are not altered to be less damaging to biodiversity.

Habitat Restoration

Habitat restoration holds considerable promise as a mechanism for restoring and maintaining biodiversity. Of course, once a species has become extinct, its restoration is impossible. However, **restoration** can improve the biodiversity of degraded ecosystems. Reintroducing wolves, a top predator, to Yellowstone National Park in 1995 led to dramatic changes in the ecosystem that increased biodiversity (Figure 6.2.4.4).

The wolves, a keystone species, function to suppress elk and coyote populations and provide more abundant resources to the guild of carrion eaters. Reducing elk populations has allowed the revegetation of riparian areas, which has increased the diversity of species in that habitat. Decreasing the coyote population has increased the populations of species that were previously suppressed by this predator. The number of species of carrion eaters has increased because of the predatory activities of the wolves.

The results from the Yellowstone experiment suggest that restoring a keystone species can have the effect of restoring biodiversity in the community. Ecologists have argued for the identification of keystone species where possible and for focusing protection efforts on those species; likewise, it also makes sense to attempt to return them to their ecosystem if they have been removed.

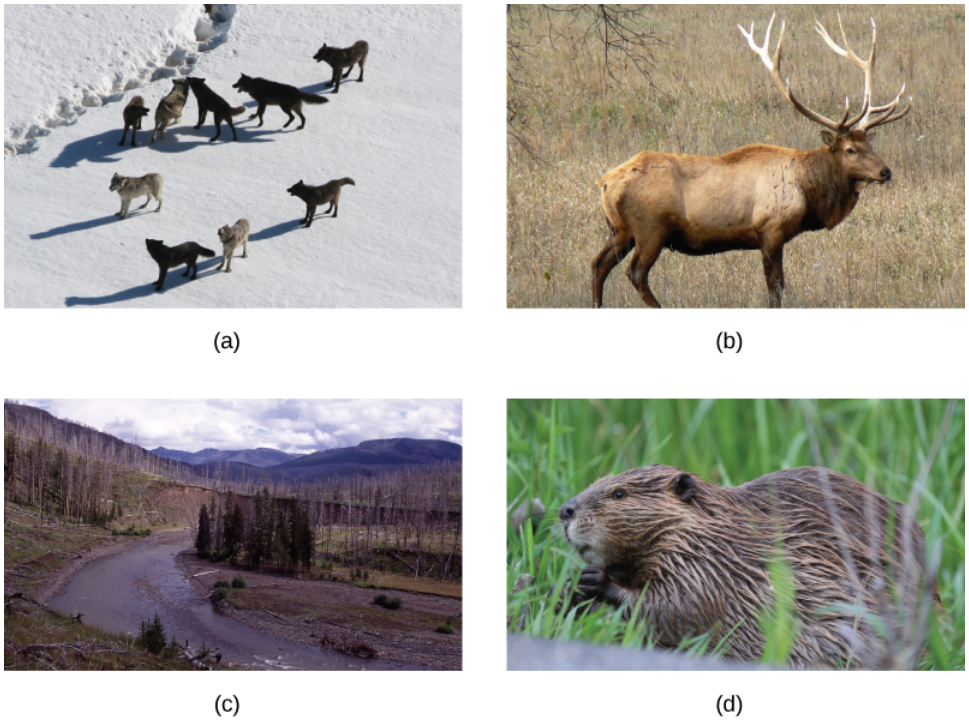


Figure 6.2.4.4: (a) The Gibbon wolf pack in Yellowstone National Park, March 1, 2007, represents a keystone species. The reintroduction of wolves into Yellowstone National Park in 1995 led to a change in the grazing behavior of (b) elk. To avoid predation, the elk no longer grazed exposed stream and riverbeds, such as (c) the Lamar Riverbed in Yellowstone. This allowed willow and cottonwood seedlings to grow. The seedlings decreased erosion and provided shading to the creek, which improved fish habitat. A new colony of (d) beaver may also have benefited from the habitat change. (credit a: modification of work by Doug Smith, NPS; credit c: modification of work by Jim Peaco, NPS; credit d: modification of work by “Shiny Things”/Flickr)

Other large-scale restoration experiments underway involve dam removal. Since the mid-1980s, many aging dams are being considered for removal rather than replacement because of shifting beliefs about the ecological value of free-flowing rivers and because many dams no longer provide the benefit and functions that they did when they were first built. The measured benefits of dam removal include restoration of naturally fluctuating water levels (the purpose of dams is frequently to reduce variation in river flows), which leads to increased fish diversity and improved water quality.

On the Pacific coast, dam removal projects are expected to increase populations of salmon, which is considered a keystone species because it transports key nutrients to inland ecosystems during its annual spawning migrations. In other regions such as the Atlantic coast, dam removal has allowed the return of other spawning anadromous fish species (species that are born in freshwater, live most of their lives in salt water, and return to freshwater to spawn). Some of the largest dam removal projects have yet to occur or have happened too recently for the consequences to be measured. The large-scale ecological experiments that these removal projects constitute will provide valuable data for other dam projects slated either for removal or construction.

Video



This 2.5-minute video highlights the work to create and restore vital habitat for pacific salmon in the Upper Pitt watershed in B.C., on the unceded territory of the Katzie First Nation.

Question after watching: How did the members restore the habitat and why were these efforts good for the salmon?

The Role of Zoos and Aquariums in Conservation

Zoos and aquariums have sought to play a role in conservation efforts both through captive breeding programs and education (Figure 6.2.4.5). The transformation of the missions of zoos and aquariums from collection and exhibition facilities to organizations that are dedicated to conservation is ongoing. In general, it has been recognized that, except in some specifically targeted cases, captive breeding programs for endangered species are inefficient and often prone to failure when the species are reintroduced to the wild. These facilities are far too limited to contemplate captive breeding programs for the number of species that are now at risk. Education, on the other hand, is a potential positive impact of zoos and aquariums on conservation efforts, particularly given the global trend to urbanization and the consequent reduction in contact between people and wildlife. A number of studies have been performed to look at the effectiveness of these facilities on people's attitudes and actions regarding conservation and at present, the results tend to be mixed.



Figure 6.2.4.5. Zoos and captive breeding programs have helped to preserve many endangered species, such as the golden lion tamarin. (credit: Garrett Ziegler)

6.2.S: Chapter Resources

Summary

Biodiversity exists at multiple levels of organization, and is measured in different ways depending on the goals of those taking the measurements. These include numbers of species, genetic diversity, chemical diversity, and ecosystem diversity. Humans use many compounds that were first discovered or derived from living organisms as medicines: secondary plant compounds, animal toxins, and antibiotics produced by bacteria and fungi. Ecosystems provide ecosystem services that support human agriculture: pollination, nutrient cycling, pest control, and soil development and maintenance. Loss of biodiversity threatens these ecosystem services and risks making food production more expensive or impossible. The core threats to biodiversity are human population growth and unsustainable resource use. Climate change is predicted to be a significant cause of extinction in the coming century. Exotic species have been the cause of a number of extinctions and are especially damaging to islands and lakes. International treaties such as CITES regulate the transportation of endangered species across international borders. In the United States, the Endangered Species Act protects listed species but is hampered by procedural difficulties and a focus on individual species. The Migratory Bird Act is an agreement between Canada and the United States to protect migratory birds. Presently, 11 percent of Earth's land surface is protected in some way. Habitat restoration has the potential to restore ecosystems to previous biodiversity levels before species become extinct. Examples of restoration include reintroduction of keystone species and removal of dams on rivers.

Review Questions

1. Bacteria that feed upon decaying organic matter in the soil would best be described as which one of the following?
   A. Eukaryotic
   B. Autotrophic
   C. Fungi
   D. Cyanobacteria
   E. Heterotrophic
2. As Darwin recognized, populations evolve through natural selection when which of the following condition(s) are met?
   A. Variation of traits among individuals
   B. Competition for limited resources
   C. More offspring are produced than can survive
   D. All of the above
3. You are the world's foremost expert on lizards. You have traveled the world extensively and have found that a particular species of lizard is found only in one desert near of the Chilean Andes. Which of following terms, with regard to its distribution, can be definitively applied to this species?
   A. Endangered
   B. Prokaryotic
   C. Endemic
   D. Disbursed
   E. Clustered
4. Which one of the following is not a major cause of biodiversity loss?
   A. Habitat loss
   B. Climate change
   C. Invasive Species
   D. Zoonotic diseases
   E. Overharvesting
5. Which one of the following statements is false?
   A. There have been five mass extinctions preserved in the fossil record
   B. Some bacteria are autotrophs
   C. Current rates of extinction are higher than background extinction rates
   D. Speciation is the process of creating new species

E. All living things can be classified into one of four taxonomic domains

6. During the middle of the 19th century, which scientist independently derived and proposed a theory of evolution that was similar to Darwin's?
   A. Gregor Mendel
   B. Alfred Wallace
   C. Isaac Newton
   D. Rachel Carson
   E. Niels Bohr
7. The study of the distribution of the world's species both in the past and in the present is known by what term?
   A. Geology
   B. Biogeography
   C. Biodiversity
   D. Biogeomorphology
   E. Ecological Succession
8. Which one of the following would be described as anthropogenic?
   A. Water backing up behind a beaver dam
   B. The dinosaurs going extinct
   C. Logging a forest
   D. A mudslide burying a stream
   E. A volcanic eruption
9. By definition, what are you most likely to find in a biodiversity hotspot?
   A. A large abundance of endangered species
   B. A large number of endemic species
   C. Mostly eukaryotic species
   D. Extremophiles
   E. Heat-loving microbes
10. You are working as a biologist for a team surveying biodiversity in the Amazon rainforest. You find a non-motile organism that grows in the soil, has eukaryotic cells, and is heterotrophic. Which one of the following could potentially describe this species?
    A. Fungus
    B. Animal
    C. Bacteria
    D. Plant
    E. Archaea

See Appendix for answers

Attributions

OpenStax College. (2013). *Concepts of biology*. Retrieved from http://cnx.org/contents/b3c1e1d2-839...9a8aafbdd@8.10. OpenStax CNX. Available under Creative Commons Attribution License 3.0 (CC BY 3.0). Modified from Original.

Page attribution: Essentials of Environmental Science by Kamala Doršner is licensed under CC BY 4.0. "Review Questions" is licensed under CC BY 4.0 by Matthew R. Fisher.

This page titled 6.2.S: Chapter Resources is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg via source content that was edited to the style and standards of the LibreTexts platform.

- **5.6: Chapter Resources** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.

CHAPTER OVERVIEW

6.3: Climate Change

Learning Objectives

- Describe the major causes of anthropogenic global climate change
- Identify impacts of global climate change on living systems and human civilization
- Suggest personal and systemic adaption and mitigation measures to address global climate change

6.3.1: Introduction to Climate Change
6.3.2: Anthropogenic Climate Change
6.3.3: Current and Future Climate Change Impacts
6.3.4: Climate Strategies

This page titled 6.3: Climate Change is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

6.3.1: Introduction to Climate Change

Introduction to Climate Change

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Define global climate change
- Summarize the effects of the Industrial Revolution on global atmospheric carbon dioxide concentration
- Describe three natural factors affecting long-term global climate
- List two or more greenhouse gases and describe their role in the greenhouse effect

Introduction

All biomes are universally affected by global conditions, such as climate, that ultimately shape each biome's environment. Scientists who study climate have noted a series of marked changes that have become increasingly evident during the last sixty years. **Climate change** refers to the complete set of climate characteristics—temperature; precipitation; pressure systems; wind patterns; and oceanic currents—that are changing locally, regionally, and globally due to human influences. It is closely related to **global warming**, also called global heating, which describes the general trend of increasing global temperatures we see under climate change. However, *climate change* is more inclusive of the totality of abiotic effects of a warming planet.

Climate and Weather

A common misconception about global climate change is that a specific weather event occurring in a particular region (for example, a very cool week in June in central Saskatchewan) is evidence of global climate change. However, a cold week in June is a weather-related event and not a climate-related one. These misconceptions often arise because of confusion over the terms climate and weather.

Video



Discover the real reason we confuse weather and climate in this 5-minute video from Hot Mess (US PBS). Question after watching: How does our personal experience of weather have an effect on how we view climate change?

Climate refers to the long-term, predictable atmospheric conditions of a specific area. The climate of a biome is characterized by having consistent temperature and annual rainfall ranges. Climate does not address the amount of rain that fell on one particular day in a biome or the colder-than-average temperatures that occurred one season. In contrast, **weather** refers to the conditions of the atmosphere during a short period of time. Weather forecasts are usually made for 48-hour cycles. Long-range weather forecasts are available but can be unreliable.

To better understand the difference between climate and weather, imagine that you are planning an outdoor event in Kamloops, BC. You would be thinking about *climate* when you plan the event in the summer rather than the winter because you have long-term knowledge that any Saturday in May through August would be a better choice for an outdoor event in Kamloops than a Saturday in January. However, you cannot determine the specific day on which that event should be held because it is difficult to accurately predict the weather. Climate can be considered "average" weather.

? Optional Activity 6.3.1.1

Which of the following is an example of climate?

A. An intense thunderstorm in Houston.
B. The average temperature in Chicago over the past 50 years.
C. An unusually hot fall in Boston.
D. A foggy day in San Francisco.

Answer

B. The average temperature in Chicago over the past 50 years.

Global Climate Change

Climate change can be understood by approaching three areas of study:

- current and past global climate change
- causes of past and present-day global climate change
- ancient and current results of climate change

It is helpful to keep these three different aspects of climate change clearly separated when consuming media reports about global climate change. It is common for reports and discussions about global climate change to confuse the data showing that Earth's climate is changing with the factors that drive this climate change.

Evidence for Past and Current Global Climate Change

Since scientists cannot go back in time to directly measure climatic variables, such as average temperature and precipitation, they must instead indirectly measure temperature. To do this, scientists rely on historical evidence of Earth's past climate.

Antarctic ice cores are a key example of such evidence. These **ice cores** are samples of polar ice obtained by means of drills that reach thousands of meters into ice sheets or high mountain glaciers. Viewing the ice cores is like traveling backwards through time; the deeper the sample, the earlier the time period. Trapped within the ice are bubbles of air and other biological evidence that can reveal temperature and carbon dioxide data. Antarctic ice cores have been collected and analyzed to indirectly estimate the temperature of the Earth over the past 400,000 years (Figure 6.3.1.1a). The 0°C on this graph refers to the long-term, modern-day average. Temperatures that are greater than 0°C exceed Earth's long-term average temperature. Conversely, temperatures that are less than 0°C are less than Earth's average temperature. This figure shows that there have been periodic cycles of increasing and decreasing temperature.

Before the late 1800s, the Earth was as much as 9°C cooler and as much as 3°C warmer. Most of the past 400,000 years have been colder than today. Most of the past warming and cooling periods happened over long enough time scales that the majority of organisms were able to adapt and evolve with the changing climate.

The graph in Figure 6.3.1.1b shows that the atmospheric concentration of carbon dioxide has also risen and fallen in periodic cycles. Note the relationship between carbon dioxide concentration and temperature. Figure 6.3.1.1b shows that carbon dioxide levels in the

atmosphere have historically cycled between 180 and 300 parts per million (ppm) by volume.

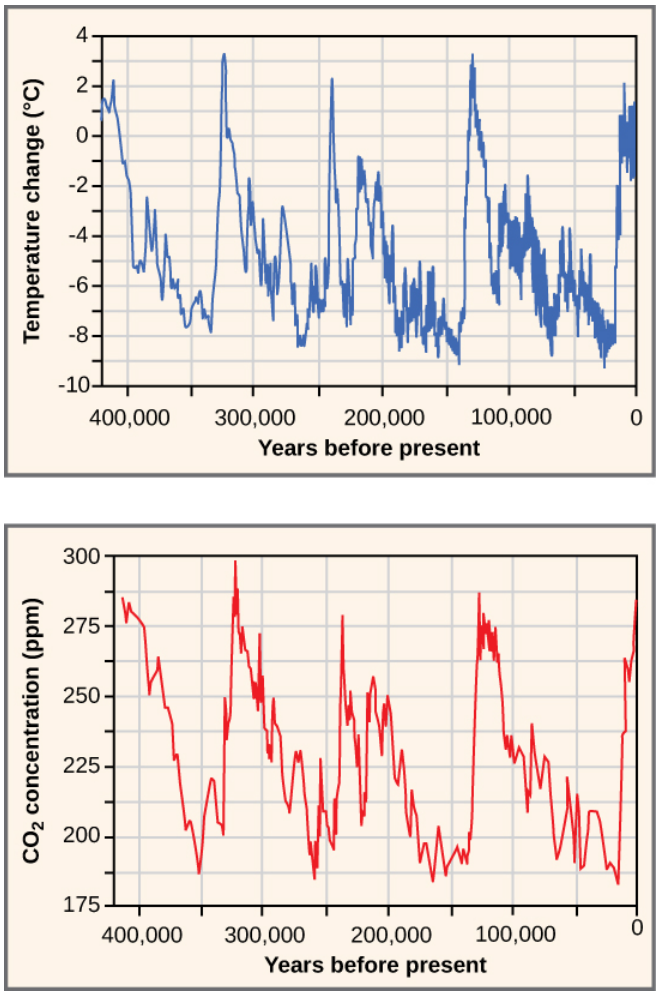


Figure 6.3.1.1**:** Ice at the Russian Vostok station in East Antarctica was laid down over the course of 420,000 years and reached a depth of over 3,000 m. By measuring the amount of CO_2 trapped in the ice, scientists have determined past atmospheric CO_2 concentrations. Temperatures relative to modern-day were determined from the amount of deuterium (an isotope of hydrogen) present.

Figure 6.3.1.1 does not show the last 2,000 years with enough detail to compare the changes in Earth's temperature during the last 400,000 years with the temperature change that has occurred in the more recent past. Three significant temperature anomalies, or irregularities, have occurred in the last 2000 years. The first two are the Medieval Climate Anomaly (or the Medieval Warm Period) and the Little Ice Age. A third temperature anomaly aligns with the Industrial Era.

The **Medieval Climate Anomaly** occurred between 900 and 1300 AD. During this time period, many climate scientists think that slightly warmer weather conditions prevailed in many parts of the world; the higher-than-average temperature changes varied between 0.10 °C and 0.20 °C above the norm. Although 0.10 °C does not seem large enough to produce any noticeable change, it did free seas of ice. Remember, the temperatures stated here are global averages. Some areas became much warmer, especially at higher latitudes, and some areas remained at their same averages. Because of the warming in the higher latitudes, the Vikings were able to colonize Greenland.

The **Little Ice Age** was a cold period that occurred between 1550 AD and 1850 AD. During this time, a slight cooling of a little less than 1°C was observed in North America, Europe, and possibly other areas of the Earth. This 1°C change in global temperature is a seemingly small deviation in temperature (as was observed during the Medieval Climate Anomaly); however, it also resulted in noticeable changes. Historical accounts reveal a time of exceptionally harsh winters with much snow and frost.

The **Industrial Revolution**, which began around 1750, was characterized by changes in much of human society. Advances in agriculture increased the food supply, which improved the standard of living for people in Europe and North America. New

technologies were invented and provided jobs and cheaper goods. These new technologies were powered using fossil fuels, especially coal. The Industrial Revolution starting in the early nineteenth century ushered in the beginning of the Industrial Era. When a **fossil fuel** (coal, oil, or natural gas) is burned, carbon dioxide is released. With the beginning of the Industrial Era, atmospheric carbon dioxide began to rise (Figure 6.3.1.2).

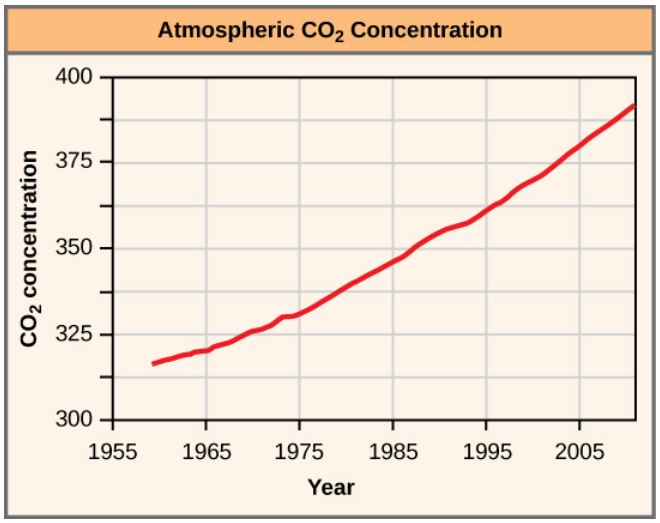


Figure 6.3.1.2: The atmospheric concentration of CO_2 has risen steadily since the beginning of industrialization, which began in 1750. Modern isotopic measurements of atmospheric CO_2 began in the late 1950s, which is reflected in this graph.

Causes of Past Climate Change

Since it is not possible to go back in time to directly observe and measure climate, scientists use indirect evidence to determine the **drivers**, or causes, that may be responsible for climate change. The indirect evidence includes data collected using ice cores, boreholes (a narrow shaft bored into the ground), tree rings, glacier lengths, pollen remains, and ocean sediments. The data shows a correlation between the timing of temperature changes and drivers of climate change: before the Industrial Era (pre-1780), there were three drivers of climate change that were not related to human activity or atmospheric gases.

The first of these is the **Milankovitch cycles**. The Milankovitch cycles describe the effects of slight changes in the Earth's orbit on Earth's climate. The length of the Milankovitch cycles ranges between 19,000 and 100,000 years. In other words, one could expect to see some predictable changes in the Earth's climate associated with changes in the Earth's orbit at a minimum of every 19,000 years and maximum every 100,000 years.

The variation in the sun's intensity is the second natural factor responsible for climate change. **Solar intensity** is the amount of solar power or energy the sun emits in a given amount of time. There is a direct relationship between solar intensity and temperature. As solar intensity increases (or decreases), the Earth's temperature correspondingly increases (or decreases). Changes in solar intensity have been proposed as one of several possible explanations for the Little Ice Age.

Finally, volcanic eruptions are a third natural driver of climate change. Volcanic eruptions can last a few days, but the solids and gases released during an eruption can influence the climate over a period of a few years, causing short-term climate changes. The gases and solids released by volcanic eruptions can include carbon dioxide, water vapor, sulfur dioxide, hydrogen sulfide, hydrogen, and carbon monoxide. Generally, volcanic eruptions cool the climate. This occurred in 1783 when volcanoes in Iceland erupted and caused the release of large volumes of sulfuric oxide. This led to **haze-effect cooling**, a global phenomenon that occurs when dust, ash, or other suspended particles block out sunlight and trigger lower global temperatures as a result; haze-effect cooling usually extends for one or more years. In Europe and North America, haze-effect cooling produced some of the lowest average winter temperatures on record in 1783 and 1784.

However, today, greenhouse gases are probably the most significant drivers of the climate. When heat energy from the sun strikes the Earth, gases known as **greenhouse gases** trap the heat in the atmosphere, just as the glass panes of a greenhouse keep heat from escaping. The greenhouse gases that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and chlorofluorocarbons (CFCs). Approximately half of the radiation from the sun passes through these gases in the atmosphere and strikes the Earth. This radiation is converted into thermal radiation on the Earth's surface, and then a portion of that energy is re-

radiated back into the atmosphere. Greenhouse gases, however, reflect much of the thermal energy back to the Earth's surface. The more greenhouse gases there are in the atmosphere, the more thermal energy is reflected back to the Earth's surface. Greenhouse gases absorb and emit radiation and are an important factor in the greenhouse effect: the warming of Earth due to carbon dioxide and other greenhouse gases in the atmosphere.

Video



Discover the intricacies of Earth's greenhouse effect in this 3-minute video.
Question after watching: How do the so-called greenhouse gases act to insulate the Earth? Why do more greenhouse gases lead to a warmer planet?

Optional Activity 6.3.1.2

What is the greenhouse effect?

A. Certain gases in the atmosphere trap heat and warm the Earth
B. Life on Earth 'exhales' gas that warms up the atmosphere
C. The tilt of the Earth changes the amount of solar energy the Earth receives
D. The Sun is putting out more radiant energy over time

Answer

A. Certain gases in the atmosphere trap heat and warm the Earth.

Results of Past Climate Change

Climate change is not a new phenomenon. Scientists have geological evidence of the consequences of long-ago climate change. Increased global temperatures and greenhouse gases have been associated with at least one planet-wide extinction event during the geological past. The Permian extinction event occurred about 251 million years ago toward the end of the roughly 50-million-year-long geological time span known as the Permian period. This geologic time period was one of the three warmest periods in Earth's geologic history. Scientists estimate that more than 90 percent of all life became extinct near the end of the Permian period. Organisms that had adapted to wet and warm climatic conditions, such as annual rainfall of 300–400 cm and 20 °C–30 °C in the tropical wet forest, may not have been able to survive the Permian climate change.

During the past 2 million years, there have been at least 10 cycles of natural warming and cooling on a planetary scale. When the polar ice caps melted during warming periods, sea levels rose to well above their earlier levels, and a larger portion of Earth experienced tropical climates. During cooling periods, the polar ice caps expanded, sea levels dropped, and tropical species' ranges contracted. Sometimes these changes occurred gradually, which enabled the affected species to adapt. But the onset of some climate change periods was abrupt, causing major ecosystem disruptions and global mass extinction events. Yet, nature recovered every time; many of the species we see today are survivors of previous climate change events. It is thus fair to ask why today's climate change is of such concern to us.

Video



A look at the history of climate change on Earth can give us some much-needed perspective on our current climate dilemma because, the surprising truth is, what we are experiencing now is different than anything this planet has encountered before. This 11-minute video gives an overview of Earth's prior climates.
Question after watching: In what way is the current climate change different than historical climate changes?

Climate Change's Impact on Humans (Past and Present)

History provides us with many lessons to illustrate the impact of climate change on human societies. These lessons start with the earliest well-documented example of a societal collapse—that of the Middle East's Natufian communities roughly 10,000 years ago—which has been attributed to climatic changes. Since then, climate change has regularly contributed to the collapse of complex human societies across the world. Notable examples of such collapses include the Akkadian Empire (the world's first empire) of the Middle East, Egypt's Old Kingdom (the builders of the pyramids), Central America's Classic Mayan civilization, the first English colony in America, several Chinese dynasties, and the Late Bronze Age societies along the Mediterranean Sea. Also, in Southern Africa, the fall of the Mapungubwe Kingdom has been attributed to crop failures and declining grazing lands due to regional droughts and warming cycles.

Similar patterns hold true today, only on a global scale. Because of humans' collective lack of response in addressing the drivers of climate change, more people will suffer the consequences than will not. Prominently, many parts of the world are already seeing higher temperatures and longer droughts. These conditions are compromising our quality of life by leading to more intense wildfires, increased incidences of vector-borne disease, increased crop failures, and increased competition for water. Many coastal areas are also seeing storms increasing in intensity and frequency, exposing people living near large rivers, deltas, and estuaries to more frequent flooding and storm surges. For example, the impacts from Cyclone Idai, one of the worst storms on record to have hit Africa, led to the deaths of more than 1,000 people (Figure 6.3.1.3). While no single flooding event can be attributed to climate change, it is undeniable that warmer oceans create conditions for hurricanes and cyclones to be stronger, bigger, and more frequent. Sea level rise is expected to leave many low-lying oceanic islands uninhabitable within a few decades. With all these impacts expected to increase the competition for space under an increasing human population, it would be wise for the world's governments to start preparing for millions of climate refugees that need to be relocated soon.

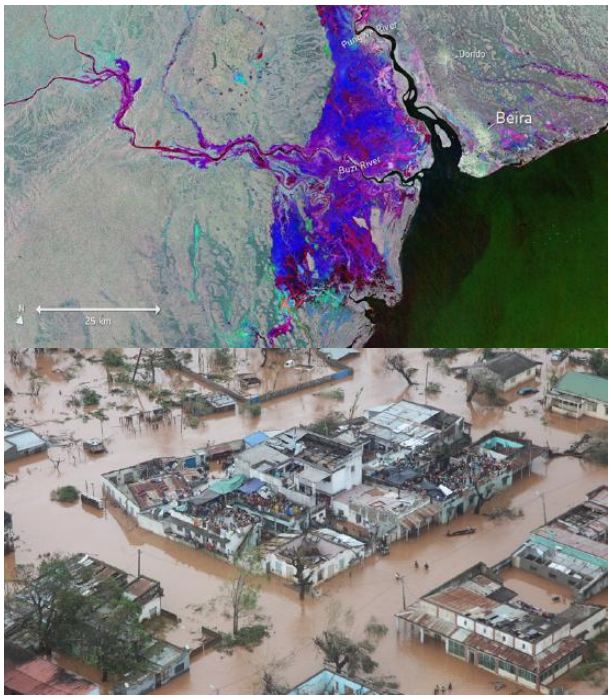


Figure 6.3.1.3: (Top) A Copernicus Sentinel-1 satellite image showing the extent of flooding (areas shown in blue) in central Mozambique after Cyclone Idai made landfall on 15 March, 2019. Photograph by European Space Agency, https://www.flickr.com/photos/europeanspaceagency/47477652401, CC BY-SA 2.0. (Bottom) People in Beira, Mozambique, taking refuge on rooftops to escape flooding brought by Cyclone Idai. Photograph by World Vision, https://www.flickr.com/photos/dfid/46570320385, CC BY 2.0.

This page titled 6.3.1: Introduction to Climate Change is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.3: The Impact of Climate Change** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **44.5: Climate and the Effects of Global Climate Change** by OpenStax is licensed CC BY 4.0.

6.3.2: Anthropogenic Climate Change

Anthropogenic Climate Change

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 2 hours.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

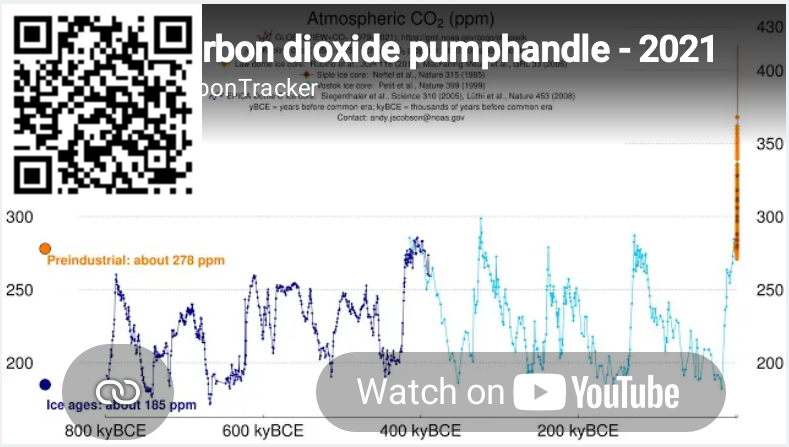
Learning Objectives

- Identify the historical beginnings of anthropogenic climate change
- Explain how current climate change is measured
- Describe the scientific consensus on anthropogenic climate change
- Identify human impacts on specific greenhouse gases

Introduction

Evidence supports the relationship between atmospheric concentrations of carbon dioxide and temperature: as carbon dioxide rises global temperature rises. Since 1950, the concentration of atmospheric carbon dioxide has increased from about 280 ppm to 382 ppm in 2006. In 2021, the atmospheric carbon dioxide concentration was 415 ppm.

Video



This 2.5-minute video shows how atmospheric CO_2 has varied recently and also over the last 800,000 years as determined by many CO_2 monitoring stations (shown on the insert map). It is also instructive to watch the CO_2 variation of the video by latitude. This shows that most of the sources of CO_2 are in the Northern Hemisphere where humans reside.

Question after watching: What general trends do you notice over the last 800,000 years? How is the current climate breaking those trends?

Scientists look at patterns in data and try to explain differences or deviations from these patterns. The atmospheric carbon dioxide data reveal a geologic pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm before decreasing again, generally over 100,000 year Malankovich cycles (see Unit 6.3.1). Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its traditionally low minimum concentration at the height of the last ice age to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. The current increases in atmospheric carbon dioxide

have happened very quickly—in a matter of hundreds of years rather than thousands of years. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide and other greenhouse gases (GHGs)?

Anthropogenic Climate Change

Anthropogenic climate change refers to the impacts of humans on the climate system. Scientists generally look to the Industrial Era as the beginning of anthropogenic climate change, which is the advent of the use of fossil fuels, beginning with coal, to power machinery in the middle of the 1700s. Some climate scientists argue that anthropogenic climate change actually begins much earlier than the Industrial Era and that humans began impacting the climate through deforestation and land clearing to grow food. This would include farming grains in Europe and the Middle East during the first Agricultural Revolution around 8,000 years BCE and developing artificial wetlands for rice cultivation in Asia around 5,000 years BCE. Clearing vegetation for crops is a type of **climate-forcing**, meaning greenhouse gases (in this case, carbon dioxide) are being released into the atmosphere. The carbon dioxide storage capacity of crops is generally lower than that of the forests originally there. Creating wetlands is also a carbon source due to the bacterial decay of organic matter within wetlands that produces methane.

In fact, whether anthropogenic climate change started with the Agricultural Revolution or the Industrial Revolution is not important, because the really significant climate changes did not start until the early part of the 20th century. Human activities and population size are intertwined. As more and more of the world's population adopts a resource-intensive lifestyle, the climate problem becomes worse. These lifestyles currently require fossil fuels, which provide relatively cheap and abundant energy and are used for everything from transportation and heating and cooling to industry and food production.

This escalating level of industrialization and mechanization of our lives has driven the anthropogenic climate change of the past century. The trend of mean global temperatures since 1880 is shown in Figure 6.3.2.1. For approximately the past 55 years, the temperature has increased at a relatively steady and rapid rate, especially compared to past changes. The average temperature now is approximately 1.0°C higher than before industrialization, and two-thirds of this warming has occurred since 1975. Since 1880, average global surface temperatures have trended upward and most of that warming has occurred since 1970. Since the ocean is absorbing a lot of the additional trapped heat, surface temperatures include both land surface and ocean temperatures.

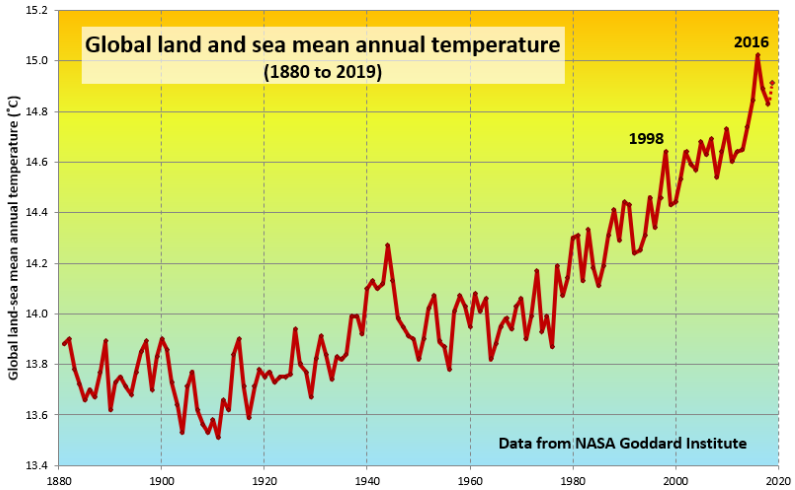
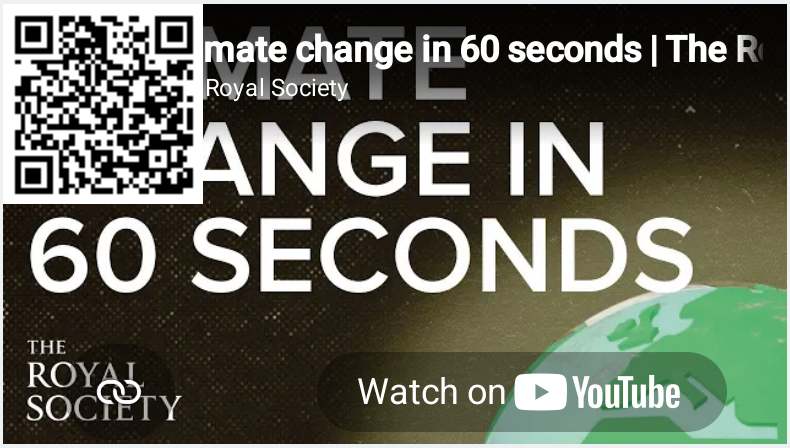


Figure 6.3.2.1: Global mean annual temperatures for the period from 1880 to 2019. The value for 2019 is projected, based on only 6 months of data. 1998 and 2016 were strong El Niño years. © Steven Earle. CC BY. Based on data from NASA.

Video



This 60-second animation from two of the world's leading science academies brings you the science behind climate change.

Question after watching: Of the graphs shown, which had you seen before (similar or the same)? Which ones were new to you? What does this make you think about?

Optional Activity 6.3.2.1

How has the global average temperature changed since the Industrial Revolution?

A. Cooler by 0.1°C
B. The temperature has gone up and down, but remains overall the same
C. Warmer by more than 1°C
D. Warmer by almost 2°C

Answer

C. Warmer by more than 1°C

How Do We Know? Measuring Current Climate Change

Changes in land surface or ocean surface temperatures can be expressed as temperature **anomalies**. A temperature anomaly is a difference in average temperature measurement from a predetermined datum (or baseline). This datum is the average temperature of a particular date range, for example, 1951 to 1980. Another common datum is the last century (1900-2000). Therefore, an anomaly of 1.25 ℃ for 2015 (last century datum) means that the average temperature for 2015 was 1.25 ℃ greater than the 1900-2000 average. In 1950, the temperature anomaly was -0.28 ℃, so this is -0.28 ℃ lower than the 1900-2000 average [3]. These temperatures are annual average surface temperatures. Figure 6.3.2.2 shows the global mean temperature estimates for the period of 1880 to 2020 using the datum of the 1951-1980 average temperature.

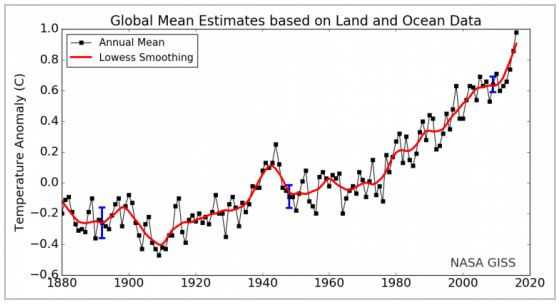


Figure 6.3.2.2: Land-ocean temperature index, 1880 to present, with a base time 1951-1980. The solid black line is the global annual mean and the solid red line is the five-year lowess smooth curve. The blue uncertainty bars (95% confidence limit) account only for incomplete spatial sampling.
[From https://opengeology.org/textbook/15-...limate-change/ Adapted from *Source:* *National Climate Data Center*]

Other valuable insights have been obtained by running sophisticated mathematical global **climate models** on high-powered supercomputers. These “virtual experiments” examine the potential climatic responses to increases in atmospheric CO_2. These computer simulations are known as three-dimensional general circulation models (GCMs). The models simulate the complex movements of energy and mass in the global circulation of the atmosphere. They also examine the interactions of these processes with physical variables that are important aspects of climate, such as temperature and precipitation. A strong tendency that emerges from these virtual experiments is that global warming and associated climate changes are a likely consequence of the well-documented increases of CO_2 and other GHGs in the atmosphere.

Many such simulation experiments have examined the scenario of a doubling of CO_2 concentration to 800 ppm from its recent concentration of just over 400 ppm. These experiments suggest that such a doubling would result in an increase of 1°C to 4°C in the average temperature of the surface atmosphere. The intensity of warming is predicted to be greatest in high-latitude regions, where the temperature increases might be two to three times greater than in the tropics.

Warming of the lower atmosphere will be one likely change that will be caused by an increased intensity of the greenhouse effect. However, there could also be important effects that occur indirectly due to increased temperatures. The most important of these would include large-scale shifts in the patterns of atmospheric circulation. Such shifts would likely result in changes in the amounts, distribution, and seasonality of precipitation. Changes in precipitation regimes would influence soil moisture, which would greatly affect the distribution and productivity of vegetation, both natural and managed. These changes in precipitation regime would likely have much greater effects on agricultural and wild ecosystems than would any direct influence of a warmed atmosphere.

Indigenous Connections: Monitoring Climate Change

"Indigenous research methodologies are "…as old as our ceremonies and our nations. They are with us and have always been with us” (Cardinel, 2001). The methodologies for Indigenous-led research are varied across and within First Nation, Inuit, and Métis communities across Canada reflecting the diversity of worldviews and ways of knowing" (First Peoples Group, 2022).

"Many Indigenous climate monitoring projects co-apply Indigenous Knowledge Systems with science bringing together the strengths of both knowledge systems. This has been described as two-eyed seeing (Etuaptmumk in Mi’kmaw), which involves 'learning to see from one eye with the strengths of Indigenous Knowledges and ways of knowing, and from the other eye with the strengths of mainstream knowledges and ways of knowing, and to use both these eyes together, for the benefit of all' (Marshall, 2020)" (First Peoples Group, 2022).

"Indicators are used by many Indigenous Peoples to understand and communicate about ecological change. They are the signs and signals that have guided understanding and decisions within Indigenous communities for hundreds if not thousands of years. Climate indicators can relate to:

- radiation (solar radiation or sunlight; surface temperature and thermal radiation)
- the atmosphere (e.g., temperature, precipitation, wind, humidity);
- the land (e.g., changes in permafrost, soil moisture, soil temperature, water-table depth)
- water quantity (e.g., flow, water depth) or quality (e.g., pH, dissolved oxygen, nitrate, phosphates, water temperature)
- ice and snow (e.g., timing of ice formation and breakup, thickness, quality; snow depth)

- plants and animals (e.g., timing of arrival of species, species population and distribution, health and body condition, taste and yield of berries, spectroscopy)" (First Peoples Group, 2022).

"Elders and Knowledge keepers hold invaluable knowledge about the changes to the land and the environment as a whole. Going out on the land with Knowledge holders can provide a natural space for intergenerational knowledge transfer and Indigenous Knowledge sharing. Participatory video is a newer method of documenting community climate observations and stories through mobilizing stories and collectively-held knowledge with diverse audiences to inform climate adaptation" (First Peoples Group, 2022).

"Many Indigenous climate monitoring projects also follow scientific methods for collecting data. Many monitoring projects incorporate sensors and automated instrumentation which remain in the field such as weather stations, hydrological sensors, trail cameras, soil temperature sensors, etc. Some community-based monitoring projects are even using observations from space-based remote sensors (e.g., Landsat 8, LIDAR)" (First Peoples Group, 2022).

In 2022, the federal government announced $800 million towards Indigenous-led conservation efforts, including those that help to mitigate climate change, like the BC Northern Shelf Bioregion: https://pm.gc.ca/en/news/news-releases/2022/12/07/protecting-more-nature-partnership-indigenous-peoples

Sources:

Cardinel, L. 2001. What is an Indigenous Perspective? Canadian Journal of Native Education, 25(2), 180-182.

Elder Dr. Albert Marshall from Reid, Andrea J Lauren E. Eckert, John-Francis Lane, Nathan Young, Scott G. Hinch, Chris T. Darimont, Steven J. Cooke, Natalie C. Ban, Albert Marshall. 2020. “Two-Eyed Seeing”: An Indigenous framework to transform fisheries research and management. Fish and Fisheries 22:2, p243-261. Available at: https://doi.org/10.1111/faf.12516



This beautifully illustrated animation video explains what climate change means for Tsay Keh Dene, the changes that elders have observed in their territories of British Columbia, and how these changes will impact local cultures and traditional practices. It describes the Tsay Keh Dene and Carcross Tagish Community-Based Climate Monitoring project funded by Crown-Indigenous Relations and Northern Affairs Canada.

Scientific Consensus: Global Anthropogenic Climate Change is Real

The **Intergovernmental Panel on Climate Change** (IPCC)—established by the United Nations Environment Programme and the World Meteorological Organization in 1988—is responsible for reviewing the scientific literature on climate change and issuing periodic reports on several topics, including the scientific basis for understanding climate change, our vulnerability to observed and predicted climate changes, and what we can do to limit climate change and minimize its impacts. The IPCC uses this information to evaluate current impacts and future risks, in addition to providing policymakers with assessments. These assessments are released about once every six years. The Panel is on their most recent Synthesis Report, the 6th Assessment Report. Working group reports were released in 2021-2022. Hundreds of leading scientists from around the world are chosen to author these reports. Over the

history of the IPCC, these scientists have reviewed thousands of peer-reviewed, publicly available studies. The scientific consensus according to the last IPCC assessment is clear: global climate change is real and humans are very likely the cause for this change.

Additionally, the major scientific agencies of Canada and the Canadian government also agree that climate change is occurring and that humans are driving it. From the Environment and Climate Change Canada: “Human activity is the main cause of climate change. Carbon dioxide is the main cause of human-induced climate change.” Many independent scientific organizations have released similar statements, both in Canada and abroad. This does not necessarily mean that every scientist agrees on the strength of each component of the climate change system, but nearly universal agreement exists that climate change is happening and is primarily caused by excess greenhouse gases from human activities.

Video



This 14-minute video from the IPCC summarizes much of the 6th Assessment Report on Impacts, Adaptation, and Vulnerability with a global focus.

Question after watching:

Climate varies naturally over a wide range of time scales. In general, climate changes prior to the Industrial Revolution in the 1700s can be explained by natural causes, such as changes in solar energy, volcanic eruptions, and natural changes in greenhouse gas (GHG) concentrations. Recent changes in climate**,** however, cannot be explained by natural causes alone. Research indicates that natural causes are very unlikely to explain most observed warming, especially warming since the mid-20th century. Rather, human activities, especially our combustion of fossil fuels, explains the current warming (Figure 6.3.2.3). The scientific consensus is clear: through alterations of the carbon cycle, humans are changing the global climate by increasing the effects of something known as the greenhouse effect.

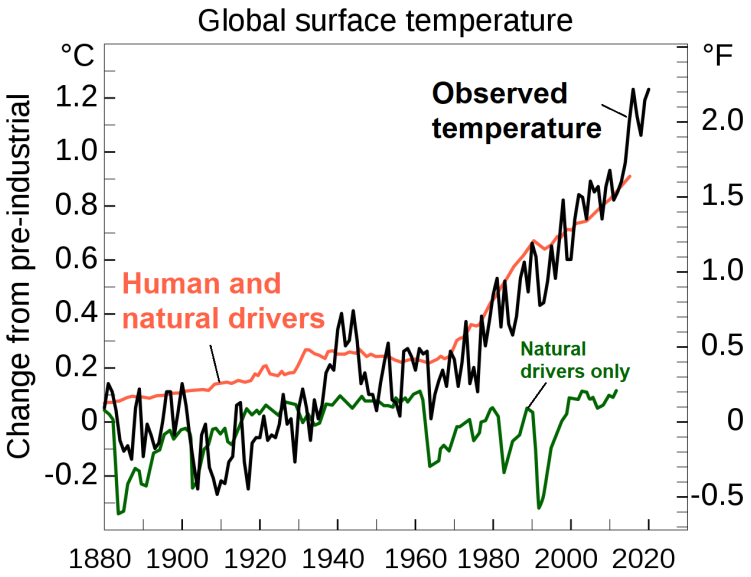


Figure 6.3.2.3: This graph shows the predicted temperatures from two climate models and observed temperatures from 1880 to 2020. The first model considered only natural factors that could influence temperature and is represented by the green line (bottom). It shows some fluctuations in temperature by no overall increase or decrease. The second model considered both human and natural factors and is represented by the orange line (top). It shows an overall increase in temperature. Actual observations (black, jagged line; middle) more closely match the second model. Overall, temperature has increased about 1.2°C since pre-industrial times. Image relabeled from Efbrazil CC-BY-SA.

Climate change forecasting is famously complex, with a great amount of uncertainty attached to the task. The general models used for climate change forecasting need to account for a great number of highly variable components, each affecting one another across the only planet we can adequately measure or examine (we have no other planet where we can test predictions). Among thousands of considerations, **climatologists**, scientists who study climate, need to account for how human activities might change over time, and how these activities will change the atmosphere's composition. They also need to account for how much CO_2 the world's oceans and plants will absorb, and how wind and fire might influence these processes. Combining all the component parts, climatologists then need to estimate how increased temperatures will affect the polar ice caps, how the melting ice will affect oceanic conditions and currents which, in turn, will affect terrestrial conditions and weather patterns. Uncertainty also exists over interactive effects of some drivers. For example, higher temperatures increase evaporation and cloud cover which, in turn, will have a moderate cooling effect. Because of the complexity of these and other variables going into climate models, a great number of research groups are encouraged to develop their own climate forecasts, each using a range of different scenarios on how human activity might change in the future.

By regularly doing extensive reviews of all the evidence and climate science literature, the IPCC has found that, despite the complexity of climate models, results of all the models taken together exhibited significant agreement with changes already observed. Climate change models have also proven reliable in predicting responses of biodiversity to climate change. While climatologists continue to improve on the finer details of their models, conservation biologists can and should confidently use the climate forecasts available for general conservation planning purposes.

Specific Human Impacts on Greenhouse Gases

Recall that GHGs are probably the most significant drivers of current climate change. The GHGs that affect Earth include carbon dioxide, methane, water vapor, nitrous oxide, and ozone. Water vapor is the most abundant greenhouse gas and also the most important in terms of its contribution to the natural greenhouse effect, despite having a short atmospheric lifetime. Some human activities can influence local water vapor levels. However, on a global scale, the concentration of water vapor is controlled by temperature, which influences overall rates of evaporation and precipitation. Therefore, the global concentration of water vapor is not substantially affected by direct human emissions.



Figure 6.3.2.6: The burning of fossil fuels in industry and by vehicles releases carbon dioxide and other greenhouse gases into the atmosphere. (CC-BY-SA 4.0 “Pöllö”/Wikimedia Commons)

Sinks and Sources

Places in the ecosystem that store GHGs are reservoirs. Places that supply and remove are **sources** and **sinks**, respectively. If more GHGs are released than stored, the place is a source. If more GHGs are absorbed than emitted, the reservoir is a sink. A reservoir can change from a sink to a source and vice versa. For example, a forest is a sink for carbon, but when the forest burns it becomes a carbon source.

Carbon Dioxide

Carbon dioxide (CO_2) is the primary greenhouse gas that is contributing to recent global climate change. Healthy living forests and the oceans act as carbon sinks. The mantle is a natural source of carbon from volcanic gases. The link between human-induced climate change and atmospheric CO_2 concentrations was first highlighted in the late 19th century by Arrhenius. However, it was not until the mid-1950s that scientists started to raise concerns about increasing CO_2 concentrations in the atmosphere. By the 1980s, as global annual mean temperatures started to rise, consensus about climate change linked to CO_2 began to spread among the broader public. Yet concrete steps to curb CO_2 emissions have only been initiated recently.

In the meantime, CO_2 emissions continue to accelerate: more than 37 billion tonnes of carbon, a new record, were released into the atmosphere in 2018. CO_2 is a natural component of the carbon cycle, involved in such activities as photosynthesis, respiration, volcanic eruptions, and ocean-atmosphere exchange. Human activities, primarily the burning of fossil fuels, deforestation, and changes in land use, release very large amounts of CO_2 to the atmosphere, causing its concentration in the atmosphere to rise, where each molecule may remain for more than 200 years. Cement manufacture, animal agriculture, the clearing of land, and the burning of forests are other human activities that release carbon dioxide.

Scientists look at patterns in data and try to explain differences or deviations from these patterns. As stated in Unit 6.3.1, the atmospheric carbon dioxide data reveal a historical pattern of carbon dioxide increasing and decreasing, cycling between a low of 180 ppm and a high of 300 ppm (Figure 6.3.2.4). Scientists have concluded that it took around 50,000 years for the atmospheric carbon dioxide level to increase from its low minimum concentration to its higher maximum concentration. However, starting recently, atmospheric carbon dioxide concentrations have increased beyond the historical maximum of 300 ppm. Atmospheric CO_2 concentrations have increased by 45% since pre-industrial times, from approximately 280 parts per million (ppm) in the 18th century to 415 ppm in 2021. What is the reason for this difference in the rate of change and the amount of increase in carbon dioxide? A key factor that must be recognized when comparing the historical data and the current data is the presence of modern human society; no other driver of climate change has yielded changes in atmospheric carbon dioxide levels at this rate or to this magnitude.

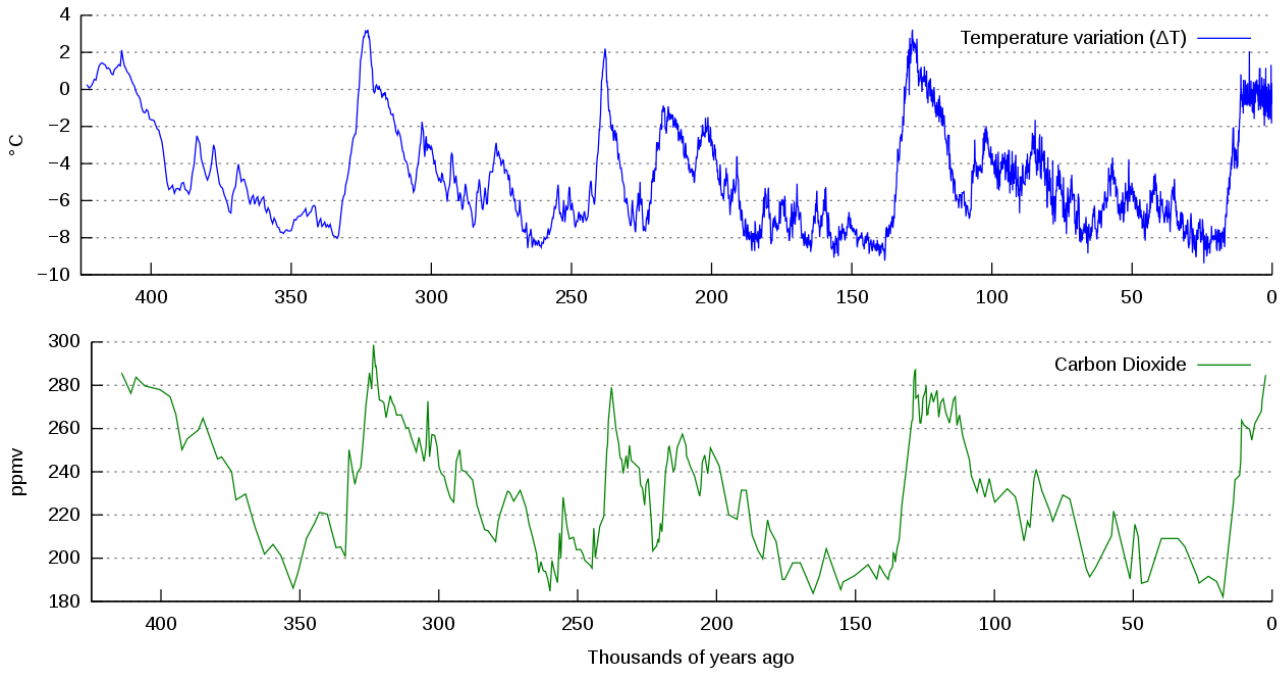
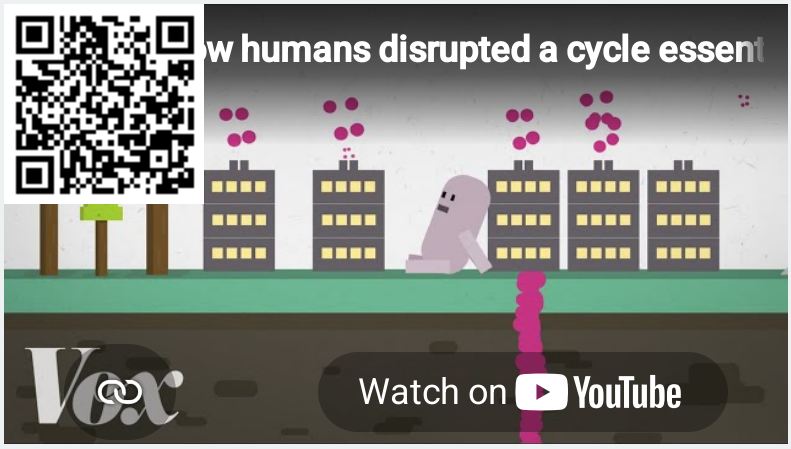


Figure 6.3.2.4: Graph of change in temperature in degrees Celsius (top, blue line) and carbon dioxide concentration in parts per million by volume (bottom, green line) measured from the Vostok, Antarctica ice core. These have been associated for over 400,000 years. As carbon dioxide concentration increased, so did temperature. As carbon dioxide concentration decreased, so did temperature. These data were collected in 1999. Since then, carbon dioxide concentrations have stabilized to over 410 ppm. Image and caption (modified) by NOAA/Autopilot (CC-BY-SA)

Video



This 4-minute animation describes the natural carbon cycle and how humans are disrupting that cycle. Question after watching: Which of the technologies to remove carbon from the atmosphere have you heard of before? Which have you not? What do these technologies do?

Optional Activity 6.3.2.2

How long does a molecule of CO_2 remain in the atmosphere?

A. CO_2 washes out of the atmosphere seasonally.
B. CO_2 remains in the atmosphere for 5-10 years.
C. CO_2 remains in the atmosphere for up to 200 years, or more.

Answer

C. CO_2 remains in the atmosphere for up to 200 years, or more.

Optional Activity 6.3.2.3

What is the primary cause of the overall rising trend in CO_2 in the atmosphere?

A. The increase in CO_2 is caused by burning of fossil fuels.
B. CO_2 is increasing because we are coming out of an ice age.
C. As human population grows, people exhale more CO_2.
D. CO_2 is released by the oceans as they warm.

Answer

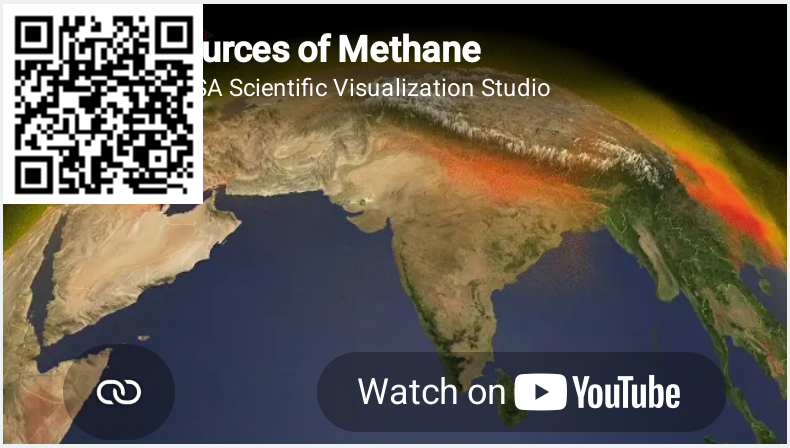
A. The increase in CO_2 is caused by burning of fossil fuels.

Methane

Although this concentration is far less than that of CO_2, **methane** (CH_4) is 28 times as potent a greenhouse gas. Methane is produced when bacteria break down organic matter under anaerobic conditions and can be released due to natural or anthropogenic processes. Anaerobic conditions can happen when organic matter is trapped underwater (such as in rice paddies) or in the intestines of herbivores. Anthropogenic causes now account for 60% of total methane release. Examples include agriculture, fossil fuel extraction and transport, mining, landfill use, and burning of forests. Methane can also be released from natural gas fields and the decomposition that occurs in landfills. Specifically, raising cattle releases methane due to fermentation in their rumens producing methane that is expelled from their GI tract. Methane is more abundant in Earth's atmosphere now than at any time in at least the past 650,000 years, and CH_4 concentrations increased sharply during most of the 20th century. They are now more than 2.5 times pre-industrial levels and increasing rapidly.

Another source of methane is the melting of clathrates (methane hydrate). **Clathrates** are frozen chunks of methane hydrate found at the bottom of the ocean. When water warms these chunks of ice melt and methane is released. As the ocean's water temperature increases, the rate at which clathrates melt is increasing, releasing even more methane. This leads to increased levels of methane in the atmosphere, which further accelerates the rate of global warming. This is an example of the positive feedback loop that is leading to the rapid rate of increase in global temperatures. There is strong evidence that warming during the Quaternary period 55 million years ago was caused, at least in part, by a massive release of clathrates.

Video



This 2-minute, 3D volumetric visualization shows the emission and transport of atmospheric methane around the globe between December 9, 2017 and December 1, 2018. (NASA)

Question after watching: What patterns do you notice based on the narrator's descriptions and the visualization?

Other Greenhouse Gases

Nitrous oxide (N_2O) is produced through natural and human activities, mainly through agricultural activities and natural biological processes. Fuel-burning and some other processes also create N_2O. Concentrations of N_2O have risen approximately 18% since the start of the Industrial Revolution, with a relatively rapid increase towards the end of the 20th century. [3] In contrast, the atmospheric concentration of N_2O varied only slightly for a period of 11,500 years before the onset of the industrial period, as shown by ice core samples.

Ground-level ozone (O_3), which also has a short atmospheric lifetime, is a potent greenhouse gas. Chemical reactions create ozone from emissions of nitrogen oxides and volatile organic compounds from automobiles, power plants, and other industrial and commercial sources in the presence of sunlight. In addition to trapping heat, ozone is a pollutant that can cause respiratory health problems and damage crops and ecosystems.

Chlorofluorocarbons (CFCs), hydrochlorofluorocarbons (HCFCs), hydrofluorocarbons (HFCs), perfluorocarbons (PFCs), and sulfur hexafluoride (SF6), together called **F-gases**, are often used in coolants, foaming agents, fire extinguishers, solvents, pesticides, and aerosol propellants. Unlike water vapor and ozone, these F-gases have a long atmospheric lifetime, and some of these emissions will affect the climate for many decades or centuries.

Human-Induced Changes in Albedo and Aerosols

When sunlight energy reaches Earth it can be reflected or absorbed. The amount that is reflected or absorbed depends on Earth's surface and atmosphere. Light-colored objects and surfaces, like snow and clouds, tend to reflect most sunlight, while darker objects and surfaces, like the ocean and forests, tend to absorb more sunlight. The term **albedo** refers to the amount of solar radiation reflected from an object or surface, often expressed as a percentage. Earth as a whole has an albedo of about 30%, meaning that 70% of the sunlight that reaches the planet is absorbed. Sunlight that is absorbed warms Earth's land, water, and atmosphere.

Albedo is also affected by aerosols. **Aerosols** are small particles or liquid droplets in the atmosphere that can absorb or reflect sunlight. Unlike greenhouse gases (GHGs), the climate effects of aerosols vary depending on what they are made of and where they are emitted. Those aerosols that reflect sunlight, such as particles from volcanic eruptions or sulfur emissions from burning coal, have a cooling effect. Those that absorb sunlight, such as black carbon (a part of soot), have a warming effect. In addition, human activities have generally increased the number of aerosol particles in the atmosphere. Overall, human-generated aerosols have a net cooling effect offsetting about one-third of the total warming effect associated with human greenhouse gas emissions. Reductions in overall aerosol emissions can therefore lead to more warming. However, targeted reductions in black carbon emissions can reduce warming.

Human changes in land use and land cover have changed Earth's albedo. Processes such as deforestation, reforestation, desertification, and urbanization often contribute to changes in climate in the places they occur. These effects may be significant regionally but are smaller when averaged over the entire globe.

Video



This 2-minute video visualizes albedo.

Question after watching: What are some human activities that change albedo as visualized in the video?

Climate Feedbacks

When sea ice melts, as it has done in the Arctic Ocean at a disturbing rate over the past decade, the albedo of the area affected changes dramatically, from around 80% down to less than 10%. This is a positive feedback (see a review of feedback loops in Unit 6.1.1) because much more solar energy is absorbed by the water than by the pre-existing ice, and the temperature increase is amplified. The same applies to ice and snow on land, but the difference in albedo is not as great.

When ice and snow on land melt, sea level rises. Sea level is also rising because the oceans are warming and that increases their volume. A higher sea level means a larger proportion of the planet is covered with water, and since water has a lower albedo than land, more heat is absorbed and the temperature goes up a little more. Since the last glaciation, sea-level rise has been about 125m; a huge area that used to be land is now flooded by heat-absorbent seawater. During the current period of anthropogenic climate change, sea level has risen only about 20 cm, and although that does not make a big change to albedo, sea-level rise is accelerating.

Video



A warming Arctic can catapult the world into drastic climate impacts through feedback loops as seen in this 3.5-minute video.

Question after watching: Why should we be concerned with permafrost melting as well as ice in the Arctic?



Figure 6.3.2.10: A degrading permafrost site on the north coast of Alaska.

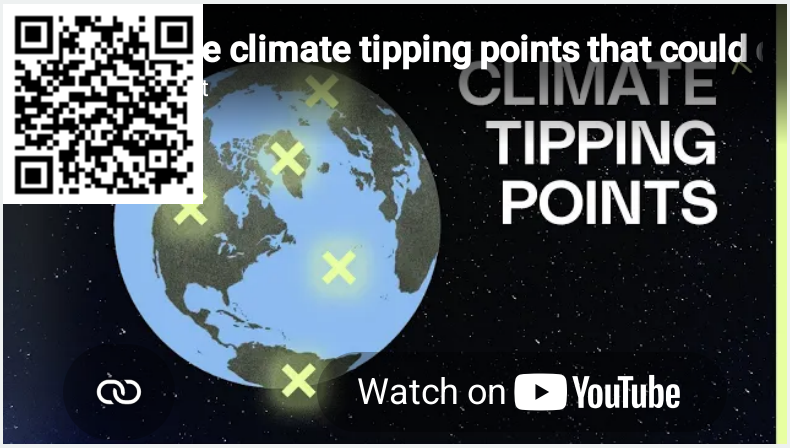
Most of northern Canada has a layer of permafrost that ranges from a few centimeters to hundreds of meters in thickness; the same applies in Alaska, Russia, and Scandinavia. Permafrost is a mixture of soil and ice (Figure 6.3.2.10), and it also contains a significant amount of trapped organic carbon that is released as CO_2 and CH_4 when the permafrost breaks down. Because the amount of carbon stored in permafrost is in the same order of magnitude as the amount released by burning fossil fuels, this is a feedback mechanism that has the potential to equal or surpass the forcing that has unleashed it. In some polar regions, including northern Canada, permafrost also includes methane hydrate. Breakdown of permafrost releases this form of methane.

There is about 45 times as much carbon in the ocean (as dissolved bicarbonate) as there is in the atmosphere (as CO_2), and there is a steady exchange of carbon between the two reservoirs. But the ability of CO_2 to dissolve in water (its **solubility**) decreases as the temperature goes up. In other words, the warmer it gets, the more oceanic bicarbonate gets released to the atmosphere as CO_2. That makes CO_2 solubility another positive feedback mechanism.

Vegetation growth responds positively to both increased temperatures and elevated CO_2 levels, and so in general, it represents negative feedback to climate change because the more the vegetation grows, the more CO_2 is taken from the atmosphere. However, trees grow bigger and more vigorously so forests have lower albedo so they absorb more heat. In addition, climate change is not just more CO2, it may mean more or less rain, extreme weather events, or drastic seasonal changes that interfere with forest health. Furthermore, climate warming isn't necessarily good for vegetation growth; some areas have become too hot, too dry, or even too wet to support the plant community that was growing there, and it might take centuries for something to replace it successfully.

All of these positive (and negative) feedbacks work both ways. For example, during climate cooling, growth of glaciers leads to higher albedos, and formation of permafrost results in storage of carbon that would otherwise have returned quickly to the atmosphere.

Video



This 3.5-minute video describes climate tipping points.
Question after watching: What is meant by a "tipping point" for climate? What types of systemic changes are studied in terms of climate tipping points? Are these positive feedbacks or negative feedbacks?

This page titled 6.3.2: Anthropogenic Climate Change is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **44.5: Climate and the Effects of Global Climate Change** by OpenStax is licensed CC BY 4.0.
- **6.3: The Impact of Climate Change** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **6.2: Predicting Earth's Future Climate** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.
- **10.4: Climate Change** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.
- **8.5: Climate Change** by Paul Webb is licensed CC BY 4.0. Original source: https://rwu.pressbooks.pub/webboceanography.

Current and Future Climate Change Impacts

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Identify current global climate impacts and their confidence level
- Explain several projected abiotic climate impacts and their effects on living organisms

Introduction

Climate change has the potential to render Earth unrecognizable from what any human has ever experienced. These changes will have an immense impact on ecosystem services, global economies, and our own quality of life. Yet, while there is much talk about these risks, there is still too little action addressing its main causes.

Current Climate Change Impacts

Some of the lack of action may be attributed to “climate change” and “future” often being used in the same sentence, giving politicians and industries a false impression that we can deal with climate change once we achieved sufficient economic growth. The reality could however not be further from the truth, as we already see signs of the changes to come here today (Table 6.3.3.1), including near-annual crop failures, record-high temperatures, and record-strength coastal storms.

Table 6.3.3.1: Some examples illustrating how climate change is already impacting our planet (IPCC, 2022).

Impact	Evidence
Increased extreme weather	The rise in weather and climate extremes has led to some irreversible impacts as natural and human systems are pushed beyond their ability to adapt. (high confidence). Widespread, pervasive impacts to ecosystems, people, settlements, and infrastructure have resulted from observed increases in the frequency and intensity of climate and weather extremes, including hot extremes on land and in the ocean, heavy precipitation events, drought, and fire weather (high confidence).
Widespread flood and droughts	Flood and drought-related acute food insecurity and malnutrition have increased in Africa (high confidence) and Central and South America (high confidence).
Rising sea levels	Continued and accelerating sea level rise will encroach on coastal settlements and infrastructure (high confidence) and commit low-lying coastal ecosystems to submergence and loss (medium confidence).
Earlier spring activity	Widespread deterioration of ecosystem structure and function, resilience, and natural adaptive capacity, as well as shifts in seasonal timing have occurred due to climate change (high confidence), with adverse socioeconomic consequences (high confidence).
Disease spread	The occurrence of climate-related food-borne and water-borne diseases has increased (very high confidence). The incidence of vector-borne diseases has increased from range expansion and/or increased reproduction of disease vectors (high confidence). Animal and human diseases, including zoonoses, are emerging in new areas (high confidence).
Shifts in species ranges	Approximately half of the species assessed globally have shifted polewards and to higher elevations on land (very high confidence).
Wildlife population declines	Climate change has caused substantial damages, and increasingly irreversible losses, in terrestrial, freshwater and coastal and open ocean marine ecosystems (high confidence). The extent and magnitude of climate change impacts are larger than estimated in previous assessments (high confidence). Hundreds of local losses of species have been driven by increases in the magnitude of heat extremes (high confidence), as well as mass mortality events on land and in the ocean (very high confidence) and loss of kelp forests (high confidence). Some losses are already irreversible, such as the first species extinctions driven by climate change (medium confidence).

Terms from Table 6.3.3.1

Risk: provides a framework for understanding the increasingly severe, interconnected, and often irreversible impacts of climate change on ecosystems, biodiversity, and human systems; differing impacts across regions, sectors, and communities; and how to best reduce adverse consequences for current and future generations.

Adaptation: in human systems, the process of adjustment to actual or expected climate and its effects in order to moderate harm or take advantage of beneficial opportunities. In natural systems, adaptation is the process of adjustment to actual climate

and its effects; human intervention may facilitate this.

Resilience: the capacity of social, economic, and ecosystems to cope with a hazardous event, trend, or disturbance, responding, or reorganizing in ways that maintain their essential function, identity, and structure as well as biodiversity in case of ecosystems while also maintaining the capacity for adaptation, learning, and transformation.

Mitigation: reducing emissions, and stabilizing the levels, of heat-trapping greenhouse gases in the atmosphere.

Confidence: each finding is grounded in an evaluation of underlying evidence and agreement. A level of confidence is expressed using five qualifiers: very low, low, medium, high and very high.

Between June 25 and July 1, 2021, British Columbia experienced a massive heat dome with temperatures reaching 49.6^{o}C in some areas. Scientists have stated that climate change was a contributing factor. More than 500 deaths were attributed to the heat. Glaciers throughout British Columbia are in retreat, with losses ranging from 6% to 34% from 1985-2005, and their melting is increasing. See more from the British Columbia Provincial Government: Change in Size of B.C. Glaciers.

A summary of the impacts of climate change on natural disasters is given in Figure 6.3.3.1. The major types of disasters related to climate are floods and storms, but the health implications of extreme temperatures are also becoming a great concern. In the decade 1971 to 1980, extreme temperatures were the fifth most common natural disasters; by 2001 to 2010, they were the third most common.

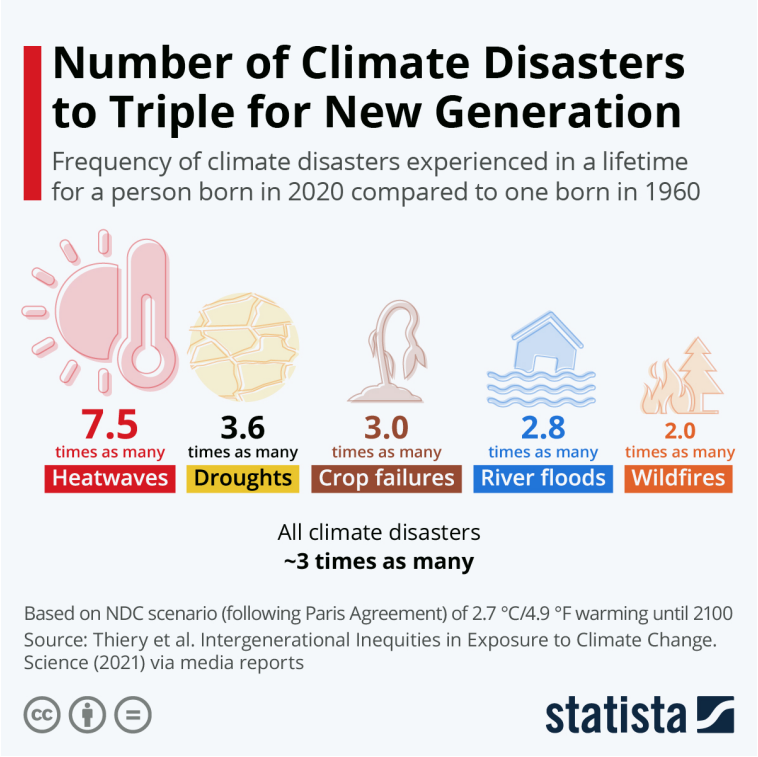
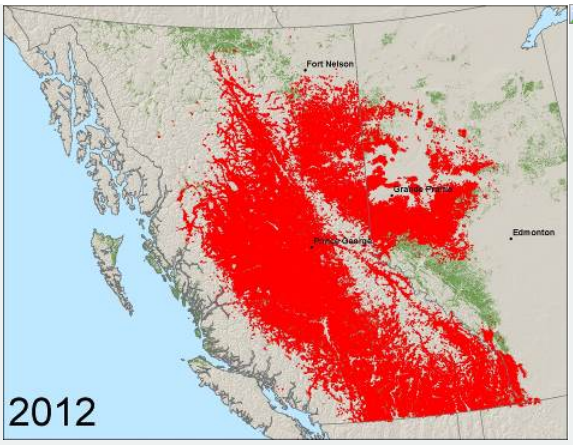


Figure 6.3.3.1: Predicted future climate disasters for someone born in 2020 versus someone born in 1960.

Canadian Perspective - The Mountain Pine Beetle

"The mountain pine beetle (*Dendroctonus ponderosae* Hopkins) is native to western North America, from northern Mexico to northern British Columbia. It is also present in an isolated population of pine that is surrounded by prairie in the Cypress Hills area of southwestern Saskatchewan, which was likely infested in the early 1980s. In the 2000s, the beetle significantly expanded its range in Canada, invading new habitat east of the Rocky Mountains in northeastern British Columbia and northern Alberta (Figure 6.3.3.2 left)."[1]



Reddened pine, caused by pine beetle attack, in central British Columbia.

Figure 6.3.3.2: Left: Observed presence of mountain pine beetle from 1999 to 2012 (Government of Canada). Right: Large area of damaged forest (Government of British Columbia)

"Most species of pine that grow in the beetle's range are readily attacked, with the exception of Jeffrey pine. In Canada, these hosts include ponderosa, western white, whitebark, limber pines, and, very recently, jack pine in the expanded range. Lodgepole pine is the most common host in the mountain pine beetle's range in British Columbia."[1]

"This small beetle attacks and kills mature trees by boring through the bark and mining the phloem (living tissue in vascular plants that carries organic nutrients). Its eggs hatch into larvae that consume the phloem, killing the tree. The beetles are killed by very cold winter weather, which historically has kept their numbers in check."[2]

"Trees will attempt to repel the beetles by releasing quantities of resin, which mixes with the boring dust and forms a soft, white or reddish pitch tube around each borehole. These pitch tubes usually appear from the duff line to a top diameter of 15cm. Infected trees' foliage turns yellow and then red by the spring of the year following the initial beetle attack. Most of the needles drop from the tree after two years, leaving a dead grey snag."[2]

"In British Columbia, the northern limit of the beetle's range has been limited by cold winter temperatures (−40°C) and cool summers. Outbreaks have been linked to favorable weather in both summer and winter. Warm, dry summers are good for beetle development and dispersal, and drought stress reduces tree defenses. In the late 1990s, after several relatively warm winters, a massive outbreak resulted in the loss of millions of hectares of pine forest in British Columbia over the next 15 years."[1,2]

Resources:

1. Government of Canada. 2021. *Mountain pine beetle (factsheet)*. Natural Resources Canada [Online]. Available from: https://www.nrcan.gc.ca/forests/fire-insects-disturbances/top-insects/13397

2. Government of British Columbia. 2022. *Mountain pine beetle*. Forest Health [Online]. Available from: https://www2.gov.bc.ca/gov/content/industry/forestry/managing-our-forest-resources/forest-health/forest-pests/bark-beetles/mountain-pine-beetle

Future Climate Change

Many greenhouse gases stay in the atmosphere for long periods of time. As a result, even if emissions stopped increasing, atmospheric greenhouse gas concentrations would continue to remain elevated for hundreds of years. Moreover, if we stabilized concentrations and the composition of today's atmosphere remained steady (which would require a dramatic reduction in current greenhouse gas emissions), surface air temperatures would continue to warm (Figure 6.3.3.3). This is because the oceans, which store heat, take many decades to fully respond to higher greenhouse gas concentrations. The ocean's response to higher greenhouse gas concentrations and higher temperatures will continue to impact climate over the next several decades to hundreds of years. Thus, past and present GHG emissions will affect climate far into the future.

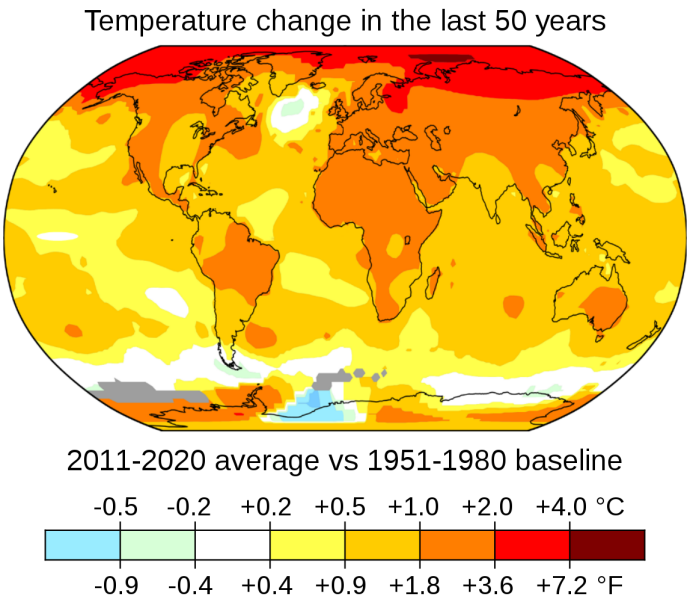


Figure 6.3.3.3: Temperature increases have been most pronounced in northern latitudes and over land masses. The colors represent the temperature difference between the 2011-2020 average and the 1951-1980 baseline, with warmer colors (yellow, orange, red) representing increases, and cool colors (green, blue) representing decreases. The image uses longer term averages of at least a decade to smooth out climate variability due to factors such as El Niño. Grey areas in the image have insufficient data for rendering. Image and caption (modified) from NASA's Scientific Visualization Studio/Eric Fisk (public domain).

Temperature Changes

Climate models project the following key temperature-related changes:

- Average global temperatures are expected to increase by 1.1°C to 6.4°C by 2100, depending on the level of future greenhouse gas emissions, and the outcomes from various climate models.
- By 2100, global average temperature is expected to warm at least twice as much as it has during the last 100 years.
- Ground-level air temperatures are expected to continue to warm more rapidly over land than oceans.
- Some parts of the world are projected to see larger temperature increases than the global average.

These changes will impact our food supply, water resources, infrastructure, ecosystems, and even our own health. The magnitude and rate of future climate change will primarily depend on the following factors:

- The rate at which levels of greenhouse gas concentrations in our atmosphere continue to increase, often known as "climate scenarios" (Figure 6.3.3.4);
- How strongly features of the climate (e.g., temperature, precipitation, and sea level) respond to the expected increase in greenhouse gas concentrations; and
- Natural influences on climate (e.g., from volcanic activity and changes in the sun's intensity) and natural processes within the climate system (e.g., changes in ocean circulation patterns).

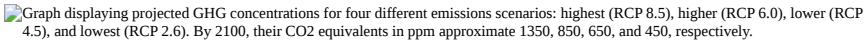

Graph displaying projected GHG concentrations for four different emissions scenarios: highest (RCP 8.5), higher (RCP 6.0), lower (RCP 4.5), and lowest (RCP 2.6). By 2100, their CO2 equivalents in ppm approximate 1350, 850, 650, and 450, respectively.

Figure 6.3.3.4: This figure shows projected greenhouse gas concentrations for four different emissions pathways. The top pathway assumes that greenhouse gas emissions will continue to rise throughout the current century. The bottom pathway assumes that emissions reach a peak between 2010 and 2020, declining thereafter. Source: Graph created from data in the Representative Concentration Pathways Database (Version 2.0.5)

Species that are highly mobile are not entirely spared from the negative impacts of climate change. Consider that migratory species rely on environmental cues, such as day length and temperature, to determine when to start moving from one area to the next. But because different species rely on different environmental cues to time their life cycles (e.g. breeding), not all species will adjust to climate change at the same rate. There is consequently a high likelihood that climate change will disrupt these synchronous

movements that the animals in particular have developed over thousands to millions of years. This disruption of timed aspects of a species' life cycle, such as migration and breeding, is called **phenological mismatch**. Researchers have already seen signs of phenological mismatch: some migratory birds that overwinter in the tropics have started to migrate to their breeding grounds at earlier dates than before. If these trends hold, they may soon start breeding before peak food availability, which could lead to lower fitness of offspring.

Resident species are also vulnerable to phenological mismatch. While these species might not be known for large-scale movements around the globe, they may still have to adjust their ranges to keep track of their climatic niches. Considering the improbability that different species will all adapt at the same pace, there is thus a danger that important mutualistic relationships might be pulled apart during these range adaptations. This is of concern for species with specialized feeding niches, as seen in some pollinators. Extinctions arising from this decoupling of mutualistic relationships are referred to as **coextinction**.

Freshwater ecosystems will generally experience temperature increases under climate change. Like their terrestrial counterparts, many freshwater species are sensitive to temperature shifts as warmer water also holds less dissolved oxygen. In addition, longer growing seasons and higher water temperatures will lead to increased nutrient loads, algae blooms, and eutrophication. All these factors will force many freshwater species—even those not sensitive to temperature shifts—to adjust their ranges to keep track of suitable conditions. For some freshwater species, the impediments to adjusting their ranges as necessary may be insurmountable.

Not all species will be impacted negatively. A variety of species are expected to benefit from climate change. These include generalist species currently limited by interactions with localized specialists that are—at least at present—better competitors for limiting resources. Some tropical species may thrive as their habitats become hotter and wetter. Species with high genetic diversity that reproduce quickly (allowing for rapid adaption to environmental changes) are also likely to benefit. Unfortunately, many species that exhibit these traits carry diseases and/or are agricultural pests. For example, populations of the coffee berry borer (*Hypothenemus hampei*)—Africa's most notorious coffee pest—are expected to greatly increase in a warmer world. This growing threat is particularly worrying given that higher temperatures have already reduced coffee harvests in countries such as Tanzania by as much as 50%.

The range of disease-carrying insects and the viruses and pathogenic parasites they harbor will increase. This spread has already been documented in North America with several different diseases including West Nile and Lyme disease. Colder temperatures typically limit the distribution of certain species, such as the mosquitoes that transmit malaria, because freezing temperatures destroy their eggs. Not only will the range of some disease-causing insects expand, but increasing temperatures will also accelerate the host lifecycles, allowing them to breed and multiply more quickly. They may even evolve pesticide resistance faster. In addition to those listed above, other diseases such as dengue fever, malaria, yellow fever, zika virus, and chikungunya are expected to spread to new regions as the global climate warms.

Climate change does not only increase the spread of diseases in humans. Rising temperatures are associated with greater amphibian mortality due to chytridiomycosis (see Unit 5.2.3). Similarly, warmer temperatures have exacerbated bark beetle infestations of coniferous trees, such as pine and spruce.

? Optional Activity 6.3.3.1

How do climate factors (temperature, precipitation, & humidity) relate to vector-borne disease?

A. Heavy rain increases the risk of animals transmitting pathogens.
B. Milder winters increase the vector density & risk of disease
C. Dry summers & drought increase the risk of vectors expanding their range
D. More intense snowstorms Snow increase vector density & risk of disease

Answer

B. Milder winters increase the vector density & risk of disease.

Precipitation and Storm Events

Patterns of precipitation and storm events, including both rain and snowfall are likely to change. However, some of these changes are less certain than the changes associated with temperature. Because warm air is able to hold more water than cold air, the general

global trend over the past century has been one of increasing precipitation (Figure 6.3.3.5).

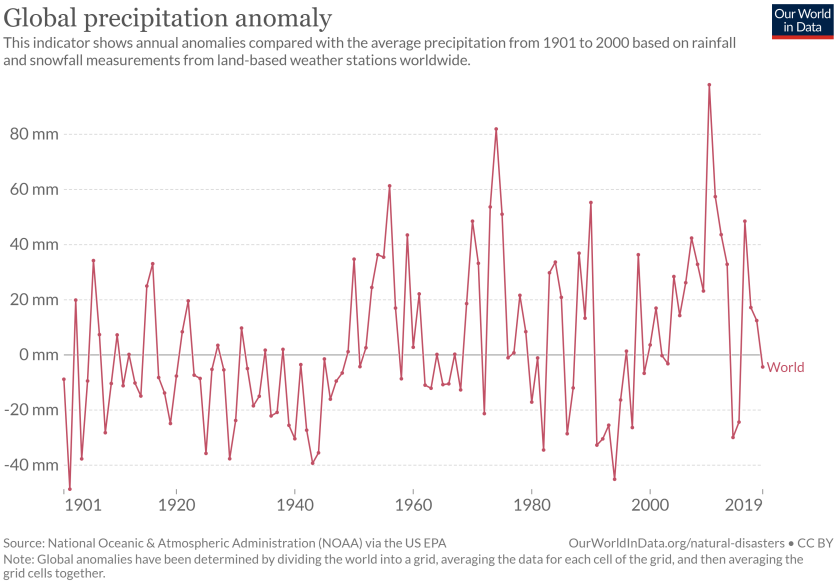


Figure 6.3.3.5: Data shows global precipitation patterns, based on rainfall and snowfall measurements from land-based weather stations worldwide. This indicator shows annual anomalies, or differences, compared with the average precipitation from 1901 to 2000. CC-BY United States Environmental Protection Agency (EPA)

Projections show that future precipitation and storm changes will vary by season and region. Some regions may have less precipitation, some may have more precipitation, and some may have little or no change. The amount of rain falling in heavy precipitation events is likely to increase in most regions, while storm tracks are projected to shift toward the poles. Climate models project the following precipitation and storm changes:

- Global average annual precipitation through the end of the century is expected to increase, although changes in the amount and intensity of precipitation will vary by region.
- The intensity of precipitation events will likely increase on average. This will be particularly pronounced in tropical and high-latitude regions, which are also expected to experience overall increases in precipitation.
- The strength of the winds associated with tropical storms is likely to increase. The amount of precipitation falling in tropical storms is also likely to increase.
- Annual average precipitation is projected to increase in some areas and decrease in others.

One of the other risks for coastal populations, besides sea-level rise, is that climate warming is also associated with an increase in the intensity of coastal storms (e.g., atmospheric rivers, hurricanes, cyclones, or typhoons), which almost always bring serious flooding from intense rain and storm surges. Some recent examples are the Vancouver floods of 2021 and the impact of Hurricane Fiona on Nova Scotia in 2022 (Figure 6.3.3.6).



Figure 6.3.3.6: Grounded barge along Vancouver's Seawall in English Bay. November 2021. CC-BY-SA 4.0 Northwest

Changing precipitation levels will have several impacts on freshwater ecosystems, particularly as it relates to changes in their flow regimes. For example, areas that are undergoing decreased precipitation will experience decreased runoff and increased drying of wetlands and small streams, while areas with increased precipitation will experience increased storm surges and flushing. Given these multiple stressors, there is a reasonable expectation that many freshwater species will go extinct or face significant population declines and range shifts over the next decades. These changes are of major concern in countries that are currently majority subsistence, where so many people depend on fish and related natural resources for their livelihoods. Many communities around the world are already finding it more difficult to meet their nutritional needs due to climate-induced freshwater fish declines. Also, at some large lakes, which may supply 20–40% of the surrounding countries' dietary protein—fish yields have decreased by 30% in recent years, also attributed to climate change.

Ice Melt and Sea Level Rise

Arctic sea ice is already declining. Sea ice is ice floating in the ocean (not on land like a glacier). Most sea ice is in the Arctic Ocean and the extent of sea ice is shrinking. Below, the NOAA animation shows how perennial sea ice has declined from 1990 to 2015. The oldest ice is white and the youngest (seasonal) ice is dark blue. The amount of old ice has declined from 20% in 1985 to 3% in 2015. For every 1°C of warming, models project about a 15% decrease in the extent of annually averaged sea ice (the total ice extent and concentration averaged over a year) and a 25% decrease in September Arctic sea ice.

Video



This 2-minute video from the US's National Oceanic and Atmospheric Association illustrates the loss of Arctic sea ice from 1990-2015.

Question after watching: What seasonal patterns do you notice? What do you notice regarding the oldest ice over the 25 years portrayed in the video?

The land-based, coastal sections of the Greenland and Antarctic ice sheets have been melting significantly and are expected to continue to do so (Figure 6.3.3.7). If the rate of this ice melting increases in the 21st century, these ice sheets could add significantly to global sea level rise and disrupt global ocean currents. Before anthropogenic warming, glacial activity was variable with some retreating and some advancing. Now, nearly all glaciers globally a retreating and expected to continue to melt, leading to freshwater shortages globally.

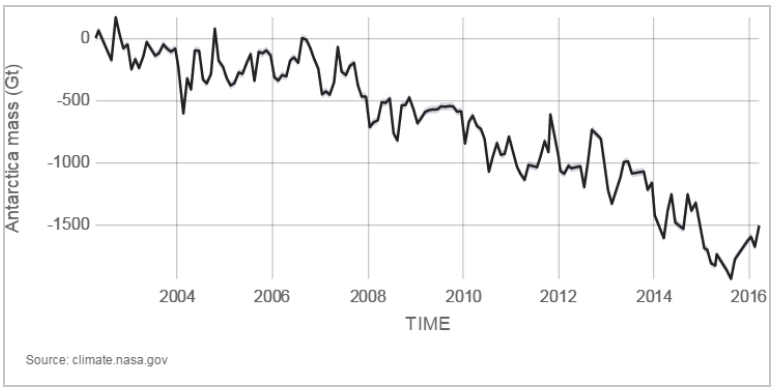


Figure 6.3.3.7: Decline of Antarctic ice mass from 2002 to 2016. (NASA)

On average, the sea is rising at a rate of 1.8 mm per year. However, between 1993 and 2010 the rate of sea level increase ranged between 2.9 and 3.4 mm per year (Figure 6.3.3.8). This is thought largely to be from both the melting of glaciers and thermal expansion. Thermal expansion means that as objects such as solids, liquids, and gases heat up, they expand in volume. Since 1970, the melting of glaciers and thermal expansion account for 75% of the sea-level rise (scientists are still researching the other 25%). As the oceans creep further inland, the extent of low-lying coastal ecosystems such as rocky shores or sandy beaches will shrink, and so also the sizes of the wildlife populations living in those areas.

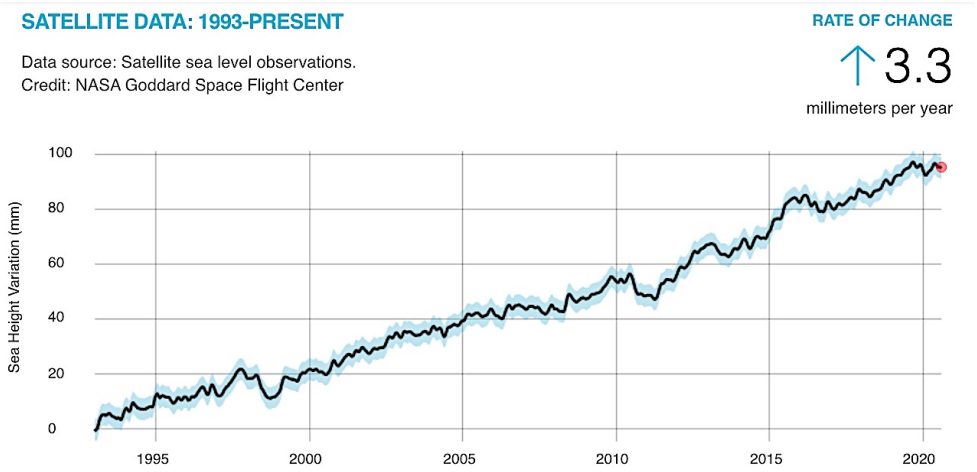


Figure 6.3.3.8: Sea height variation (mm) over time. Sea height has increased about 3.3 millimeters per year on average since 1993. Data is from satellite sea level observations by the NASA Goddard Space Flight Center. Image by NASA (public domain)

Projections for sea level rise to the end of this century vary widely. This is in large part because we do not know which of the above climate change scenarios (Figure 6.3.3.3) we will most closely follow, but many are in the range from 0.5 m to 2.0 m. One of the problems in predicting sea level rise is that we do not have a strong understanding of how large ice sheets, such as Greenland and Antarctica, will respond to future warming. Another issue is that the oceans do not respond immediately to warming. For example, with the current amount of warming, we are already committed to a future sea level rise of between 1.3 m and 1.9 m, even if we could stop climate change today.

? Optional Activity 6.3.3.2

What are the major causes of sea level rise?

A. Melting sea ice
B. Melting glaciers and ice sheets
C. Seawater expanding as it gets warmer
D. A and B
E. B and C

Answer

B and C. Melting glaciers and ice sheets and seawater expanding as it gets warmer.

Ocean Acidification and Deoxygenation

Since 1750, the ocean has absorbed about 30% of all anthropogenic carbon dioxide sources. When carbon dioxide gets absorbed in the ocean, it creates carbonic acid which makes the ocean more acidic. **Ocean acidification** is the process of ocean waters' decreasing pH (lower values are more acidic on the pH scale). The pH level of the oceans has decreased by approximately 0.1 pH units since pre-industrial times, which is equivalent to a 25% increase in acidity. The pH level of the oceans is projected to decrease even more by the end of the century as CO_2 concentrations are expected to increase for the foreseeable future.

Ocean acidification adversely affects many marine species, including plankton, mollusks, shellfish, and corals. As ocean acidification increases, the availability of calcium carbonate will decline. Calcium carbonate is a key building block for the shells and skeletons of many marine organisms. Most tropical oceans have experienced extensive coral bleaching events in recent years due to increased sea surface temperatures and ocean acidification. Ocean acidification also disturbs predator-prey dynamics by impairing the senses of prey species and compromising the ability of marine creatures to communicate with those within their same species.

Marine fish and invertebrates rely on dissolved oxygen that enters the water either through the atmosphere or by photosynthetic plankton. But because warmer water absorbs less oxygen, scientists predict that some areas of the ocean will see a 3–6% drop in dissolved oxygen concentrations under climate change. This process, known as **ocean deoxygenation**, will leave parts of the ocean unsuitable for marine fishes and invertebrates, leading to dead zones. The impact of ocean deoxygenation will also be felt by economically important fisheries where climate change is predicted to lead to fisheries-related economic losses upwards of $415 million each year.

Acidification combined with warmer temperatures and lower oxygen levels is expected to have severe impacts on marine ecosystems, especially coral reefs, and associated fisheries possibly affecting our ocean-derived food sources.

? Optional Activity 6.3.3.3

What causes ocean acidification?

A. Deoxygenated ocean water.
B. Ocean pollution.
C. Warm freshwater from land.
D. CO_2 dissolved in ocean water.

Answer

D. CO_2 dissolved in ocean water.

Climate Change Affects Everyone

We have all experienced the effects of climate change over the past decade. However, it is not straightforward for climatologists to make the connection between a warming climate and specific weather events, and most are justifiably reluctant to ascribe any

specific event to climate change. In this respect, the best measures of climate change are those that we can detect over several decades, such as the temperature changes shown in Figure 6.3.3.2, or the sea level rise shown in Figure 6.3.3.7.

Our lives are connected to the climate**.** Human societies have adapted to the relatively stable climate we have enjoyed since the last ice age which ended several thousand years ago. A warming climate will bring changes that can affect our water supplies, agriculture, power and transportation systems, the natural environment, and even our own health and safety. Carbon dioxide can stay in the atmosphere for nearly a century, on average, so Earth will continue to warm in the coming decades. The warmer it gets, the greater the risk for more severe changes to the climate and Earth's system. Although it is difficult to predict the exact impacts of climate change, what is clear is that the climate we are accustomed to is no longer a reliable guide for what to expect in the future.

Indigenous Connections: Climate Change Vulnerabilities

In 2019, the Tsleil-Waututh Nation published a report entitled, "Understanding Our Community's Climate Change Vulnerabilities: Community Climate Change Resilience Planning | PHASE 1 Summary". As noted in the report, "Climate change has the potential to profoundly impact the Tsleil-Waututh Nation (TWN) and many key aspects of community life. It influences the ability of our community to harvest some wild foods and medicinal plants, how we access the shoreline and marine waters, and how we connect with Nature. It poses community health risks, influence our ability to practice spiritual and cultural ceremonies, and share cultural teachings...This report serves to build an understanding of community vulnerability to climate change and begins to explore potential climate adaptation actions" (Tsleil-Waututh Nation, 2019).

The project focused on "climate change impacts to Tsleil-Waututh, also known as Burrard Inlet IR#3, which is the current village site for the Nation. In the future, TWN hopes to expand the assessment to consider the vulnerability of other areas within its traditional territory" (Tsleil-Waututh Nation, 2019).

Below is a summary of some of what this report details as possible impacts of climate change on the Tsleil-Waututh Nation:

- Coastal flood hazard modeling results showed that most waterfront properties may experience flooding during an extreme flood under a 2 m sea level rise scenario.
- Coastal erosion may affect waterfront properties and natural habitats, and threaten buildings, archeological, and other cultural sites.
- Ocean acidification from climate change poses an acute threat to species (particularly shellfish) along the mudflats and beaches of Burrard Inlet IR#3.
- [Loss of intertidal areas] will have significant impacts on species that live in the intertidal zone (e.g., shellfish) or that forage for food in these areas (e.g., marine birds and salmon). Many of these species are critically important as sources of food for TWN community and cultural health and serve as important opportunities to share traditional teachings (Figure 6.3.3.9).
- The waters of Burrard Inlet will be increasingly vulnerable to harmful algal blooms as water temperatures rise and summer precipitation decreases.
- Climate change has the potential to make local waters more habitable for invasive non-native species, particularly those from warmer waters.
- Extended periods of extreme heat can cause heat exhaustion or heat stroke, particularly among vulnerable groups.
- Community member health and the opportunity for recreation, cultural practices, and job productivity is also impacted by poor air quality and smoke from wildfires across BC.
- Ongoing changes to air temperatures and precipitation patterns from climate change could increase the success and abundance of some invasive species.



Figure 6.3.3.9: A keystone species, the ochre sea star (*Pisaster ochraceus*) taken at Ganges Harbour, Salt Spring Island, British Columbia, CC-BY-SA D. Gordon E. Robertson

Reference:

Tsleil-Waututh Nation. 2019. "Understanding Our Community's Climate Change Vulnerabilities: Community Climate Change Resilience Planning | PHASE 1 Summary" British Columbia, Canada. Available from: https://twnation.ca/wp-content/uploa...e-Jan-2020.pdf

Video



Learn how climate change will transform the world at a 2°C of warming in this 7-minute video by PBS. Question after watching: Which of the changes will affect you directly? Which of the changes will affect you indirectly?

Suggested Supplementary Reading

Intergovernmental Panel on Climate Change. 2021. 6th Assessment: Summary for Policymakers.

NASA. 2022. Global Climate Change: Vital Signs of the Planet. This website by NASA provides a multi-media smorgasbord of engaging content. Learn about climate change using data collected by NASA satellites and more.

This page titled 6.3.3: Current and Future Climate Change Impacts is shared under a CC BY-NC-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.0: Prelude to Our Warming World** has no license indicated.
- **10.4: Climate Change** by Matthew R. Fisher is licensed CC BY 4.0. Original source: https://openoregon.pressbooks.pub/envirobiology.
- **6.3: The Impact of Climate Change** by John W. Wilson & Richard B. Primack is licensed CC BY 4.0. Original source: https://doi.org/10.11647/OBP.0177.

6.3.4: Climate Strategies

Climate Strategies

- Please read and watch the following Learning Resources
- Reading the material for understanding, and taking notes during videos, will take approximately 1 hour.
- Optional Activities are embedded.
- To navigate to the next section, use the Contents menu at the top of the page OR the right arrow on the side of the page.
  - If on a mobile device, use the Contents menu at the top of the page OR the links at the bottom of the page.

Learning Objectives

- Explain the global efforts to communicate about, and combat, climate change
- Describe the differences between adaptation and mitigation strategies

Introduction

With the increase in understanding that our activities are creating a global crisis of epic proportions, the impacts of climate change are now being actively debated in the corridors of governments and major corporations. Politicians, the media, and others are also increasingly replacing “climate change” with more vivid language, like “climate crisis” and “climate emergency.” This will hopefully encourage even more governments and industries to come to the table and cooperate like never before to address the fundamental drivers of climate change. Solving this global crisis requires an international multi-pronged approach that should include ecosystem protection, restoration, and direct species management, reduction of carbon emissions, sustainable planning, and legislative action.

International Agreements

On the international front, key initiatives related to research and planning are being led by the United Nations Environment Programme (UNEP) and the World Meteorological Organization (WMO), which in 1988 established the Intergovernmental Panel on Climate Change (IPCC). The IPCC undertakes comprehensive reviews of the science of global warming, with a focus on likely scenarios of climatic, ecological, and economic consequences. The IPCC also does research on ways to slow or prevent the increases in GHGs and on how economic and ecological systems might adapt to predicted climate change. At the international level, the IPCC is the most credible source of information about climate change.

Because of concerns about the potentially disastrous consequences of global warming, in 1990 the IPCC and other groups of climate specialists recommended that the United Nations (UN) mobilize global leadership to negotiate an international agreement to reduce emissions of GHGs. The UN then established an Intergovernmental Negotiating Committee to draft the terms of a **UN Framework Convention on Climate Change (UNFCCC)**. After a series of difficult international negotiations, the UNFCCC was drafted and then adopted in 1992 at the UN Conference on Environment and Development (UNCED) held in Rio de Janeiro, Brazil.

The objective of the UNFCCC is to stabilize atmospheric GHGs at concentrations that would prevent a dangerous intensification of the planetary greenhouse effect. Signatory nations to the UNFCCC, known as “parties to the convention,” have agreed to undertake certain actions to compile information on emissions of GHGs, develop policies to decrease emissions, prepare strategies to adapt to anticipated effects of climate change, and provide financial and scientific support to developing countries. Moreover, the 140 countries that signed the UNFCCC in Rio agreed to discuss its implementation at a global forum, which was held in Berlin in 1995. At that meeting, it was agreed that global emissions of GHGs should be reduced and a further series of international negotiations was needed to reach consensus on an implementation strategy. Those negotiations were completed at another meeting, held in Kyoto, Japan, in 1997. The outcome of that key meeting was the **Kyoto Protocol**.

Most years, since 1992, the world's countries have come together to renegotiate and discuss climate change at an UN-organized **Conference of the Parties** (Parties meaning those who signed to the UNFCCC), also known as "COP". As of 2022, COP27 was

held in Egypt celebrating the 30th Anniversary of the ratification of the UNFCCC where attendees from 197 countries met to discuss solutions, financing, and collaboration.

National and Local Action

While the United States never fully ratified the Kyoto Protocol, it has made some commitments to reduce its emissions of CO_2 through COP agreements. The **Environmental Protection Agency** is the federal agency largely tasked with setting these goals and targets. Some of these goals and targets include:

- Reducing U.S. greenhouse gas emissions 50-52% below 2005 levels in 2030.
- Reaching 100% carbon pollution-free electricity by 2035.
- Achieving a net-zero emissions economy by 2050.
- On September 23, 2021, the EPA issued a final rule that will phase down the U.S. production and consumption of hydroflourocarbons (HFCs) by 85% by 2035, as mandated by the American Innovation and Manufacturing Act of 2020. A global phasedown of HFCs is expected to avoid up to 0.5°C of global warming by 2100.
- On December 20, 2021, EPA finalized federal greenhouse gas emissions standards for passenger cars and light trucks for Model Years (MY) 2023 through 2026. EPA also announced plans to reduce greenhouse gas emissions and other harmful air pollutants from heavy-duty trucks for MY 2027 and beyond.
- EPA is implementing CO_2 emission standards for airplanes used in commercial aviation and for large business jets. These standards are consistent with international standards set by the United Nations' International Civil Aviation Organization.
- The Renewable Fuel Standard (RFS) program was created under the Energy Policy Act of 2005 (EPAct), which amended the Clean Air Act (CAA). The RFS program is a national policy that requires a certain volume of renewable fuel to replace or reduce the quantity of petroleum-based transportation fuel, heating oil, or jet fuel.

To accomplish any reductions is a formidable challenge as the United States has the highest per capita production of greenhouse gasses in the world. In fact, the US has not made most of its previously set targets, largely due to expanding use of natural gas and oil.

This is largely due to the fact that, like most other developed countries, the US has not produced an effective strategy for meeting its agreements. There is a great deal of intense political and economic controversies associated with the actions that would be necessary. In addition, there is a great deal of argument between countries about who should make the most changes. Moreover, the federal government and some other jurisdictions, are focusing on intensity-based targets, which encourage improved technological efficiencies but do not necessarily reduce the aggregate emissions of GHGs. Such tactics do little to reduce the rapid increase of emissions from new fossil-fuel enterprises.

To combat climate change, the leadership of many states and cities have started to enact laws to reduce greenhouse gas emissions and habitat destruction. Many industries are also hard at work developing “greener” technologies to enable us to live more sustainably. Communities are coming together to implement solutions that are a best-fit for local environments and economies. Conservation biologists also play a crucial role in mitigating the negative impacts of climate change. In addition to highlighting the plight of the natural world to society at large, we could work towards reducing the loss of ecosystem services and preventing species extinctions. To accomplish this task, we need to identify which species and ecosystems are most sensitive to climate change and develop strategies that will ensure the continued persistence of as many sensitive species and their habitats as possible.

While the situation surrounding global climate change is in serious need of our attention, it is important to realize that many scientists, leaders, and concerned citizens are making solutions to climate change part of their life’s work (Figure 6.3.4.1). The two solutions to the problems caused by climate change are mitigation and adaptation, and we will likely need a combination of both in order to prosper in the future.



Figure 6.3.4.1: Young people demand action to protect their futures at the 2021 UN Climate Change Conference, also known as COP26, held in Glasgow, Scotland. Photograph by UNFCCC, https://ukcop26.org/young-people-dem...ures-at-cop26/, Open Government Licence(OGL).

Video



The UN's Sustainable Development Goals (SDGs) outline issues and strategies for the future of humans and natural systems.

This 8.5-minute video describes SDG 13, which is focused on Climate Action.

Question after watching: Which of the strategies have you heard of before? Which strategies are new to you? What barriers to change resonate with you? What actions can you take to make change happen?

Climate Mitigation Strategies

In general, a strategy to mitigate climate change is one that reduces the amount of greenhouse gases in the atmosphere or prevents additional emissions. Mitigation strategies attempt to “fix” the problems caused by climate change.

Greenhouse Gas Reduction

There are many options for reducing the adverse impacts to society from CO_2 and other greenhouse gas emissions, such as switching to sources of electricity that do not contribute to the CO_2 problem, trying to generate fossil-based electricity by not releasing the CO_2 into the atmosphere, or exploring ways to reduce the demand for products that produce greenhouse gas emissions. Governmental regulations regarding the fuel efficiency of vehicles is one example of an institutionalized mitigation strategy already in place in many countries around the world.

Putting a price on carbon is the method many economists favor for reducing or controlling greenhouse gas emissions. Pricing carbon provides producers and consumers with a monetary incentive to reduce greenhouse gas emissions by placing a value on each unit of carbon dioxide or carbon dioxide equivalent that is emitted into the atmosphere. In Canada, for example, there are **carbon taxes,** or charges for burning fossil fuels. This is known as the "carbon pollution pricing system" and has been in place since 2019. This does not exist in the US because of political and economic controversies.

In Canada (and some other nations), however, it works well. Their federal pricing system has two parts: a regulatory charge on fossil fuels like gasoline and natural gas, known as the **Fuel Charge**, and a performance-based system for industries, known as the **Output-Based Pricing System**. Each province or territory can design its own pricing structure or the region will default to the Canadian government's minimum national stringency standards (known as the Federal Backstop) (Figure 6.3.4.2). Currently, this pricing mechanism is in place for the burning of fossil fuels such as gasoline or natural gas and for industries.

"Proceeds from the federal carbon pricing system remain in the jurisdiction where they were collected. Provinces and territories that requested the federal system receive these proceeds directly and can use them as they see fit. In other jurisdictions, the federal government delivers all proceeds to individuals, families, and businesses through payments and climate action programs. This helps make carbon pricing affordable, and enables households to make investments to increase energy efficiency and further reduce emissions" (Government of Canada, 2022). This type of governmental mitigation strategy has been shown to be effective in many other countries including India, Japan, France, Costa Rica, Canada, and the United Kingdom.



Figure 6.3.4.2: The provinces and territories on the map of Canada are one of three colors depending on whether the federal backstop applies in full, in part or not at all. CC-BY-SA Government of Canada

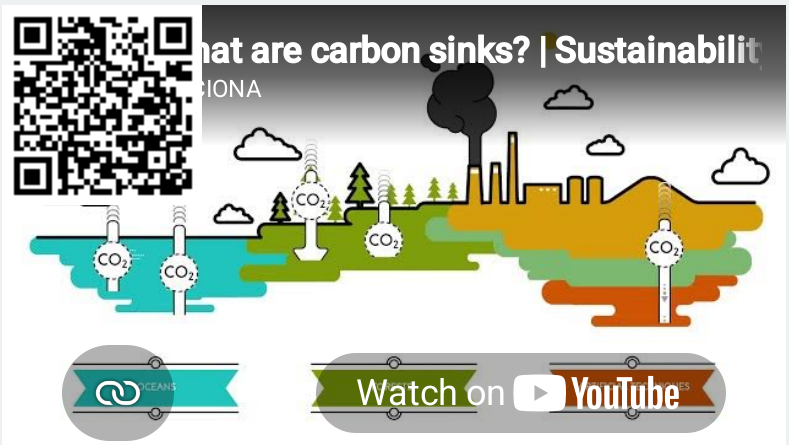
Carbon Capture and Sequestration

In addition to government measures and incentives, technology can also be harnessed to mitigate climate change. One strategy for this is the use of **carbon capture and sequestration** (CCS). Through CCS, 80-90% of the CO_2 that would have been emitted to the atmosphere from sources such as a coal-fired power plant is instead captured and then stored deep beneath the Earth's surface. The CO_2 is often injected and sequestered hundreds of miles underground into porous rock formations sealed below an impermeable layer, where it is stored permanently.

Scientists are also looking into the use of soils and vegetation for carbon storage potential. Proper management of soil and forest ecosystems has been shown to create additional carbon sinks for atmospheric carbon, reducing the overall atmospheric CO_2 burden. Increasing soil carbon further benefits communities by providing better-quality soil for agriculture and cultivation.

Technologies related to alternative energy sources mitigate climate change by providing people with energy not derived from the combustion of fossil fuels. Finally, simple activities such as energy conservation, choosing to walk or bike instead of driving, and disposing of waste properly are activities that, when done by large numbers of people, actively mitigate climate change by preventing carbon emissions.

Video



This 2-minute video describes using natural and artificial carbon sinks to help mitigate climate change but notes that these do not solve it.

Question after watching: What is the ultimate solution to mitigating climate change?

? Optional Activity 6.3.4.1

Why are forests important for mitigating climate change?

A. Forests serve as a sink in the carbon cycle.
B. Trees provide building materials.
C. Trees are an important food source.
D. Leaves of trees reflect all sunlight away from the Earth.

Answer

A. Forests serve as a sink in the carbon cycle.

Climate Adaptation Strategies

Beyond mitigation, we know that climate change is already occurring as we can see and feel its effects. For this reason, it is essential to also adapt to our changing environment. This means that we must change our behaviors in response to the changing environment around us. Adaptation strategies will vary greatly by region, depending on the largest specific impacts in that area. For example, in the city of Delhi, India, a dramatic decrease in rainfall is projected over the next century. This city will likely need to implement policies and practices relating to the conservation of water like rainwater harvesting, water re-use, and increased irrigation efficiency. Rain-limited cities near oceans, such as Los Angeles, California may choose to use desalination to provide drinking water to their citizens. **Desalination** involves taking the salt out of seawater to make it potable. Cities with low elevations near oceans may need to implement adaptation strategies to rising sea levels, from seawalls and levees to relocation of citizens. One adaptation strategy gaining use is the creation or conservation of wetlands, which provide natural protection against storm surges and flooding.

The IPCC 6th Assessment Report (2022) outlines just some of the following global strategies for adaptation to climate change:

- Sustainable land use and urban planning
- Water use efficiency and water resource management
- Integrated coastal zone management
- Resilient power systems
- Health and health systems adaptation
- Planned relocation and resettlement
- Disaster risk management
- Climate services, including Early Warning Systems

Want to know more? Visit this site for short courses on Climate Change Adaptation Fundamentals: https://pcs.royalroads.ca/climate-change-adaptation-fundamentals-online

Indigenous Connections: Climate Action

"First Nations are seriously threatened by the climate emergency but are also essential drivers of effective climate change action. Indigenous ecological knowledge, authority and deep responsibilities to traditional lands and waters are critical to achieving world targets for greenhouse gas emission reductions and developing effective climate adaptation strategies.

The BC Assembly of First Nations (BCAFN), as part of the First Nations Leadership Council, strongly advocates for First Nations in BC to be true partners with the Provincial and Federal Governments to tackle the climate emergency. This approach is consistent with the *UN Declaration on the Rights of Indigenous Peoples* and respectful of First Nations' inherent Aboriginal Title, Rights and Treaty Rights.

In recognition of the climate emergency, the Union of BC Indian Chiefs (UBCIC) Chiefs Council and the BCAFN Chiefs-in-Assembly have passed resolutions mandating that the FNLC take action to respond to climate change. In addition to previous resolutions, the UBCIC passed Resolution no. 2019-02,***Climate Emergency and BC First Nations Climate Emergency Plan***, and the BCAFN passed Resolution no. 2019-04, ***Climate Emergency and Support for the Development of a BC First Nations Climate Change Strategy***.

Since 2019, the FNLC has worked with First Nations in BC to develop the First Nations Climate Change Strategy and Action Plan, endorsed by Chiefs in February and March of 2022.

The Strategy is designed to be a living and flexible document for use and implementation in different contexts. It is a means for collective advocacy on climate change while respecting the autonomy and self-determination of each Nation to address climate change on their own terms and through their own processes." (British Columbia Assembly of First Nations, 2022)

Below are just some of the adaptation measures included in the First Nations Climate Change Strategy and Action Plan:

- Ensuring long-term and stable climate funding for First Nations communities. Specifically, by establishing a BC First Nations Climate Fund.
- Implementing effective climate data governance and management systems within and between Indigenous communities broadly.
- Ensuring mechanisms are in place to restore the lands, waters, and ecosystems that have been impacted by human activity and climate change. This involves strengthening First Nation-led conservation efforts and implementing accountability measures for environmentally impactful human actions.
- Effectively responding to climate-related emergencies and associated risks and impacts by strengthening First Nation-led emergency management and preparedness mechanisms and increasing collaboration between relevant entities.
- Assessing impacts of climate change on First Nations health and wellness and developing appropriate responses to ensure long-term resiliency. As an immediate action, this involves ensuring that all First Nations have long-term and reliable access to safe and clean food and water sources.

The Executive Summary of the Plan can be found here: https://www.bcafn.ca/sites/default/files/2022-04/Executive%20Summary%20v2.pdf

Resource:

British Columbia Assembly of First Nations. 2022. Climate Emergency. British Columbia, Canada. Available from: https://www.bcafn.ca/priority-areas/environment/climate-emergency



B.C.'s climate is changing, and Indigenous peoples are taking action to help their communities prepare and adapt to these impacts. In this 5-minute video, some actions are highlighted including helping the Klinse-Za caribou thrive in a new environment, adapting traditional food systems at T'eqt"aqutn'mux and Fort Nelson First Nation returning to fish camp.

Question after watching: Which of the adaptation measures listed above did you see in the video?

If we are to mitigate and adapt to the far-reaching impacts of climate change, we must carefully monitor and study changes in biological communities and ecosystem functioning, and how they relate to changes in climate and other stressors. While we may lose some species in a warmer world, we can also prevent many extinctions with proactive wildlife management (Unit 6.2.4). It is likely that many existing protected areas will no longer preserve some of the rare and threatened species that currently live in them,

necessitating careful planning when establishing new protected areas. Even if climate change is not as severe as predicted, the steps we take now to safeguard biodiversity and our own future can only help.

Read these additional articles:

- Individual actions (via EPA)
- UN's 2022 Conference of the Parties 27th Annual Meeting (COP 27)
- 10 Solutions to Climate Change (Scientific American)

This page titled 6.3.4: Climate Strategies is shared under a CC BY-SA 4.0 license and was authored, remixed, and/or curated by Tara Jo Holmberg.

- **6.0: Prelude to Our Warming World** has no license indicated.
- **17: Atmospheric Gases and Climate Change** by Bill Freedman is licensed CC BY-NC 4.0.

Index

A

abiotic
1.1.1: Themes and Concepts of Biology
aboveground biomass
6.1.2: Energy Flow through Ecosystems
absorption spectrum
2.5.3: The Light-Dependent Reactions of Photosynthesis
abstract
1.1.2: The Nature of Science
abyssal zone
6.1.4: Aquatic Biomes
Acanthostega
5.8.4: Amphibians
accessory pigments
5.1.4: Eukaryotic Origins
acellular
5.2: Acellular Entities - Viruses, Prions, and Viroids
acetyl CoA
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
acid
1.2.3: Water
acid rain
6.1.5: Biogeochemical Cycles
acidophile
5.1.3: Evidence for Early Life
acoelomate
5.6.4: Features Used to Classify Animals
Actinopterygii
5.8.3: Fishes
activation energy
2.3.3: Potential, Kinetic, Free, and Activation Energy
activator
3.6.3: Prokaryotic Gene Regulation
active site
2.3.6: Enzymes
active transport
2.2.4: Active Transport
adaptation
1.1.1: Themes and Concepts of Biology
4.1.1: Understanding Evolution
6.3.3: Current and Future Climate Change Impacts
adhesion
1.2.3: Water
aerobic respiration
2.4.3: Glycolysis
5.1.4: Eukaryotic Origins
aerosol
6.3.2: Anthropogenic Climate Change
Age
5.1.1: Deep Time
air pollution
6.2.3: The Biodiversity Crisis - HIPPPOC
albedo
6.3.2: Anthropogenic Climate Change
algal bloom
6.1.4: Aquatic Biomes
aliphatic hydrocarbon
1.2.4: Carbon
alkilophile
5.1.3: Evidence for Early Life
allantois
5.8.5: Reptiles
allele
3.2.3: Characteristics and Traits
allosteric inhibition
2.3.6: Enzymes
alternation of generations
3.1.3: Sexual Reproduction
5.9.2: Kingdom Plantae - Adaptations
Alvarez Hypothesis
5.1.1: Deep Time
amino acid
1.3.5: Proteins
aminoacyl tRNA synthetase
3.5.6: Ribosomes and Protein Synthesis
amnion
5.8.5: Reptiles
amniote
5.8.5: Reptiles
amoebocyte
5.7.2: Phylum Porifera
Amphibia
5.8.4: Amphibians
amphiphilic
2.2.2: Components and Structure
ampulla of Lorenzini
5.8.3: Fishes
anabolic
2.3.2: Energy and Metabolism
anaerobic
2.4.3: Glycolysis
anaerobic cellular respiration
2.4.6: Metabolism without Oxygen
analytical model
6.1.1: Ecology of Ecosystems
anaphase
2.7.3: The Cell Cycle
anapsid
5.8.5: Reptiles
aneuploid
3.3.3: Chromosomal Basis of Inherited Disorders
aneuploidy
3.3.3: Chromosomal Basis of Inherited Disorders
angiosperm
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Animalia
4.4.1: Systematics and Classification
anion
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Annelida
5.7.4: Superphylum Lophotrochozoa
anomalies
6.3.2: Anthropogenic Climate Change
antenna protein
2.5.3: The Light-Dependent Reactions of Photosynthesis
antheridium
5.9.2: Kingdom Plantae - Adaptations
Anthocerotophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Anthropocene
5.1.1: Deep Time
anthropogenic
6.2.1: Introduction to Biodiversity
anthropogenic climate change
6.2.3: The Biodiversity Crisis - HIPPPOC
6.3.2: Anthropogenic Climate Change
anthropoid
5.8.8: The Evolution of Primates
antibiotic resistance
3.7.2: Biotechnology
anticodon
3.5.5: RNA Processing in Eukaryotes
antiporter
2.2.4: Active Transport
Anura
5.8.4: Amphibians
apex consumer
6.1.2: Energy Flow through Ecosystems
aphotic zone
6.1.4: Aquatic Biomes
apical meristem
5.9.2: Kingdom Plantae - Adaptations
apocrine gland
5.8.7: Mammals
Apoda
5.8.4: Amphibians
apoptosis
2.6.4: Response to the Signal
5.2: Acellular Entities - Viruses, Prions, and Viroids
applied science
1.1.3: The Role of Science in Society
aquaporin
2.2.3: Passive Transport
archaea
4.4.1: Systematics and Classification
Archaeopteryx
5.8.6: Birds
archegonium
5.9.2: Kingdom Plantae - Adaptations
archenteron
5.7.6: Superphylum Deuterostomia
archosaur
5.8.5: Reptiles
arctic tundra
6.1.3: Terrestrial Biomes
aromatic hydrocarbon
1.2.4: Carbon
Arthropoda
5.7.5: Superphylum Ecdysozoa
assimilation
6.1.2: Energy Flow through Ecosystems
assortative mating
4.3.2: Evolution in Populations
atom
1.1.1: Themes and Concepts of Biology
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
atomic mass
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks

atomic number
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
ATP
2.3.5: ATP- Adenosine Triphosphate
ATP synthase
2.4.5: Oxidative Phosphorylation
Australopithecus
5.8.8: The Evolution of Primates
autocrine signal
2.6.2: Signaling Molecules and Cellular Receptors
autoinducer
2.6.5: Signaling in Single-Celled Organisms
autosome
3.3.3: Chromosomal Basis of Inherited Disorders
autosomes
3.2.3: Characteristics and Traits

B

background extinction rate
6.2.1: Introduction to Biodiversity
bacteria
4.4.1: Systematics and Classification
bacteriophage
5.2: Acellular Entities - Viruses, Prions, and Viroids
balanced chemical equation
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Baltimore classification
5.2: Acellular Entities - Viruses, Prions, and Viroids
basal angiosperms
5.9.1: Kingdom Plantae - Evolution and Phylogeny
basal taxon
4.4.2: Phylogeny and Cladistics
base
1.2.3: Water
basic science
1.1.3: The Role of Science in Society
behavioral isolation
4.2.1: Species Defined
benthic realm
6.1.4: Aquatic Biomes
bilateral symmetry
5.6.4: Features Used to Classify Animals
binary fission
2.7.6: Prokaryotic Cell Division
binomial nomenclature
4.4.1: Systematics and Classification
bioaccumulation
6.1.2: Energy Flow through Ecosystems
biochemistry
1.1.1: Themes and Concepts of Biology
biodiversity
6.2.1: Introduction to Biodiversity
biodiversity hotspot
6.2.4: Preserving Biodiversity
biodiversity loss
6.2.2: Importance of Biodiversity
bioenergetics
2.3.2: Energy and Metabolism
biofilms
5.1.3: Evidence for Early Life
Biogeochemical cycle
6.1: Ecosystems and the Biosphere
6.1.5: Biogeochemical Cycles
biogeography
6.1: Ecosystems and the Biosphere
6.1.6: Biogeography
biological macromolecule
1.3.2: Synthesis of Biological Macromolecules
biological species
4.2.1: Species Defined
biology
1.1.2: The Nature of Science
Biomagnification
6.1.2: Energy Flow through Ecosystems
biomarker
3.7.6: Genomics and Proteomics
biomes
6.1: Ecosystems and the Biosphere
6.1.3: Terrestrial Biomes
biosphere
1.1.1: Themes and Concepts of Biology
biotechnology
3.7.2: Biotechnology
biotic
1.1.1: Themes and Concepts of Biology
biramous
5.7.5: Superphylum Ecdysozoa
blastopore
5.6.4: Features Used to Classify Animals
blastula
5.6.3: Features of the Animal Kingdom
bleaching
6.1.4: Aquatic Biomes
blending theory of inheritance
3.2.2: Mendel's Experiments and the Laws of Probability
body plan
5.6.3: Features of the Animal Kingdom
bog
6.1.4: Aquatic Biomes
boreal forest
6.1.3: Terrestrial Biomes
botany
1.1.1: Themes and Concepts of Biology
brachiation
5.8.8: The Evolution of Primates
brackish
6.1.4: Aquatic Biomes
brumation
5.8.5: Reptiles
Bryophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
bryophytes
5.9.1: Kingdom Plantae - Evolution and Phylogeny
budding
5.2: Acellular Entities - Viruses, Prions, and Viroids
buffer
1.2.3: Water

C

CAAT box
3.5.4: Eukaryotic Transcription
Calvin cycle
2.5.2: Overview of Photosynthesis
2.5.4: Using Light Energy to Make Organic Molecules
Cambrian explosion
5.6.2: The Evolutionary History of the Animal Kingdom
cAMP
2.6.3: Propagation of the Signal
cancer
3.6.8: Cancer and Gene Regulation
canopy
6.1.3: Terrestrial Biomes
CAP
3.6.3: Prokaryotic Gene Regulation
capillary action
1.2.3: Water
capsid
5.2: Acellular Entities - Viruses, Prions, and Viroids
captacula
5.7.4: Superphylum Lophotrochozoa
carbohydrate
1.3.3: Carbohydrates
carbon capture and sequestration
6.3.4: Climate Strategies
carbon dioxide
6.3.2: Anthropogenic Climate Change
carbon fixation
2.5.4: Using Light Energy to Make Organic Molecules
carbon footprint
6.1.5: Biogeochemical Cycles
carbon taxes
6.3.4: Climate Strategies
carotenoid
2.5.3: The Light-Dependent Reactions of Photosynthesis
carrier protein
2.2.3: Passive Transport
Casineria
5.8.5: Reptiles
catabolic
2.3.2: Energy and Metabolism
catabolite activator protein
3.6.3: Prokaryotic Gene Regulation
Catarrhini
5.8.8: The Evolution of Primates
cation
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
caveolin
2.2.5: Bulk Transport
cDNA library
3.7.3: Mapping Genomes
cell
1.1.1: Themes and Concepts of Biology
2: Unit II- The Cell
cell communication
2.6: Cell Communication
cell cycle
2.7.2: Cell Division
2.7.3: The Cell Cycle
cell cycle checkpoint
2.7.4: Control of the Cell Cycle

cell plate
2.7.3: The Cell Cycle
cell reproduction
2.7: Cell Reproduction
cell theory
2.1.2: Studying Cells
cell wall
2.1.4: Eukaryotic Cells
cellular cloning
3.7.2: Biotechnology
cellular respiration
2.4: Cellular Respiration
cellulose
1.3.3: Carbohydrates
centimorgan
3.3.2: Chromosomal Theory and Genetic Linkage
central dogma
3.5.2: The Genetic Code
central vacuole
2.1.4: Eukaryotic Cells
centriole
2.7.3: The Cell Cycle
centromere
2.7.2: Cell Division
centrosome
2.1.4: Eukaryotic Cells
Cephalochordata
5.8.2: Chordates
cephalothorax
5.7.5: Superphylum Ecdysozoa
chaeta
5.7.4: Superphylum Lophotrochozoa
chain termination method
3.7.4: Whole-Genome Sequencing
channel
6.1.4: Aquatic Biomes
channel protein
2.2.3: Passive Transport
chaparral
6.1.3: Terrestrial Biomes
chaperones
1.3.5: Proteins
charismatic species
6.2.2: Importance of Biodiversity
Charophyte
5.9.1: Kingdom Plantae - Evolution and Phylogeny
chelicera
5.7.5: Superphylum Ecdysozoa
chemical bond
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
chemical energy
2.3.3: Potential, Kinetic, Free, and Activation Energy
chemical reaction
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
chemical reactivity
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
chemical synapse
2.6.2: Signaling Molecules and Cellular Receptors
chemiosmosis
2.4.2: Energy in Living Systems
chemoautotroph
2.5.2: Overview of Photosynthesis
6.1.2: Energy Flow through Ecosystems
chiasmata
3.1.2: The Process of Meiosis
chitin
1.3.3: Carbohydrates
chlorophyll
2.1.4: Eukaryotic Cells
chlorophyll a
2.5.3: The Light-Dependent Reactions of Photosynthesis
chlorophyll b
2.5.3: The Light-Dependent Reactions of Photosynthesis
chloroplast
2.1.4: Eukaryotic Cells
2.5.2: Overview of Photosynthesis
chloroplasts
5.1.4: Eukaryotic Origins
choanocyte
5.7.2: Phylum Porifera
Chondrichthyes
5.8.3: Fishes
chordata
5.7.6: Superphylum Deuterostomia
5.8.2: Chordates
chorion
5.8.5: Reptiles
chromatid
2.7.2: Cell Division
chromatin
2.1.4: Eukaryotic Cells
Chromosomal Theory of Inheritance
3.3.2: Chromosomal Theory and Genetic Linkage
chromosome
2.1.4: Eukaryotic Cells
chromosome inversion
3.3.3: Chromosomal Basis of Inherited Disorders
cilium
2.1.6: The Cytoskeleton
CITES
6.2.4: Preserving Biodiversity
citric acid cycle
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
clade
4.4.2: Phylogeny and Cladistics
cladistics
4.4.2: Phylogeny and Cladistics
cladogram
4.4.2: Phylogeny and Cladistics
class
4.4.1: Systematics and Classification
clathrin
2.2.5: Bulk Transport
cleavage
5.6.3: Features of the Animal Kingdom
cleavage furrow
2.7.3: The Cell Cycle
climate
6.3: Climate Change
6.3.1: Introduction to Climate Change
climate change
6.2.3: The Biodiversity Crisis - HIPPPOC
6.2.4: Preserving Biodiversity
6.3.1: Introduction to Climate Change
climate model
6.3.2: Anthropogenic Climate Change
climatologist
6.3.2: Anthropogenic Climate Change
clitellum
5.7.4: Superphylum Lophotrochozoa
clone
3.7.2: Biotechnology
club mosses
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Cnidaria
5.7.3: Phylum Cnidaria
cnidocyte
5.7.3: Phylum Cnidaria
codominance
3.2.3: Characteristics and Traits
codon
3.5.2: The Genetic Code
coelom
5.6.4: Features Used to Classify Animals
coenzyme
2.3.6: Enzymes
coextinction
6.3.3: Current and Future Climate Change Impacts
cofactor
2.3.6: Enzymes
cohesin
3.1.2: The Process of Meiosis
cohesion
1.2.3: Water
colinear
3.5.2: The Genetic Code
common ancestor
4.4.2: Phylogeny and Cladistics
community
1.1.1: Themes and Concepts of Biology
competitive inhibition
2.3.6: Enzymes
compound
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
concentration gradient
2.2.3: Passive Transport
conceptual model
6.1.1: Ecology of Ecosystems
conclusion
1.1.2: The Nature of Science
condensin
2.7.3: The Cell Cycle
Conference of the Parties
6.3.4: Climate Strategies
confidence
6.3.3: Current and Future Climate Change Impacts
Coniferophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
conispiral
5.7.4: Superphylum Lophotrochozoa
consensus
3.5.3: Prokaryotic Transcription

conservation biology
6.2.2: Importance of Biodiversity
contig
3.7.4: Whole-Genome Sequencing
continental drift
5.1.1: Deep Time
continuous variation
3.2.2: Mendel's Experiments and the Laws of Probability
contour feather
5.8.6: Birds
control
1.1.2: The Nature of Science
Convention on Biological Diversity
6.2.4: Preserving Biodiversity
convergent evolution
4.1.1: Understanding Evolution
coral reef
6.1.4: Aquatic Biomes
core enzyme
3.5.3: Prokaryotic Transcription
corona
5.7.4: Superphylum Lophotrochozoa
COSEWIC
6.2.4: Preserving Biodiversity
cotelydons
5.9.1: Kingdom Plantae - Evolution and Phylogeny
covalent bond
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
Craniata
5.8.2: Chordates
cranium
5.8.2: Chordates
critically imperiled
6.2.4: Preserving Biodiversity
Crocodilia
5.8.5: Reptiles
crossover
3.1.2: The Process of Meiosis
Cryogenian period
5.6.2: The Evolutionary History of the Animal Kingdom
cryptofauna
6.1.4: Aquatic Biomes
ctenidium
5.7.4: Superphylum Lophotrochozoa
culture
1.1.3: The Role of Science in Society
cupule
5.9.1: Kingdom Plantae - Evolution and Phylogeny
cutaneous respiration
5.8.4: Amphibians
cuticle
5.7.5: Superphylum Ecdysozoa
5.9.2: Kingdom Plantae - Adaptations
Cycadophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
cyclic AMP
2.6.3: Propagation of the Signal
cyclin
2.7.4: Control of the Cell Cycle
cypris
5.7.5: Superphylum Ecdysozoa
cytochrome complex
2.5.3: The Light-Dependent Reactions of Photosynthesis
cytogenetic mapping
3.7.3: Mapping Genomes
cytokinesis
2.7.3: The Cell Cycle
cytopathic
5.2: Acellular Entities - Viruses, Prions, and Viroids
cytoplasm
2.1.4: Eukaryotic Cells
cytoskeleton
2.1.6: The Cytoskeleton
cytosol
2.1.4: Eukaryotic Cells

D

DAG
2.6.3: Propagation of the Signal
Darwin
4.1.1: Understanding Evolution
dead zone
6.1.4: Aquatic Biomes
6.1.5: Biogeochemical Cycles
decomposer
6.1.2: Energy Flow through Ecosystems
deductive reasoning
1.1.2: The Nature of Science
degeneracy
3.5.2: The Genetic Code
dehydration synthesis
1.3.2: Synthesis of Biological Macromolecules
denaturation
1.3.5: Proteins
denature
2.3.6: Enzymes
dentary
5.8.7: Mammals
deoxynucleotide
3.7.4: Whole-Genome Sequencing
deoxyribonucleic acid
1.3.6: Nucleic Acids
dephosphorylation
2.4.2: Energy in Living Systems
desalination
6.3.4: Climate Strategies
descriptive science
1.1.2: The Nature of Science
desmosome
2.1.7: Connections between Cells and Cellular Activities
determinate cleavage
5.6.4: Features Used to Classify Animals
detrital food web
6.1.2: Energy Flow through Ecosystems
detritivore
6.1.2: Energy Flow through Ecosystems
deuterostome
5.6.4: Features Used to Classify Animals
development
1.1.1: Themes and Concepts of Biology
diacylglycerol
2.6.3: Propagation of the Signal
diapsid
5.8.5: Reptiles
Dicer
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
dicots
5.9.1: Kingdom Plantae - Evolution and Phylogeny
dideoxynucleotide
3.7.4: Whole-Genome Sequencing
diffusion
2.2.3: Passive Transport
dihybrid
3.2.4: Laws of Inheritance
dimer
2.6.3: Propagation of the Signal
dimerization
2.6.3: Propagation of the Signal
dioecious
5.9.2: Kingdom Plantae - Adaptations
diphyodont
5.8.7: Mammals
diploblast
5.6.4: Features Used to Classify Animals
diploid
2.7.2: Cell Division
diplontic
5.9.2: Kingdom Plantae - Adaptations
disaccharide
1.3.3: Carbohydrates
discontinuous variation
3.2.2: Mendel's Experiments and the Laws of Probability
discussion
1.1.2: The Nature of Science
dispersive model
3.4.4: Basics of DNA Replication
dissociation
1.2.3: Water
divergent evolution
4.1.1: Understanding Evolution
Divisons
5.9.1: Kingdom Plantae - Evolution and Phylogeny
DNA
1.3.6: Nucleic Acids
3.4.2: Historical Basis of Modern Understanding
3.4.3: DNA Structure and Sequencing
DNA methylation
3.6.8: Cancer and Gene Regulation
DNA microarray
3.7.4: Whole-Genome Sequencing
DNA polymerase II
3.4.7: DNA Repair
DNA replication
3.4.4: Basics of DNA Replication
3.4.6: DNA Replication in Eukaryotes
DNA structure
3.4.3: DNA Structure and Sequencing
domain
4.4.1: Systematics and Classification
Domain Archaea
5.1.3: Evidence for Early Life
Domain Bacteria
5.1.3: Evidence for Early Life

Domain Eukarya
5.1.3: Evidence for Early Life
dominant
3.2.2: Mendel’s Experiments and the Laws of Probability
dominant lethal
3.2.3: Characteristics and Traits
dorsal hollow nerve cord
5.8.2: Chordates
down feather
5.8.6: Birds
downstream
3.5.3: Prokaryotic Transcription
driver
6.3.1: Introduction to Climate Change

E

eccrine gland
5.8.7: Mammals
Ecdysozoa
5.6.5: Animal Phylogeny
Echinodermata
5.7.6: Superphylum Deuterostomia
ecological pyramid
6.1.2: Energy Flow through Ecosystems
ecology
6: Unit VI- Ecology
ecosystem
1.1.1: Themes and Concepts of Biology
6.1.1: Ecology of Ecosystems
ecosystem diversity
6.2.1: Introduction to Biodiversity
ecosystem dynamics
6.1.1: Ecology of Ecosystems
ecosystem ecology
6.1: Ecosystems and the Biosphere
Ediacaran period
5.6.2: The Evolutionary History of the Animal Kingdom
electrochemical gradient
2.2.4: Active Transport
electrogenic pump
2.2.4: Active Transport
electrolyte
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electromagnetic spectrum
2.5.3: The Light-Dependent Reactions of Photosynthesis
electron configuration
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electron microscope
2.1.2: Studying Cells
electron orbital
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electron transfer
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electron transport chain
2.5.3: The Light-Dependent Reactions of Photosynthesis
electronegativity
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
electrophoresis
3.4.3: DNA Structure and Sequencing
element
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
embryophyte
5.9.2: Kingdom Plantae - Adaptations
emergent vegetation
6.1.4: Aquatic Biomes
enantiomers
1.2.4: Carbon
Enantiornithes
5.8.6: Birds
endangered
6.2.2: Importance of Biodiversity
endemic
6.1.6: Biogeography
endergonic
2.3.3: Potential, Kinetic, Free, and Activation Energy
endocrine cell
2.6.2: Signaling Molecules and Cellular Receptors
endocrine signal
2.6.2: Signaling Molecules and Cellular Receptors
endocytosis
2.2.5: Bulk Transport
endomembrane system
2.1.5: The Endomembrane System and Proteins
endoplasmic reticulum
2.1.5: The Endomembrane System and Proteins
endosymbiosis
5.1.4: Eukaryotic Origins
endosymbiotic theory
5.1.4: Eukaryotic Origins
ENGO
6.2.4: Preserving Biodiversity
enhancer
3.6.5: Eukaryotic Transcription Gene Regulation
enterocoelom
5.7.6: Superphylum Deuterostomia
enterocoely
5.6.4: Features Used to Classify Animals
entropy
2.3.4: The Laws of Thermodynamics
enzyme
1.3.5: Proteins
Eon
5.1.1: Deep Time
epidermis
5.7.3: Phylum Cnidaria
epigenetic
3.6.2: Regulation of Gene Expression
Epigenetic mechanisms
3.6.4: Eukaryotic Epigenetic Gene Regulation
epiphyte
6.1.3: Terrestrial Biomes
epistasis
3.2.4: Laws of Inheritance
Epoch
5.1.1: Deep Time
equilibrium
6.1.1: Ecology of Ecosystems
Era
5.1.1: Deep Time
EST
3.7.3: Mapping Genomes
estuary
6.1.4: Aquatic Biomes
eucoelomate
5.6.4: Features Used to Classify Animals
eukarya
4.4.1: Systematics and Classification
eukaryote
1.1.1: Themes and Concepts of Biology
eukaryotes
3.4.6: DNA Replication in Eukaryotes
eukaryotic cell
2.1.4: Eukaryotic Cells
Eumetazoa
5.6.5: Animal Phylogeny
euploid
3.3.3: Chromosomal Basis of Inherited Disorders
eutherian mammal
5.8.7: Mammals
eutrophication
6.1.4: Aquatic Biomes
evaporation
1.2.3: Water
6.1.5: Biogeochemical Cycles
evolution
1.1.1: Themes and Concepts of Biology
4.1.1: Understanding Evolution
exergonic
2.3.3: Potential, Kinetic, Free, and Activation Energy
exocytosis
2.2.5: Bulk Transport
exon
3.5.5: RNA Processing in Eukaryotes
experiemnt
1.1.2: The Nature of Science
expressed sequence tag
3.7.3: Mapping Genomes
extant
5.1.4: Eukaryotic Origins
extinct
6.2.4: Preserving Biodiversity
extirpated
6.2.4: Preserving Biodiversity
extracellular digestion
5.7.3: Phylum Cnidaria
extracellular domain
2.6.2: Signaling Molecules and Cellular Receptors
extracellular matrix
2.1.7: Connections between Cells and Cellular Activities
extracellular matrix (ECM)
5.1.3: Evidence for Early Life
extremophile
5.1.3: Evidence for Early Life

F

F1
3.2.2: Mendel’s Experiments and the Laws of Probability

F2
3.2.2: Mendel’s Experiments and the Laws of Probability
facilitated transport
2.2.3: Passive Transport
facilitates chromatin transcription
3.5.4: Eukaryotic Transcription
FACT
3.5.4: Eukaryotic Transcription
fallout
6.1.5: Biogeochemical Cycles
false negative
3.7.6: Genomics and Proteomics
falsifiable
1.1.2: The Nature of Science
family
4.4.1: Systematics and Classification
feedback inhibition
2.3.6: Enzymes
fermentation
2.4.6: Metabolism without Oxygen
fern
5.9.1: Kingdom Plantae - Evolution and Phylogeny
fertilization
3.1.2: The Process of Meiosis
flagellum
2.1.6: The Cytoskeleton
flavenoids
5.9.2: Kingdom Plantae - Adaptations
flight feather
5.8.6: Birds
flower
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Fluid Mosaic Model
2.2.2: Components and Structure
food chain
6.1.2: Energy Flow through Ecosystems
food web
6.1.2: Energy Flow through Ecosystems
forb
6.1.3: Terrestrial Biomes
foreign DNA
3.7.2: Biotechnology
fossil fuel
6.3.1: Introduction to Climate Change
frameshift mutation
3.4.7: DNA Repair
Frederick Griffith
3.4.2: Historical Basis of Modern Understanding
free energy
2.3.3: Potential, Kinetic, Free, and Activation Energy
Friedrich Miescher
3.4.2: Historical Basis of Modern Understanding
frog
5.8.4: Amphibians
FtsZ
2.7.6: Prokaryotic Cell Division
fuel charge
6.3.4: Climate Strategies
functional group
1.2.4: Carbon
fungi
4.4.1: Systematics and Classification
5.5: Fungi
furcula
5.8.6: Birds

G

G0 phase
2.7.3: The Cell Cycle
G1 phase
2.7.3: The Cell Cycle
G2 phase
2.7.3: The Cell Cycle
gametangia
5.9.2: Kingdom Plantae - Adaptations
gamete
2.7.2: Cell Division
gametic barrier
4.2.1: Species Defined
gametophyte
3.1.3: Sexual Reproduction
5.9.1: Kingdom Plantae - Evolution and Phylogeny
gap junction
2.1.7: Connections between Cells and Cellular Activities
gastrodermis
5.7.3: Phylum Cnidaria
gastrovascular cavity
5.7.3: Phylum Cnidaria
gastrula
5.6.3: Features of the Animal Kingdom
GDP
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
gel electrophoresis
3.7.2: Biotechnology
gemmule
5.7.2: Phylum Porifera
gene
2.7.2: Cell Division
gene expression
3.6.2: Regulation of Gene Expression
gene pool
4.2.1: Species Defined
4.3.2: Evolution in Populations
gene regulation
3.6.4: Eukaryotic Epigenetic Gene Regulation
3.6.8: Cancer and Gene Regulation
gene targeting
3.7.2: Biotechnology
gene therapy
3.7.2: Biotechnology
genetic diagnosis
3.7.2: Biotechnology
genetic diversity
4.1.1: Understanding Evolution
6.2.1: Introduction to Biodiversity
genetic drift
4.3.2: Evolution in Populations
genetic engineering
3.7.2: Biotechnology
genetic map
3.7.3: Mapping Genomes
genetic marker
3.7.3: Mapping Genomes
genetic recombination
3.7.3: Mapping Genomes
genetic testing
3.7.2: Biotechnology
genetically modified organism
3.7.2: Biotechnology
genetics
3: Unit III- Genetics
4.1.1: Understanding Evolution
genome
2.7.2: Cell Division
genome annotation
3.7.4: Whole-Genome Sequencing
genome mapping
3.7.3: Mapping Genomes
genomic library
3.7.3: Mapping Genomes
genomics
3.7.3: Mapping Genomes
genotype
3.2.3: Characteristics and Traits
4.1.1: Understanding Evolution
genus
4.4.1: Systematics and Classification
geologic time scale
5.1.1: Deep Time
geometric isomer
1.2.4: Carbon
geosphere
6.1.5: Biogeochemical Cycles
germ cells
3.1.3: Sexual Reproduction
germ layer
5.6.3: Features of the Animal Kingdom
Ginkophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
global climate change
6.3: Climate Change
global warming
6.3.1: Introduction to Climate Change
glucose catabolism
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
glycogen
1.3.3: Carbohydrates
glycolipid
2.2.2: Components and Structure
glycolysis
2.4.3: Glycolysis
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
glycoprotein
2.2.2: Components and Structure
glycosidic bond
1.3.3: Carbohydrates
GMO
3.7.2: Biotechnology
gnathostome
5.8.3: Fishes
Gnetophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Golgi apparatus
2.1.5: The Endomembrane System and Proteins
Gondwana
5.1.1: Deep Time

Gorilla
5.8.8: The Evolution of Primates
granum
2.5.2: Overview of Photosynthesis
grazing food web
6.1.2: Energy Flow through Ecosystems
Great Oxygenation Event (GOE)
5.1.4: Eukaryotic Origins
greenhouse gases
6.3.1: Introduction to Climate Change
gross national product
6.2.3: The Biodiversity Crisis - HIPPPOC
gross primary productivity
6.1.2: Energy Flow through Ecosystems
growth
1.1.1: Themes and Concepts of Biology
growth factor
2.6.4: Response to the Signal
GTP
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
guanine diphosphate
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
guanine triphosphate
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
gymnosperm
5.9.1: Kingdom Plantae - Evolution and Phylogeny

H

habitat isolation
4.2.1: Species Defined
hagfish
5.8.3: Fishes
hairpin
3.5.3: Prokaryotic Transcription
halophile
5.1.3: Evidence for Early Life
halophyte
6.1.4: Aquatic Biomes
haplodiplodontic
5.9.2: Kingdom Plantae - Adaptations
haploid
2.7.2: Cell Division
haplontic
5.9.2: Kingdom Plantae - Adaptations
heat
2.3.4: The Laws of Thermodynamics
heat energy
2.3.3: Potential, Kinetic, Free, and Activation Energy
heat of vaporization of water
1.2.3: Water
helicase
3.4.5: DNA Replication in Prokaryotes
hemizygous
3.2.3: Characteristics and Traits
hemocoel
5.7.5: Superphylum Ecdysozoa
herbaceous
5.9.2: Kingdom Plantae - Adaptations
hermaphrodite
5.7.5: Superphylum Ecdysozoa
heterodont tooth
5.8.7: Mammals
heterotroph
2.5.2: Overview of Photosynthesis
heterozygous
3.2.3: Characteristics and Traits
HIPPPOC
6.2.3: The Biodiversity Crisis - HIPPPOC
histone
2.7.2: Cell Division
histone acetylation
3.6.8: Cancer and Gene Regulation
holistic ecosystem model
6.1.1: Ecology of Ecosystems
holoenzyme
3.5.3: Prokaryotic Transcription
homeostasis
1.1.1: Themes and Concepts of Biology
hominin
5.8.8: The Evolution of Primates
hominoid
5.8.8: The Evolution of Primates
Homo
5.8.8: The Evolution of Primates
Homo sapiens
5.8.8: The Evolution of Primates
Homo sapiens sapiens
5.8.8: The Evolution of Primates
homologous chromosomes
2.7.2: Cell Division
homologous recombination
3.3.2: Chromosomal Theory and Genetic Linkage
hormone
1.3.5: Proteins
hornworts
5.9.1: Kingdom Plantae - Evolution and Phylogeny
horsetail
5.9.1: Kingdom Plantae - Evolution and Phylogeny
host DNA
3.7.2: Biotechnology
Hox gene
5.6.3: Features of the Animal Kingdom
humus
6.1.3: Terrestrial Biomes
hybrid inviability
4.2.1: Species Defined
hybrid sterility
4.2.1: Species Defined
hybridization
3.2.2: Mendel's Experiments and the Laws of Probability
hydrocarbon
1.2.4: Carbon
hydrogen bond
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
hydrolysis
1.3.2: Synthesis of Biological Macromolecules
hydrophilic
1.2.3: Water
2.2.2: Components and Structure
hydrophobic
1.2.3: Water
2.2.2: Components and Structure
Hydrosphere
6.1.5: Biogeochemical Cycles
hydrothermal vent
5.1.3: Evidence for Early Life
Hylobatidae
5.8.8: The Evolution of Primates
Hylonomus
5.8.5: Reptiles
hypersaline
5.1.3: Evidence for Early Life
hypertonic
2.2.3: Passive Transport
hypothesis
1.1.2: The Nature of Science
4.1.1: Understanding Evolution
hypotonic
2.2.3: Passive Transport

I

ice core
6.3.1: Introduction to Climate Change
imperiled
6.2.4: Preserving Biodiversity
IMRaD
1.1.3: The Role of Science in Society
inbreeding
4.3.2: Evolution in Populations
incomplete dominance
3.2.3: Characteristics and Traits
incomplete ingestion
6.1.2: Energy Flow through Ecosystems
indeterminate cleavage
5.6.4: Features Used to Classify Animals
Indigenous
1.1.3: The Role of Science in Society
Indigenous science
1.1.3: The Role of Science in Society
indoor air pollution
6.2.3: The Biodiversity Crisis - HIPPPOC
induced fit
2.3.6: Enzymes
induced mutation
3.4.7: DNA Repair
inducible operon
3.6.3: Prokaryotic Gene Regulation
inductive reasoning
1.1.2: The Nature of Science
Industrial Revolution
6.3.1: Introduction to Climate Change
inert gas
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
infiltration
6.1.5: Biogeochemical Cycles
ingroup
4.4.2: Phylogeny and Cladistics
inheritance
3.3: Modern Understandings of Inheritance
inhibitor
2.6.4: Response to the Signal
initiation complex
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation

initiation site
3.5.3: Prokaryotic Transcription
initiator tRNA
3.5.6: Ribosomes and Protein Synthesis
inositol phospholipid
2.6.3: Propagation of the Signal
inositol triphosphate
2.6.3: Propagation of the Signal
integral protein
2.2.2: Components and Structure
intercellular signaling
2.6.2: Signaling Molecules and Cellular Receptors
Intergovernmental Panel on Climate Change
6.3.2: Anthropogenic Climate Change
interkinesis
3.1.2: The Process of Meiosis
intermediate filament
2.1.6: The Cytoskeleton
internal receptor
2.6.2: Signaling Molecules and Cellular Receptors
interphase
2.7.3: The Cell Cycle
intertidal zone
6.1.4: Aquatic Biomes
intracellular mediator
2.6.2: Signaling Molecules and Cellular Receptors
intracellular signaling
2.6.2: Signaling Molecules and Cellular Receptors
introduction
1.1.2: The Nature of Science
intron
3.5.5: RNA Processing in Eukaryotes
invasive species
6.2.3: The Biodiversity Crisis - HIPPPOC
invertebrata
5.7.2: Phylum Porifera
invertebrates
5.7: Invertebrates
ionic bond
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
irreversible chemical reaction
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
isomerase
2.4.3: Glycolysis
isomers
1.2.4: Carbon
isotonic
2.2.3: Passive Transport
isotope
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
IUCN
6.2.4: Preserving Biodiversity

K

karyogram
3.3.3: Chromosomal Basis of Inherited Disorders
karyotype
3.3.3: Chromosomal Basis of Inherited Disorders
kinase
2.6.3: Propagation of the Signal
kinetic energy
2.3.3: Potential, Kinetic, Free, and Activation Energy
kinetochore
2.7.3: The Cell Cycle
kingdom
4.4.1: Systematics and Classification
Kozak's rules
3.5.6: Ribosomes and Protein Synthesis
Krebs cycle
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
Kyoto Protocol
6.3.4: Climate Strategies

L

lac operon
3.6.3: Prokaryotic Gene Regulation
lagging strand
3.4.5: DNA Replication in Prokaryotes
lake
6.1.4: Aquatic Biomes
lamprey
5.8.3: Fishes
lancelet
5.8.2: Chordates
large 60S ribosomal subunit
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
lateral line
5.8.3: Fishes
lateral meristem
5.9.2: Kingdom Plantae - Adaptations
Laurasia
5.1.1: Deep Time
law of dominance
3.2.4: Laws of Inheritance
Law of Independent Assortment
3.2.4: Laws of Inheritance
law of segregation
3.2.4: Laws of Inheritance
leading strand
3.4.5: DNA Replication in Prokaryotes
lepidosaur
5.8.5: Reptiles
life cycle
3.1.3: Sexual Reproduction
life science
1.1.2: The Nature of Science
ligand
2.6.2: Signaling Molecules and Cellular Receptors
ligase
3.4.5: DNA Replication in Prokaryotes
light harvesting complex
2.5.3: The Light-Dependent Reactions of Photosynthesis
light microscope
2.1.2: Studying Cells
lignin
5.9.2: Kingdom Plantae - Adaptations
linkage
3.2.4: Laws of Inheritance
linkage analysis
3.7.3: Mapping Genomes
lipid
1.3.4: Lipids
litmus paper
1.2.3: Water
Little Ice Age
6.3.1: Introduction to Climate Change
liverwort
5.9.1: Kingdom Plantae - Evolution and Phylogeny
locus
2.7.2: Cell Division
Lophotrochozoa
5.6.5: Animal Phylogeny
Lycopodiophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
lysis
5.2: Acellular Entities - Viruses, Prions, and Viroids
lysis buffer
3.7.2: Biotechnology
lysosome
2.1.4: Eukaryotic Cells

M

macroevolution
4.1.1: Understanding Evolution
macromolecule
1.1.1: Themes and Concepts of Biology
madreporite
5.7.6: Superphylum Deuterostomia
mammal
5.8.7: Mammals
mammary gland
5.8.7: Mammals
mantle
5.7.4: Superphylum Lophotrochozoa
Marchantiophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
marsh
6.1.4: Aquatic Biomes
marsupial
5.8.7: Mammals
mass extinction
5.6.2: The Evolutionary History of the Animal Kingdom
5.1.1: Deep Time
mastax
5.7.4: Superphylum Lophotrochozoa
materials and methods
1.1.2: The Nature of Science
mating factor
2.6.5: Signaling in Single-Celled Organisms
matter
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
maximum parsimony
4.4.2: Phylogeny and Cladistics
MCS
3.7.2: Biotechnology
mechanical isolation
4.2.1: Species Defined
Medieval Climate Anomaly
6.3.1: Introduction to Climate Change

medusa
5.7.3: Phylum Cnidaria
megaspore
5.9.2: Kingdom Plantae - Adaptations
meiosis
3.1.2: The Process of Meiosis
meiosis I
3.1.2: The Process of Meiosis
meiosis II
3.1.2: The Process of Meiosis
mesocosm
6.1.1: Ecology of Ecosystems
mesoglea
5.7.3: Phylum Cnidaria
mesohyl
5.7.2: Phylum Porifera
mesophyll
2.5.2: Overview of Photosynthesis
messenger RNA
1.3.6: Nucleic Acids
metabolic pathways
2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways
metabolism
2.3: Metabolism
2.3.2: Energy and Metabolism
metabolome
3.7.6: Genomics and Proteomics
metabolomics
3.7.6: Genomics and Proteomics
metagenomics
3.7.5: Applying Genomics
metamerism
5.7.4: Superphylum Lophotrochozoa
metaphase
2.7.3: The Cell Cycle
metaphase plate
2.7.3: The Cell Cycle
metazoa
5.6.5: Animal Phylogeny
methane
6.3.2: Anthropogenic Climate Change
microbiology
1.1.1: Themes and Concepts of Biology
microcosm
6.1.1: Ecology of Ecosystems
microevolution
4.1.1: Understanding Evolution
microfilament
2.1.6: The Cytoskeleton
microRNA
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
microsatellite polymorphism
3.7.3: Mapping Genomes
microscope
2.1.2: Studying Cells
microspore
5.9.2: Kingdom Plantae - Adaptations
microtubule
2.1.6: The Cytoskeleton
migration
6.1.6: Biogeography
Milankovitch cycles
6.3.1: Introduction to Climate Change
miRNA
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
mismatch repair
3.4.7: DNA Repair
mitigation
6.3.3: Current and Future Climate Change Impacts
mitochondria
2.1.4: Eukaryotic Cells
5.1.4: Eukaryotic Origins
mitosis
2.7.3: The Cell Cycle
mitotic phase
2.7.3: The Cell Cycle
mitotic spindle
2.7.3: The Cell Cycle
model organism
3.7.4: Whole-Genome Sequencing
model system
3.2.2: Mendel's Experiments and the Laws of Probability
modern synthesis
4.1.1: Understanding Evolution
molecular biology
1.1.1: Themes and Concepts of Biology
molecular characters
4.4.2: Phylogeny and Cladistics
molecular cloning
3.7.2: Biotechnology
molecular systematics
4.4.2: Phylogeny and Cladistics
molecule
1.1.1: Themes and Concepts of Biology
mollusca
5.7.4: Superphylum Lophotrochozoa
monocots
5.9.1: Kingdom Plantae - Evolution and Phylogeny
monoecious
5.9.2: Kingdom Plantae - Adaptations
monohybrid
3.2.3: Characteristics and Traits
monomer
1.3.2: Synthesis of Biological Macromolecules
monophyletic
4.4.2: Phylogeny and Cladistics
Monosaccharide
1.3.3: Carbohydrates
monosomy
3.3.3: Chromosomal Basis of Inherited Disorders
monotreme
5.8.7: Mammals
moss
5.9.1: Kingdom Plantae - Evolution and Phylogeny
multiple cloning site
3.7.2: Biotechnology
mutation
3.4.7: DNA Repair
4.1.1: Understanding Evolution
myc
3.6.8: Cancer and Gene Regulation
Myxini
5.8.3: Fishes

N

nacre
5.7.4: Superphylum Lophotrochozoa
natural science
1.1.2: The Nature of Science
natural selection
4.1.1: Understanding Evolution
nauplius
5.7.5: Superphylum Ecdysozoa
negative regulator
3.6.3: Prokaryotic Gene Regulation
nematocyst
5.7.3: Phylum Cnidaria
Nematoda
5.7.5: Superphylum Ecdysozoa
Nematodes
5.7.5: Superphylum Ecdysozoa
Nemertea
5.7.4: Superphylum Lophotrochozoa
Neognathae
5.8.6: Birds
Neornithes
5.8.6: Birds
neritic zone
6.1.4: Aquatic Biomes
net consumer productivity
6.1.2: Energy Flow through Ecosystems
net primary productivity
6.1.2: Energy Flow through Ecosystems
net production efficiency
6.1.2: Energy Flow through Ecosystems
neurobiology
1.1.1: Themes and Concepts of Biology
neurotransmitter
2.6.2: Signaling Molecules and Cellular Receptors
neutron
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
nitrous oxide
6.3.2: Anthropogenic Climate Change
noble gas
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
nocturnal
6.1.3: Terrestrial Biomes
node
4.4.2: Phylogeny and Cladistics
nondisjunction
3.3.3: Chromosomal Basis of Inherited Disorders
nonparental type
3.3.2: Chromosomal Theory and Genetic Linkage
nonpolar covalent bond
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
nonsense codon
3.5.2: The Genetic Code
nontemplate strand
3.5.3: Prokaryotic Transcription
northern blotting
3.7.2: Biotechnology
notochord
5.8.2: Chordates
nuclear envelope
2.1.4: Eukaryotic Cells

nucleic acid
1.3.6: Nucleic Acids
nucleoid
2.1.3: Prokaryotic Cells
nucleolus
2.1.4: Eukaryotic Cells
nucleoplasm
2.1.4: Eukaryotic Cells
nucleosome
2.7.2: Cell Division
nucleotide
1.3.6: Nucleic Acids
nucleotide excision repair
3.4.7: DNA Repair
nucleus
2.1.4: Eukaryotic Cells

O

ocean acidfication
6.3.3: Current and Future Climate Change Impacts
ocean deoxygenation
6.3.3: Current and Future Climate Change Impacts
oceanic zone
6.1.4: Aquatic Biomes
Octamer box
3.5.4: Eukaryotic Transcription
Okazaki fragment
3.4.5: DNA Replication in Prokaryotes
omega fat
1.3.4: Lipids
oncogene
2.7.5: Cancer and the Cell Cycle
operator
3.6.3: Prokaryotic Gene Regulation
operons
3.6.3: Prokaryotic Gene Regulation
order
4.4.1: Systematics and Classification
organ
1.1.1: Themes and Concepts of Biology
organ system
1.1.1: Themes and Concepts of Biology
organelle
1.1.1: Themes and Concepts of Biology
2.1.4: Eukaryotic Cells
organic molecule
1.2.4: Carbon
organism
1.1.1: Themes and Concepts of Biology
organogenesis
5.6.3: Features of the Animal Kingdom
ORI
2.7.6: Prokaryotic Cell Division
origin
2.7.6: Prokaryotic Cell Division
Ornithorhynchidae
5.8.7: Mammals
osculum
5.7.2: Phylum Porifera
osmolarity
2.2.3: Passive Transport
osmosis
2.2.3: Passive Transport
Osteichthyes
5.8.3: Fishes
ostium
5.7.2: Phylum Porifera
ostracoderm
5.8.3: Fishes
outdoor air pollution
6.2.3: The Biodiversity Crisis - HIPPPOC
outgroup
4.4.2: Phylogeny and Cladistics
ovary
5.9.1: Kingdom Plantae - Evolution and Phylogeny
overharvesting
6.2.3: The Biodiversity Crisis - HIPPPOC
oviger
5.7.5: Superphylum Ecdysozoa
ovule
5.9.1: Kingdom Plantae - Evolution and Phylogeny
oxidative phosphorylation
2.4.2: Energy in Living Systems
2.4.5: Oxidative Phosphorylation

P

P0
3.2.2: Mendel’s Experiments and the Laws of Probability
p21
2.7.4: Control of the Cell Cycle
p53
2.7.4: Control of the Cell Cycle
P680
2.5.3: The Light-Dependent Reactions of Photosynthesis
P700
2.5.3: The Light-Dependent Reactions of Photosynthesis
paleobotanist
5.9.2: Kingdom Plantae - Adaptations
Paleognathae
5.8.6: Birds
paleontology
1.1.1: Themes and Concepts of Biology
Pan
5.8.8: The Evolution of Primates
Pangea
5.1.1: Deep Time
paracentric
3.3.3: Chromosomal Basis of Inherited Disorders
paracrine signal
2.6.2: Signaling Molecules and Cellular Receptors
parapodium
5.7.4: Superphylum Lophotrochozoa
Parazoa
5.6.5: Animal Phylogeny
parental types
3.3.2: Chromosomal Theory and Genetic Linkage
passive transport
2.2.3: Passive Transport
pathogen
5.2: Acellular Entities - Viruses, Prions, and Viroids
PCR
3.7.2: Biotechnology
pedipalp
5.7.5: Superphylum Ecdysozoa
pelagic realm
6.1.4: Aquatic Biomes
peptide bond
1.3.5: Proteins
peptidyl transferase
3.5.6: Ribosomes and Protein Synthesis
percolation
6.1.4: Aquatic Biomes
pericentric
3.3.3: Chromosomal Basis of Inherited Disorders
Period
5.1.1: Deep Time
periodic table
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
peripheral protein
2.2.2: Components and Structure
permafrost
6.1.3: Terrestrial Biomes
permissive
5.2: Acellular Entities - Viruses, Prions, and Viroids
peroxisome
2.1.4: Eukaryotic Cells
Petromyzontidae
5.8.3: Fishes
pH paper
1.2.3: Water
pH scale
1.2.3: Water
Phanerozoic
5.1.1: Deep Time
pharmacogenomics
3.7.5: Applying Genomics
pharyngeal slit
5.8.2: Chordates
phenological mismatch
6.3.3: Current and Future Climate Change Impacts
phenotype
3.2.3: Characteristics and Traits
4.1.1: Understanding Evolution
phloem
5.9.2: Kingdom Plantae - Adaptations
Phosphatase
2.6.4: Response to the Signal
phosphoanhydride bond
2.3.5: ATP- Adenosine Triphosphate
phosphodiester
1.3.6: Nucleic Acids
phosphodiesterase
2.6.4: Response to the Signal
phospholipid
1.3.4: Lipids
phosphorylation
2.4.2: Energy in Living Systems
photic zone
6.1.4: Aquatic Biomes
photoact
2.5.3: The Light-Dependent Reactions of Photosynthesis
photoautotroph
2.5.2: Overview of Photosynthesis
6.1.2: Energy Flow through Ecosystems

photon
2.5.3: The Light-Dependent Reactions of Photosynthesis
photosynthesis
2.5: Photosynthesis
5.1.4: Eukaryotic Origins
photosystem
2.5.3: The Light-Dependent Reactions of Photosynthesis
photosystem I
2.5.3: The Light-Dependent Reactions of Photosynthesis
photosystem II
2.5.3: The Light-Dependent Reactions of Photosynthesis
phylogenetic tree
1.1.1: Themes and Concepts of Biology
phylogenetic trees
4.4.2: Phylogeny and Cladistics
phylogeny
4.4.2: Phylogeny and Cladistics
physical map
3.7.3: Mapping Genomes
physical science
1.1.2: The Nature of Science
pigment
2.5.2: Overview of Photosynthesis
pilidium
5.7.4: Superphylum Lophotrochozoa
pinacocyte
5.7.2: Phylum Porifera
pinocytosis
2.2.5: Bulk Transport
pKa
2.6.3: Propagation of the Signal
plagiarism
1.1.2: The Nature of Science
planktivore
6.1.4: Aquatic Biomes
planospiral
5.7.4: Superphylum Lophotrochozoa
Plantae
4.4.1: Systematics and Classification
5.9.1: Kingdom Plantae - Evolution and Phylogeny
planuliform
5.7.4: Superphylum Lophotrochozoa
plasma membrane
2.1.4: Eukaryotic Cells
plasmid
3.5.3: Prokaryotic Transcription
plasmodesma
2.1.7: Connections between Cells and Cellular Activities
plasmolysis
2.2.3: Passive Transport
plastid
5.1.4: Eukaryotic Origins
Platyrrhini
5.8.8: The Evolution of Primates
Plesiadapis
5.8.8: The Evolution of Primates
pneumatic bone
5.8.6: Birds
point mutation
3.4.7: DNA Repair
pollen
5.9.2: Kingdom Plantae - Adaptations
pollination
5.9.1: Kingdom Plantae - Evolution and Phylogeny
pollutant residence time
6.2.3: The Biodiversity Crisis - HIPPPOC
polygenic
3.7.5: Applying Genomics
polymer
1.3.2: Synthesis of Biological Macromolecules
polymerase chain reaction (PCR)
3.7.2: Biotechnology
polymorphic
4.1.1: Understanding Evolution
5.7.3: Phylum Cnidaria
polynucleotide
1.3.6: Nucleic Acids
polyp
5.7.3: Phylum Cnidaria
polypeptide
1.3.5: Proteins
polyploid
3.3.3: Chromosomal Basis of Inherited Disorders
polysaccharide
1.3.3: Carbohydrates
polysome
3.5.6: Ribosomes and Protein Synthesis
polytomy
4.4.2: Phylogeny and Cladistics
pond
6.1.4: Aquatic Biomes
Pongo
5.8.8: The Evolution of Primates
population
1.1.1: Themes and Concepts of Biology
population variation
4.1.1: Understanding Evolution
Porifera
5.7.2: Phylum Porifera
positive regulator
3.6.3: Prokaryotic Gene Regulation
postzygotic barrier
4.2.1: Species Defined
potential energy
2.3.3: Potential, Kinetic, Free, and Activation Energy
potocytosis
2.2.5: Bulk Transport
Precambrian
5.1.1: Deep Time
precipitation
6.1.5: Biogeochemical Cycles
preinitiation complex
3.5.4: Eukaryotic Transcription
preserves
6.2.4: Preserving Biodiversity
prezygotic barrier
4.2.1: Species Defined
primary active transport
2.2.4: Active Transport
primary consumer
6.1.2: Energy Flow through Ecosystems
primary electron acceptor
2.5.3: The Light-Dependent Reactions of Photosynthesis
primary feather
5.8.6: Birds
primary pollutants
6.2.3: The Biodiversity Crisis - HIPPPOC
primary producer
6.1.2: Energy Flow through Ecosystems
primary structure
1.3.5: Proteins
primase
3.4.5: DNA Replication in Prokaryotes
Primates
5.8.8: The Evolution of Primates
primer
3.4.5: DNA Replication in Prokaryotes
prion
5.2: Acellular Entities - Viruses, Prions, and Viroids
probe
3.7.2: Biotechnology
product
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
product rule
3.2.2: Mendel’s Experiments and the Laws of Probability
productivity
6.1.2: Energy Flow through Ecosystems
prognathic jaw
5.8.8: The Evolution of Primates
progressive hypothesis
5.2: Acellular Entities - Viruses, Prions, and Viroids
prokaryote
1.1.1: Themes and Concepts of Biology
2.1.3: Prokaryotic Cells
5.1.3: Evidence for Early Life
prokaryotes
3.4.5: DNA Replication in Prokaryotes
prometaphase
2.7.3: The Cell Cycle
promoter
3.5.3: Prokaryotic Transcription
proofreading
3.4.7: DNA Repair
prophase
2.7.3: The Cell Cycle
prosimian
5.8.8: The Evolution of Primates
prosthetic group
2.4.5: Oxidative Phosphorylation
protease
3.7.2: Biotechnology
proteasome
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
protein
1.3.5: Proteins
protein kinase A
2.6.3: Propagation of the Signal
protein signature
3.7.6: Genomics and Proteomics
proteome
3.7.6: Genomics and Proteomics
proteomics
3.7.6: Genomics and Proteomics

Protista
4.4.1: Systematics and Classification
protists
5.4: Protists
proton
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
protostome
5.6.4: Features Used to Classify Animals
pseudocoelomate
5.6.4: Features Used to Classify Animals
pseudoscience
1.1.2: The Nature of Science
Pteridophyta
5.9.1: Kingdom Plantae - Evolution and Phylogeny
pterophytes
5.9.1: Kingdom Plantae - Evolution and Phylogeny
pump
2.2.4: Active Transport
Punnett square
3.2.3: Characteristics and Traits
pure culture
3.7.5: Applying Genomics
pylum
4.4.1: Systematics and Classification
pyramid of biomass
6.1.2: Energy Flow through Ecosystems
pyramid of energy
6.1.2: Energy Flow through Ecosystems
pyramid of numbers
6.1.2: Energy Flow through Ecosystems
pyrimidine
1.3.6: Nucleic Acids
pyrimidine dimers
3.4.7: DNA Repair
pyruvate
2.4.3: Glycolysis

Q

quaternary structure
1.3.5: Proteins
quiescent
2.7.3: The Cell Cycle
quorum sensing
2.6.5: Signaling in Single-Celled Organisms

R

radial cleavage
5.6.4: Features Used to Classify Animals
radial symmetry
5.6.4: Features Used to Classify Animals
radiation hybrid mapping
3.7.3: Mapping Genomes
radioisotope
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
radula
5.7.4: Superphylum Lophotrochozoa
reaction center
2.5.3: The Light-Dependent Reactions of Photosynthesis
reading frame
3.5.2: The Genetic Code
receptor
2.6.2: Signaling Molecules and Cellular Receptors
recessive
3.2.2: Mendel's Experiments and the Laws of Probability
recessive lethal
3.2.3: Characteristics and Traits
reciprocal cross
3.2.2: Mendel's Experiments and the Laws of Probability
recombinant DNA
3.7.2: Biotechnology
recombinant protein
3.7.2: Biotechnology
recombinant type
3.3.2: Chromosomal Theory and Genetic Linkage
recombination frequency
3.3.2: Chromosomal Theory and Genetic Linkage
redox reaction
2.4.2: Energy in Living Systems
Reduction
2.5.4: Using Light Energy to Make Organic Molecules
reduction division
3.1.2: The Process of Meiosis
regressive hypothesis
5.2: Acellular Entities - Viruses, Prions, and Viroids
regulation
1.1.1: Themes and Concepts of Biology
relative abundance
6.2.1: Introduction to Biodiversity
replication fork
3.4.5: DNA Replication in Prokaryotes
repressor
3.6.3: Prokaryotic Gene Regulation
reproduction
1.1.1: Themes and Concepts of Biology
reproductive cloning
3.7.2: Biotechnology
reproductive isolation
4.2.1: Species Defined
residence time
6.1.5: Biogeochemical Cycles
resilience
6.3.3: Current and Future Climate Change Impacts
resilience (ecological)
6.1.1: Ecology of Ecosystems
resistance (ecological)
6.1.1: Ecology of Ecosystems
restoration
6.2.4: Preserving Biodiversity
restriction endonuclease
3.7.2: Biotechnology
restriction fragment length polymorphism
3.7.3: Mapping Genomes
results
1.1.2: The Nature of Science
retinoblastoma protein
2.7.4: Control of the Cell Cycle
reverse genetics
3.7.2: Biotechnology
reverse transcriptase PCR
3.7.2: Biotechnology
RFLP
3.7.3: Mapping Genomes
rhynchocoel
5.7.4: Superphylum Lophotrochozoa
ribonuclease
3.7.2: Biotechnology
ribonucleic acid
1.3.6: Nucleic Acids
ribosomal RNA
1.3.6: Nucleic Acids
ribosome
2.1.4: Eukaryotic Cells
ribozymes
5.1.2: Origins of Life
RISC
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
risk
6.3.3: Current and Future Climate Change Impacts
river
6.1.4: Aquatic Biomes
RNA
1.3.6: Nucleic Acids
RNA editing
3.5.5: RNA Processing in Eukaryotes
RNA stability
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
RNA world hypothesis
5.1.2: Origins of Life
rooted tree
4.4.2: Phylogeny and Cladistics
rough endoplasmic reticulum
2.1.5: The Endomembrane System and Proteins
runoff
6.1.5: Biogeochemical Cycles

S

S phase
2.7.3: The Cell Cycle
salamander
5.8.4: Amphibians
Sarcopterygii
5.8.3: Fishes
Saturated fatty acid
1.3.4: Lipids
sauropsid
5.8.5: Reptiles
savanna
6.1.3: Terrestrial Biomes
schizocoelom
5.7.4: Superphylum Lophotrochozoa
schizocoely
5.6.4: Features Used to Classify Animals
science
1.1.2: The Nature of Science
scientific method
1.1.2: The Nature of Science
scientific name
4.4.1: Systematics and Classification
scientific paper
1.1.3: The Role of Science in Society

sclerocyte
5.7.2: Phylum Porifera
sebaceous gland
5.8.7: Mammals
Second Law of Thermodynamics
6.1.2: Energy Flow through Ecosystems
second messenger
2.6.3: Propagation of the Signal
secondary active transport
2.2.4: Active Transport
secondary cambium
5.9.1: Kingdom Plantae - Evolution and Phylogeny
secondary consumer
6.1.2: Energy Flow through Ecosystems
secondary feather
5.8.6: Birds
secondary messenger
2.6.3: Propagation of the Signal
secondary metabolite
5.9.2: Kingdom Plantae - Adaptations
secondary pollutants
6.2.3: The Biodiversity Crisis - HIPPPOC
secondary structure
1.3.5: Proteins
seed
5.9.2: Kingdom Plantae - Adaptations
seedless nonvascular
5.9.1: Kingdom Plantae - Evolution and Phylogeny
seedless plants
5.9: Plantae
seedless vascular
5.9.1: Kingdom Plantae - Evolution and Phylogeny
segment
5.2: Acellular Entities - Viruses, Prions, and Viroids
selection pressure
4.1.1: Understanding Evolution
selectively permeable
2.2.3: Passive Transport
septum
2.7.6: Prokaryotic Cell Division
sequence mapping
3.7.3: Mapping Genomes
serendipity
1.1.2: The Nature of Science
1.1.3: The Role of Science in Society
seta
5.7.4: Superphylum Lophotrochozoa
shared ancestral character
4.4.2: Phylogeny and Cladistics
shared derived character
4.4.2: Phylogeny and Cladistics
shotgun sequencing
3.7.4: Whole-Genome Sequencing
signal integration
2.6.3: Propagation of the Signal
signal sequence
3.5.6: Ribosomes and Protein Synthesis
signal transduction
2.6.3: Propagation of the Signal
signaling cell
2.6.2: Signaling Molecules and Cellular Receptors
signaling pathway
2.6.3: Propagation of the Signal
silent mutation
3.4.7: DNA Repair
simulation model
6.1.1: Ecology of Ecosystems
single nucleotide polymorphism
3.7.3: Mapping Genomes
sink
6.3.2: Anthropogenic Climate Change
siphonophore
5.7.3: Phylum Cnidaria
sister taxon
4.4.2: Phylogeny and Cladistics
sliding clamp
3.4.5: DNA Replication in Prokaryotes
small 40S ribosomal subunit
3.6.7: Eukaryotic Translational and Post-translational Gene Regulation
small nuclear RNA
3.5.4: Eukaryotic Transcription
smooth endoplasmic reticulum
2.1.5: The Endomembrane System and Proteins
SNP
3.7.3: Mapping Genomes
solar intensity
6.3.1: Introduction to Climate Change
solubility
6.3.2: Anthropogenic Climate Change
solute
2.2.3: Passive Transport
solvent
1.2.3: Water
somatic cell
3.1.2: The Process of Meiosis
Southern blotting
3.7.2: Biotechnology
species
4.4.1: Systematics and Classification
species diversity
6.2.1: Introduction to Biodiversity
specific heat capacity
1.2.3: Water
spectrophotometer
2.5.3: The Light-Dependent Reactions of Photosynthesis
spermatophyte
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Sphenodontia
5.8.5: Reptiles
sphere of hydration
1.2.3: Water
spicule
5.7.2: Phylum Porifera
spiral cleavage
5.6.4: Features Used to Classify Animals
splicing
3.5.5: RNA Processing in Eukaryotes
spongocoel
5.7.2: Phylum Porifera
spontaneous mutation
3.4.7: DNA Repair
sporangium
5.9.1: Kingdom Plantae - Evolution and Phylogeny
spore
3.1.2: The Process of Meiosis
sporophyll
5.9.1: Kingdom Plantae - Evolution and Phylogeny
sporophyte
3.1.3: Sexual Reproduction
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Squamata
5.8.5: Reptiles
Stanley Miller
5.1.2: Origins of Life
starch
1.3.3: Carbohydrates
start codon
3.5.6: Ribosomes and Protein Synthesis
stereoscopic vision
5.8.8: The Evolution of Primates
steroid
1.3.4: Lipids
stimuli
1.1.1: Themes and Concepts of Biology
stoma
2.5.2: Overview of Photosynthesis
stomata
5.9.2: Kingdom Plantae - Adaptations
stratification
6.1.4: Aquatic Biomes
stream
6.1.4: Aquatic Biomes
strobilus
5.9.1: Kingdom Plantae - Evolution and Phylogeny
stroma
2.5.2: Overview of Photosynthesis
stromatolite
5.1.3: Evidence for Early Life
structural isomers
1.2.4: Carbon
subduction
6.1.5: Biogeochemical Cycles
sublimation
6.1.5: Biogeochemical Cycles
substituted hydrocarbon
1.2.4: Carbon
substrate
2.3.6: Enzymes
subtropical desert
6.1.3: Terrestrial Biomes
sum rule
3.2.2: Mendel’s Experiments and the Laws of Probability
surface tension
1.2.3: Water
swamp
6.1.4: Aquatic Biomes
swim bladder
5.8.3: Fishes
symporter
2.2.4: Active Transport
synapsid
5.8.5: Reptiles
synapsis
3.1.2: The Process of Meiosis
synaptic signal
2.6.2: Signaling Molecules and Cellular Receptors
synaptonemal complex
3.1.2: The Process of Meiosis

systematics
4.4.2: Phylogeny and Cladistics
systems biology
3.7.6: Genomics and Proteomics

T

Tachyglossidae
5.8.7: Mammals
tadpole
5.8.4: Amphibians
taiga
6.1.3: Terrestrial Biomes
target cell
2.6.2: Signaling Molecules and Cellular Receptors
TATA box
3.5.3: Prokaryotic Transcription
taxon
4.4.1: Systematics and Classification
TCA cycle
2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle
telomerase
3.4.6: DNA Replication in Eukaryotes
telomere
3.4.6: DNA Replication in Eukaryotes
telophase
2.7.3: The Cell Cycle
temperate forest
6.1.3: Terrestrial Biomes
temperate grassland
6.1.3: Terrestrial Biomes
template strand
3.5.3: Prokaryotic Transcription
temporal fenestra
5.8.5: Reptiles
temporal isolation
4.2.1: Species Defined
tertiary consumer
6.1.2: Energy Flow through Ecosystems
tertiary structure
1.3.5: Proteins
test cross
3.2.3: Characteristics and Traits
Testudines
5.8.5: Reptiles
tetrad
3.1.2: The Process of Meiosis
tetrapod
5.8.2: Chordates
theory
1.1.2: The Nature of Science
4.1.1: Understanding Evolution
thermocline
6.1.6: Biogeography
thermodynamics
2.3.4: The Laws of Thermodynamics
thermophile
5.1.3: Evidence for Early Life
theropod
5.8.6: Birds
thylakoid
2.5.2: Overview of Photosynthesis
thylakoid lumen
2.5.2: Overview of Photosynthesis
Ti plasmid
3.7.2: Biotechnology
tight junction
2.1.7: Connections between Cells and Cellular Activities
tissue
1.1.1: Themes and Concepts of Biology
tonicity
2.2.3: Passive Transport
topoisomerase
3.4.5: DNA Replication in Prokaryotes
tracheid
5.9.1: Kingdom Plantae - Evolution and Phylogeny
tracheophyte
5.9.1: Kingdom Plantae - Evolution and Phylogeny
Traditional Ecological Knowledge
1.1.3: The Role of Science in Society
TRAFFIC
6.2.4: Preserving Biodiversity
trait
3.2.2: Mendel's Experiments and the Laws of Probability
4.1.1: Understanding Evolution
trans fat
1.3.4: Lipids
transcription
1.3.6: Nucleic Acids
transcription factor
3.6.4: Eukaryotic Epigenetic Gene Regulation
transcription factor binding site
3.6.5: Eukaryotic Transcription Gene Regulation
transfer RNA
1.3.6: Nucleic Acids
transformation
3.4.2: Historical Basis of Modern Understanding
transgenic
3.7.2: Biotechnology
transition state
2.3.3: Potential, Kinetic, Free, and Activation Energy
transition substitution
3.4.7: DNA Repair
translation
1.3.6: Nucleic Acids
translocation
3.3.3: Chromosomal Basis of Inherited Disorders
transport protein
2.2.3: Passive Transport
transporter
2.2.4: Active Transport
transversion substitution
3.4.7: DNA Repair
triacylglycerol
1.3.4: Lipids
triglyceride
1.3.4: Lipids
triploblast
5.6.4: Features Used to Classify Animals
trisomy
3.3.3: Chromosomal Basis of Inherited Disorders
trochophore
5.7.4: Superphylum Lophotrochozoa
trophic cascade
6.2.3: The Biodiversity Crisis - HIPPPOC
trophic level transfer efficiency
6.1.2: Energy Flow through Ecosystems
tropical wet forest
6.1.3: Terrestrial Biomes
Trp operon
3.6.3: Prokaryotic Gene Regulation
tryptophan
3.6.3: Prokaryotic Gene Regulation
tubulin
2.7.6: Prokaryotic Cell Division
tumor suppressor gene
2.7.5: Cancer and the Cell Cycle
tunicate
5.8.2: Chordates
turnover
6.1.6: Biogeography

U

ubiquinone
2.4.5: Oxidative Phosphorylation
UN Framework Convention on Climate Change
6.3.4: Climate Strategies
understory
6.1.3: Terrestrial Biomes
UNESCO World Heritage Site
6.2.4: Preserving Biodiversity
unified cell theory
2.1.2: Studying Cells
uniporter
2.2.4: Active Transport
uniramous
5.7.5: Superphylum Ecdysozoa
unsaturated fatty acid
1.3.4: Lipids
untranslated region
3.6.6: Eukaryotic Post-transcriptional Gene Regulation
upstream
3.5.3: Prokaryotic Transcription
upwelling
6.1.6: Biogeography
Urochordata
5.8.2: Chordates
Urodela
5.8.4: Amphibians

V

vacuole
2.1.4: Eukaryotic Cells
van der Waals interaction
1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks
variable
1.1.2: The Nature of Science
variable number of tandem repeats
3.7.3: Mapping Genomes
variation
4.1.1: Understanding Evolution

vascular tissue
5.9.1: Kingdom Plantae - Evolution and Phylogeny
5.9.2: Kingdom Plantae - Adaptations
veliger
5.7.4: Superphylum Lophotrochozoa
vertebral column
5.8.2: Chordates
Vertebrata
5.8.2: Chordates
vertebrates
5.8: Vertebrates
Vesicle
2.1.4: Eukaryotic Cells
viral core
5.2: Acellular Entities - Viruses, Prions, and Viroids
viral receptor
5.2: Acellular Entities - Viruses, Prions, and Viroids
virion
5.2: Acellular Entities - Viruses, Prions, and Viroids
viroid
5.2: Acellular Entities - Viruses, Prions, and Viroids
virus
5.2: Acellular Entities - Viruses, Prions, and Viroids
virus molecular systematics
5.2: Acellular Entities - Viruses, Prions, and Viroids
VNTRs
3.7.3: Mapping Genomes
vulnerable
6.2.4: Preserving Biodiversity

W

wallace
4.1.1: Understanding Evolution
water pollution
6.2.3: The Biodiversity Crisis - HIPPPOC
water residence time
6.2.3: The Biodiversity Crisis - HIPPPOC
water vascular system
5.7.6: Superphylum Deuterostomia
Watson and Crick
3.4.3: DNA Structure and Sequencing
wavelength
2.5.3: The Light-Dependent Reactions of Photosynthesis
wax
1.3.4: Lipids
weather
6.3.1: Introduction to Climate Change
Western science
1.1.3: The Role of Science in Society
wetland
6.1.4: Aquatic Biomes
whisk fern
5.9.1: Kingdom Plantae - Evolution and Phylogeny

X

X inactivation
3.3.3: Chromosomal Basis of Inherited Disorders
xylem
5.9.2: Kingdom Plantae - Adaptations

Z

zoea
5.7.5: Superphylum Ecdysozoa
zoology
1.1.1: Themes and Concepts of Biology
zygote
4.2.1: Species Defined

Glossary

Sample Word 1 | Sample Definition 1

Detailed Licensing

Overview

Title: General Biology I and II

Webpages: 218

Applicable Restrictions: Noncommercial

All licenses found:

- CC BY-SA 4.0: 95% (207 pages)
- Undeclared: 4.6% (10 pages)
- CC BY-NC-SA 4.0: 0.5% (1 page)

By Page

- General Biology I and II - *CC BY-SA 4.0*
  - Front Matter - *Undeclared*
    - TitlePage - *Undeclared*
    - InfoPage - *Undeclared*
    - Table of Contents - *Undeclared*
    - Licensing - *Undeclared*
  - 1: Unit I- Biology, Science, and the Chemistry of Life - *CC BY-SA 4.0*
    - 1.1: The Study of Life - *CC BY-SA 4.0*
      - 1.1.1: Themes and Concepts of Biology - *CC BY-SA 4.0*
      - 1.1.2: The Nature of Science - *CC BY-SA 4.0*
      - 1.1.3: The Role of Science in Society - *CC BY-SA 4.0*
      - 1.E: The Study of Life (Exercises) - *CC BY-SA 4.0*
      - 1.G: Unit 1.1 Glossary - *CC BY-SA 4.0*
    - 1.2: The Chemical Foundation of Life - *CC BY-SA 4.0*
      - 1.2.1: Prelude to The Chemical Foundation of Life - *CC BY-SA 4.0*
      - 1.2.2: Atoms, Isotopes, Ions, and Molecules - The Building Blocks - *CC BY-SA 4.0*
      - 1.2.3: Water - *CC BY-SA 4.0*
      - 1.2.4: Carbon - *CC BY-SA 4.0*
      - 1.2.E: The Chemical Foundation of Life (Exercises) - *CC BY-SA 4.0*
    - 1.3: Biological Macromolecules - *CC BY-SA 4.0*
      - 1.3.1: Prelude to Biological Macromolecules - *CC BY-SA 4.0*
      - 1.3.2: Synthesis of Biological Macromolecules - *CC BY-SA 4.0*
      - 1.3.3: Carbohydrates - *CC BY-SA 4.0*
      - 1.3.4: Lipids - *CC BY-SA 4.0*
      - 1.3.5: Proteins - *CC BY-SA 4.0*
      - 1.3.6: Nucleic Acids - *CC BY-SA 4.0*
      - 1.3.E: Biological Macromolecules (Exercises) - *CC BY-SA 4.0*
  - 2: Unit II- The Cell - *CC BY-SA 4.0*
    - 2.1: Cell Structure - *CC BY-SA 4.0*
      - 2.1.1: Prelude to Cell Structure - *CC BY-SA 4.0*
      - 2.1.2: Studying Cells - *CC BY-SA 4.0*
      - 2.1.3: Prokaryotic Cells - *CC BY-SA 4.0*
      - 2.1.4: Eukaryotic Cells - *CC BY-SA 4.0*
      - 2.1.5: The Endomembrane System and Proteins - *CC BY-SA 4.0*
      - 2.1.6: The Cytoskeleton - *CC BY-SA 4.0*
      - 2.1.7: Connections between Cells and Cellular Activities - *CC BY-SA 4.0*
      - 2.1.E: Cell Structure (Exercises) - *CC BY-SA 4.0*
    - 2.2: Structure and Function of Plasma Membranes - *CC BY-SA 4.0*
      - 2.2.1: Prelude to Structure and Function of Plasma Membranes - *CC BY-SA 4.0*
      - 2.2.2: Components and Structure - *CC BY-SA 4.0*
      - 2.2.3: Passive Transport - *CC BY-SA 4.0*
      - 2.2.4: Active Transport - *CC BY-SA 4.0*
      - 2.2.5: Bulk Transport - *CC BY-SA 4.0*
      - 2.2.E: Structure and Function of Plasma Membranes (Exercises) - *CC BY-SA 4.0*
    - 2.3: Metabolism - *CC BY-SA 4.0*
      - 2.3.1: Prelude to Metabolism - *CC BY-SA 4.0*
      - 2.3.2: Energy and Metabolism - *CC BY-SA 4.0*
      - 2.3.3: Potential, Kinetic, Free, and Activation Energy - *CC BY-SA 4.0*
      - 2.3.4: The Laws of Thermodynamics - *CC BY-SA 4.0*
      - 2.3.5: ATP- Adenosine Triphosphate - *CC BY-SA 4.0*

- 2.3.6: Enzymes - *CC BY-SA 4.0*
- 2.3.E: Metabolism (Exercises) - *CC BY-SA 4.0*

- 2.4: Cellular Respiration - *CC BY-SA 4.0*
  - 2.4.1: Prelude to Cellular Respiration - *CC BY-SA 4.0*
  - 2.4.2: Energy in Living Systems - *CC BY-SA 4.0*
  - 2.4.3: Glycolysis - *CC BY-SA 4.0*
  - 2.4.4: Oxidation of Pyruvate and the Citric Acid Cycle - *CC BY-SA 4.0*
  - 2.4.5: Oxidative Phosphorylation - *CC BY-SA 4.0*
  - 2.4.6: Metabolism without Oxygen - *CC BY-SA 4.0*
  - 2.4.7: Connections of Carbohydrate, Protein, and Lipid Metabolic Pathways - *CC BY-SA 4.0*
  - 2.4.E: Cellular Respiration (Exercises) - *CC BY-SA 4.0*
- 2.5: Photosynthesis - *CC BY-SA 4.0*
  - 2.5.1: Prelude to Photosynthesis - *CC BY-SA 4.0*
  - 2.5.2: Overview of Photosynthesis - *CC BY-SA 4.0*
  - 2.5.3: The Light-Dependent Reactions of Photosynthesis - *CC BY-SA 4.0*
  - 2.5.4: Using Light Energy to Make Organic Molecules - *CC BY-SA 4.0*
  - 2.5.E: Photosynthesis (Exercises) - *CC BY-SA 4.0*
- 2.6: Cell Communication - *CC BY-SA 4.0*
  - 2.6.1: Prelude to Cell Communication - *CC BY-SA 4.0*
  - 2.6.2: Signaling Molecules and Cellular Receptors - *CC BY-SA 4.0*
  - 2.6.3: Propagation of the Signal - *CC BY-SA 4.0*
  - 2.6.4: Response to the Signal - *CC BY-SA 4.0*
  - 2.6.5: Signaling in Single-Celled Organisms - *CC BY-SA 4.0*
  - 2.6.E: Cell Communication (Exercises) - *CC BY-SA 4.0*
- 2.7: Cell Reproduction - *CC BY-SA 4.0*
  - 2.7.1: Preface - *CC BY-SA 4.0*
  - 2.7.2: Cell Division - *CC BY-SA 4.0*
  - 2.7.3: The Cell Cycle - *CC BY-SA 4.0*
  - 2.7.4: Control of the Cell Cycle - *CC BY-SA 4.0*
  - 2.7.5: Cancer and the Cell Cycle - *CC BY-SA 4.0*
  - 2.7.6: Prokaryotic Cell Division - *CC BY-SA 4.0*
  - 2.7.E: Cell Reproduction (Exercises) - *CC BY-SA 4.0*

- 3: Unit III- Genetics - *CC BY-SA 4.0*
  - 3.1: Meiosis and Sexual Reproduction - *CC BY-SA 4.0*
    - 3.1.1: Prelude to Meiosis and Sexual Reproduction - *CC BY-SA 4.0*
    - 3.1.2: The Process of Meiosis - *CC BY-SA 4.0*
    - 3.1.3: Sexual Reproduction - *CC BY-SA 4.0*
    - 3.1.E: Meiosis and Sexual Reproduction (Exercises) - *CC BY-SA 4.0*
  - 3.2: Mendel's Experiments and Heredity - *CC BY-SA 4.0*
    - 3.2.1: Prelude to Mendel's Experiments and Heredity - *CC BY-SA 4.0*
    - 3.2.2: Mendel’s Experiments and the Laws of Probability - *CC BY-SA 4.0*
    - 3.2.3: Characteristics and Traits - *CC BY-SA 4.0*
    - 3.2.4: Laws of Inheritance - *CC BY-SA 4.0*
    - 3.2.E: Mendel's Experiments and Heredity (Exercises) - *CC BY-SA 4.0*
  - 3.3: Modern Understandings of Inheritance - *CC BY-SA 4.0*
    - 3.3.1: Prelude to Modern Understandings of Inheritance - *CC BY-SA 4.0*
    - 3.3.2: Chromosomal Theory and Genetic Linkage - *CC BY-SA 4.0*
    - 3.3.3: Chromosomal Basis of Inherited Disorders - *CC BY-SA 4.0*
    - 3.3.E: Modern Understandings of Inheritance (Exercises) - *CC BY-SA 4.0*
  - 3.4: DNA Structure and Function - *CC BY-SA 4.0*
    - 3.4.1: Prelude to DNA Structure and Function - *CC BY-SA 4.0*
    - 3.4.2: Historical Basis of Modern Understanding - *CC BY-SA 4.0*
    - 3.4.3: DNA Structure and Sequencing - *CC BY-SA 4.0*
    - 3.4.4: Basics of DNA Replication - *CC BY-SA 4.0*
    - 3.4.5: DNA Replication in Prokaryotes - *CC BY-SA 4.0*
    - 3.4.6: DNA Replication in Eukaryotes - *CC BY-SA 4.0*
    - 3.4.7: DNA Repair - *CC BY-SA 4.0*
    - 3.4.E: DNA Structure and Function (Exercises) - *CC BY-SA 4.0*
  - 3.5: Genes Expression - *CC BY-SA 4.0*
    - 3.5.1: Prelude to Genes and Proteins - *CC BY-SA 4.0*
    - 3.5.2: The Genetic Code - *CC BY-SA 4.0*
    - 3.5.3: Prokaryotic Transcription - *CC BY-SA 4.0*
    - 3.5.4: Eukaryotic Transcription - *CC BY-SA 4.0*

- 3.5.5: RNA Processing in Eukaryotes - *CC BY-SA 4.0*
- 3.5.6: Ribosomes and Protein Synthesis - *CC BY-SA 4.0*
- 3.5.E: Genes and Proteins (Exercises) - *CC BY-SA 4.0*

- 3.6: Gene Regulation - *CC BY-SA 4.0*
  - 3.6.1: Prelude to Gene Expression - *CC BY-SA 4.0*
  - 3.6.2: Regulation of Gene Expression - *CC BY-SA 4.0*
  - 3.6.3: Prokaryotic Gene Regulation - *CC BY-SA 4.0*
  - 3.6.4: Eukaryotic Epigenetic Gene Regulation - *CC BY-SA 4.0*
  - 3.6.5: Eukaryotic Transcription Gene Regulation - *CC BY-SA 4.0*
  - 3.6.6: Eukaryotic Post-transcriptional Gene Regulation - *CC BY-SA 4.0*
  - 3.6.7: Eukaryotic Translational and Post-translational Gene Regulation - *CC BY-SA 4.0*
  - 3.6.8: Cancer and Gene Regulation - *CC BY-SA 4.0*
  - 3.6.E: Gene Expression (Exercises) - *CC BY-SA 4.0*
- 3.7: Biotechnology and Genomics - *CC BY-SA 4.0*
  - 3.7.1: Prelude - *CC BY-SA 4.0*
  - 3.7.2: Biotechnology - *CC BY-SA 4.0*
  - 3.7.3: Mapping Genomes - *CC BY-SA 4.0*
  - 3.7.4: Whole-Genome Sequencing - *CC BY-SA 4.0*
  - 3.7.5: Applying Genomics - *CC BY-SA 4.0*
  - 3.7.6: Genomics and Proteomics - *CC BY-SA 4.0*
  - 3.7.E: Biotechnology and Genomics (Exercises) - *CC BY-SA 4.0*

- 4: Unit IV- Evolutionary Processes - *CC BY-SA 4.0*
  - 4.1: Evolution - History, Evidence, and Mechanisms - *CC BY-SA 4.0*
    - 4.1.1: Understanding Evolution - *CC BY-SA 4.0*
    - 4.1.2: Evidence of Evolution - *CC BY-SA 4.0*
    - 4.1.3: Natural Selection and Adaptive Evolution - *CC BY-SA 4.0*
    - 4.1.4: Additional Mechanisms of Evolution - *CC BY-SA 4.0*
  - 4.2: The Origin of Species - *CC BY-SA 4.0*
    - 4.2.1: Species Defined - *CC BY-SA 4.0*
    - 4.2.2: Speciation - *CC BY-SA 4.0*
    - 4.2.3: Rates of Speciation and Extinction - *CC BY-SA 4.0*
  - 4.3: Genes Within Populations - *CC BY-SA 4.0*
    - 4.3.1: Evolution of Genomes - *CC BY-SA 4.0*
    - 4.3.2: Evolution in Populations - *CC BY-SA 4.0*
  - 4.4: Systematics, Phylogeny and Comparative Biology - *CC BY-SA 4.0*
    - 4.4.1: Systematics and Classification - *CC BY-SA 4.0*
    - 4.4.2: Phylogeny and Cladistics - *CC BY-SA 4.0*
- 5: Unit V- Biological Diversity - *CC BY-SA 4.0*
  - 5.1: The Origin and Diversity of Life - *CC BY-SA 4.0*
    - 5.1.1: Deep Time - *CC BY-SA 4.0*
    - 5.1.2: Origins of Life - *CC BY-SA 4.0*
    - 5.1.3: Evidence for Early Life - *CC BY-SA 4.0*
    - 5.1.4: Eukaryotic Origins - *CC BY-SA 4.0*
  - 5.2.E: Viruses (Exercises) - *CC BY-SA 4.0*
  - 5.2: Acellular Entities - Viruses, Prions, and Viroids - *CC BY-SA 4.0*
  - 5.3: Prokaryotes - Bacteria and Archaea - *CC BY-SA 4.0*
    - 5.3.E: Prokaryotes - Bacteria and Archaea (Exercises) - *CC BY-SA 4.0*
  - 5.4: Protists - *CC BY-SA 4.0*
    - 5.4.E: Protists (Exercises) - *CC BY-SA 4.0*
  - 5.5: Fungi - *CC BY-SA 4.0*
    - 5.5.E: Fungi (Exercises) - *CC BY-SA 4.0*
  - 5.6: Introduction to Animal Diversity - *CC BY-SA 4.0*
    - 5.6.1: Introduction - *CC BY-SA 4.0*
    - 5.6.2: The Evolutionary History of the Animal Kingdom - *CC BY-SA 4.0*
    - 5.6.3: Features of the Animal Kingdom - *CC BY-SA 4.0*
    - 5.6.4: Features Used to Classify Animals - *CC BY-SA 4.0*
    - 5.6.5: Animal Phylogeny - *CC BY-SA 4.0*
    - 5.6.E: Introduction to Animal Diversity (Exercises) - *CC BY-SA 4.0*
  - 5.7: Invertebrates - *CC BY-SA 4.0*
    - 5.7.1: Prelude to Invertebrates - *CC BY-SA 4.0*
    - 5.7.2: Phylum Porifera - *CC BY-SA 4.0*
    - 5.7.3: Phylum Cnidaria - *CC BY-SA 4.0*
    - 5.7.4: Superphylum Lophotrochozoa - *CC BY-SA 4.0*
    - 5.7.5: Superphylum Ecdysozoa - *CC BY-SA 4.0*
    - 5.7.6: Superphylum Deuterostomia - *CC BY-SA 4.0*
    - 5.7.E: Invertebrates (Exercises) - *CC BY-SA 4.0*
  - 5.8: Vertebrates - *CC BY-SA 4.0*
    - 5.8.1: Prelude to Vertebrates - *CC BY-SA 4.0*

- 5.8.2: Chordates - *CC BY-SA 4.0*
- 5.8.3: Fishes - *CC BY-SA 4.0*
- 5.8.4: Amphibians - *CC BY-SA 4.0*
- 5.8.5: Reptiles - *CC BY-SA 4.0*
- 5.8.6: Birds - *CC BY-SA 4.0*
- 5.8.7: Mammals - *CC BY-SA 4.0*
- 5.8.8: The Evolution of Primates - *CC BY-SA 4.0*
- 5.8.E: Vertebrates (Exercises) - *CC BY-SA 4.0*

- 5.9: Plantae - *CC BY-SA 4.0*
  - 5.9.1: Kingdom Plantae - Evolution and Phylogeny - *CC BY-SA 4.0*
  - 5.9.2: Kingdom Plantae - Adaptations - *CC BY-SA 4.0*
  - 5.9.E1: Seedless Plants (Exercises) - *CC BY-SA 4.0*
  - 5.9.E2: Seed Plants (Exercises) - *CC BY-SA 4.0*

- 6: Unit VI- Ecology - *CC BY-SA 4.0*
  - 6.1: Ecosystems and the Biosphere - *CC BY-SA 4.0*
    - 6.1.1: Ecology of Ecosystems - *CC BY-SA 4.0*
    - 6.1.2: Energy Flow through Ecosystems - *Undeclared*
    - 6.1.3: Terrestrial Biomes - *CC BY-SA 4.0*
    - 6.1.4: Aquatic Biomes - *CC BY-SA 4.0*
    - 6.1.5: Biogeochemical Cycles - *CC BY-SA 4.0*
    - 6.1.6: Biogeography - *CC BY-SA 4.0*
    - 6.1.S: Chapter Resources - *CC BY-SA 4.0*
  - 6.2: Biodiversity and HIPPPOC - *CC BY-SA 4.0*
    - 6.2.1: Introduction to Biodiversity - *CC BY-SA 4.0*
    - 6.2.2: Importance of Biodiversity - *CC BY-SA 4.0*
    - 6.2.3: The Biodiversity Crisis - HIPPPOC - *CC BY-SA 4.0*
    - 6.2.4: Preserving Biodiversity - *CC BY-SA 4.0*
    - 6.2.S: Chapter Resources - *CC BY-SA 4.0*
  - 6.3: Climate Change - *CC BY-SA 4.0*
    - 6.3.1: Introduction to Climate Change - *CC BY-SA 4.0*
    - 6.3.2: Anthropogenic Climate Change - *CC BY-SA 4.0*
    - 6.3.3: Current and Future Climate Change Impacts - *CC BY-NC-SA 4.0*
    - 6.3.4: Climate Strategies - *CC BY-SA 4.0*
- Back Matter - *Undeclared*
  - Index - *Undeclared*
  - Glossary - *Undeclared*
  - Detailed Licensing - *Undeclared*